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The evolution of plant–insect mutualisms

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Summary

Mutualisms (cooperative interactions between species) have had a central role in the generation and maintenance of life on earth. Insects and plants are involved in diverse forms of mutualism. Here we review evolutionary features of three prominent insect–plant mutualisms: pollination, protection and seed dispersal. We focus on addressing five central phenomena: evolutionary origins and maintenance of mutualism; the evolution of mutualistic traits; the evolution of specialization and generalization; coevolutionary processes; and the existence of cheating. Several features uniting very diverse insect–plant mutualisms are identified and their evolutionary implications are discussed: the involvement of one mobile and one sedentary partner; natural selection on plant rewards; the existence of a continuum from specialization to generalization; and the ubiquity of cheating, particularly on the part of insects. Plant–insect mutualisms have apparently both arisen and been lost repeatedly. Many adaptive hypotheses have been proposed to explain these transitions, and it is unlikely that any one of them dominates across interactions differing so widely in natural history. Evolutionary theory has a potentially important, but as yet largely unfilled, role to play in explaining the origins, maintenance, breakdown and evolution of insect–plant mutualisms.

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I. Introduction

Mutualisms, or cooperative interactions between species, have long received attention from natural history enthusiasts, forming a centerpiece of both nature documentaries and biology textbooks. After a prolonged delay, mutualisms have also begun to receive serious attention from ecologists and evolutionary biologists. It is now believed that virtually every species on earth is involved in one or more of these interactions. For example, in tropical rainforests the large majority of plants depend on animals for pollination and seed dispersal. Over 80% of all flowering plants are involved in mutualisms with beneficial mycorrhizal fungi that live on and in their roots. In the ocean, both coral reef communities and deep-sea vents are exceptionally rich with mutualisms. In fact, corals themselves obligately depend on the photosynthetic algae that inhabit them. Key events in the history of life have also been linked to mutualism, including the origin of the eukaryotic cell, and the invasion of the land by plants. The study of mutualism therefore has a major role to play in illuminating both the diversity and the evolutionary diversification of life on Earth.

Mutualisms between insects and plants are among the most thoroughly studied interactions (Bronstein, 1994). They are particularly critical to understanding from the perspective of plant evolution. First, reproduction of many vascular plants is clearly linked with attracting insect mutualists. Second, studying plant–insect mutualisms sheds light on the evolution and function of a diverse suite of plant traits, as well as on plant mating systems. Third, these mutualisms have been implicated in patterns of evolutionary diversification of certain groups of plants. Finally, plant–insect mutualisms have taken on particular importance in the realm of conservation: threats to critical mutualists can potentially endanger the evolutionary persistence of the plants that depend on them.

This review is organized as follows. In Section II we provide a historical overview of the study of mutualism, focusing particularly on the roles that plant–insect interactions have played. We introduce five issues of particular interest regarding mutualism evolution. The following sections use these issues to orient a review of the three major classes of plant–insect mutualisms: pollination (Section III); protection (Section IV); and seed dispersal (Section V). While a few other plant–insect mutualisms have been identified (Davidson & Epstein, 1989; Pemberton & Lee, 1996; Sabelis *et al.*, 1999), so little is known of their evolutionary histories that we do not discuss them here. Finally, Section VI synthesizes our knowledge across these interactions. We point to parallels and differences among them, as well as to major unresolved issues regarding the evolution of plant–insect mutualisms.

II. A historical perspective on mutualism

The oldest, and perhaps most culturally universal, ecological theory is the ‘balance of nature’ (Egerton, 1973; Sapp, 1994),

that is, the idea that natural forces prevent species from either becoming too abundant or going extinct. This concept can be found in even the most ancient scientific writings, and mutualisms were commonly cited as support for it. For example, Herodotus discussed how plovers removed leeches from crocodiles’ mouths (‘The crocodile enjoys this, and never, in consequence, hurts the bird’). Aristotle, Cicero and Pliny added other examples, drawing moral lessons that showed the importance of ‘friendships’ in maintaining nature’s balance. Mutualisms, then, were well known long before they had a name.

The idea that the harmony of society mirrored an underlying harmony of nature persisted in the western world throughout the Middle Ages. Each species was seen to have a preordained role assigned by the Creator. Plants provided food for animals which, in turn, decayed in order to fertilize the soil for plants. Linnaeus discussed at length how animals were created to serve plants by both feeding on them and dispersing their seeds.

The well ordered universe postulated by Christian natural theology began to unravel during the upheavals of the Industrial Revolution. Ideas of competition and struggle as forces of progress came to pervade the political and economic analyses of the time, spurred by the work of Thomas Malthus. At the same time, Alphonse de Candolle and others, possibly stimulated by an acquaintance with Malthus’s work, were documenting the importance of competition as a force in nature (Egerton, 1977).

These lines of thought came together to form the underlying thesis of Charles Darwin’s life work. Accounting for cooperation in nature was critically important to Darwin, because its existence challenged his contention that organisms did not perform actions strictly to benefit others. One of the better known passages from *The Origin of Species* (Darwin, 1859) occurs in a discussion of pollination and seed dispersal:

‘Natural selection cannot possibly produce any modification in a species exclusively for the good of another species; though throughout nature one species incessantly takes advantage of, and profits by, the structures of others. If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection.’

To develop this idea further, Darwin analysed the evolution of fruits and flowers, showing how traits that benefit animals function first and foremost to increase plants’ own reproductive success. In showing that mutualisms could arise strictly through selfish actions, limited by costs and driven by conflicts of interest between partners, Darwin laid the foundation for our current view of mutualism. He pointed out cases in which the interests of mutualists could come into conflict, discussing how cheating behaviors such as nectar-robbing might become favored. It was also in the context of mutualism that he explicitly pointed to the possibility of coevolution (reciprocal evolutionary modification of traits) (Darwin, 1859):

'Thus I can understand how a flower and a bee might slowly become, either simultaneously or one after the other, modified and adapted to each other in the most perfect manner, by the continued preservation of all the individuals which presented slight deviations of structure mutually favourable to each other.'

Despite Darwin's lead, the concept of mutualism did not develop further until the middle of the 20th century. However, by the end of the 19th century hundreds of articles had been published describing the natural history of various mutualisms (Schneider, 1897). The term 'mutualism' was first used in a biological context in 1873 (by Pierre van Beneden, a Belgian zoologist, in a communication to the Royal Academy of Belgium). From the 1840s through the 1880s, lichens and both mycorrhizal and rhizobial interactions with plants were recognized to be mutualistic. It was even argued that the eukaryotic cell was the result of a mutualistic symbiosis (Sapp, 1994). Huge compendia on pollination biology were published (Kerner, 1878; Müller, 1883); and the basics of pollination of yucca (Riley, 1892) and fig (King, 1888) were worked out. Boucher *et al.* (1982) believe that, by this point, there was 'a general recognition of the fundamental similarity of interactions ranging from mycorrhizas to cleaner fish'.

Despite the wealth of available information, mutualism was not a prominent concept in ecology or evolutionary biology through most of the 20th century. Evolutionary biologists of the time were concerned with the genetic basis of individual traits; they did not turn their attention to any form of interspecific interaction until mid-century. However, natural history studies of mutualism, particularly between plants and insects, continued (Robertson, 1895; Knuth, 1906). Economically important mutualisms, such as bee pollination of crop plants, were studied in particular depth.

The first major conceptual advances in our broad understanding of mutualism began in the 1960s. During these years, investigations of coevolution, many of which focused on plant–insect mutualisms, flourished. In particular, Janzen's (1966, 1967) experimental studies on protective mutualisms between acacias and ants provided outstanding evidence for the role of coevolution in species interactions; they also offered an unparalleled model for how the benefits and costs of mutualism could be measured in the field. In the following two decades, interest in the conditions that favor the evolution, maintenance and breakdown of cooperation began to grow, stimulated in part by the seminal work of Axelrod & Hamilton (1981). But most of this work focused on cooperation among individuals within species. Only in the past decade has a body of theory begun to develop that deals explicitly with beneficial interactions between species (see Section VI).

In the past two decades, studies of the evolution of mutualism have crystallized around five central questions. We return to these questions in Section VI in summarizing the current state of knowledge on insect–plant mutualisms.

(i) Evolutionary origins and maintenance of mutualism. How does mutualism arise? What conditions foster the

evolution of mutualism, impede its evolution, and lead to its breakdown?

(ii) Evolution of mutualistic traits. How do traits central to the functioning of mutualism, particularly traits that attract mutualists and substances that reward them, arise and evolve?

(iii) Specialization and generalization. What conditions favor the evolution and maintenance of different degrees of specialization and generalization in mutualisms?

(iv) Coevolution and cospeciation. When are mutualists likely to coevolve and cospeciate? What factors foster and impede these processes?

(v) Cheating. How commonly are mutualisms exploited by cheaters? How can mutualism persist evolutionarily in the face of cheating?

III. Insect pollination

Pollination is the transfer of pollen from an anther to the stigma of a carpel for the purpose of fertilizing ovules. Preserved gymnosperm pollen in insect guts provides direct evidence that insects were consuming pollen as far back as the Permian, well before the appearance of angiosperms in the late Jurassic to early Cretaceous (Crane *et al.*, 1995; Labandeira, 1997, 1998; Grimaldi, 1999; Grimaldi & Engel, 2005). Excess pollen probably evolved as the first reward for early insect mutualists by the Late Paleozoic (Labandeira, 1998; Grimaldi, 1999). Nectar appeared later, sometime before the Late Jurassic, as inferred from the evolution of specialized nectar-sucking mouthparts in Diptera (Labandeira, 1997; Ren, 1998; Thien *et al.*, 2000). Early angiosperms probably coopted as generalized pollinators insects that lacked adaptations for flower feeding, such as wasps, moths, thrips, beetles and flies, from other seed plants possessing flower-like structures, including Gnetales, Bennettitales and Cycads. Parallel radiation of angiosperms and the more plant-dependent insects such as bees and butterflies followed in the Mid-Cretaceous and into the Tertiary (Crane *et al.*, 1995; Crepet, 1996; Grimaldi, 1999; Bernhardt, 2000; Thien *et al.*, 2000; Grimaldi & Engel, 2005).

The congruent rise of flowering plants and insects, in conjunction with the observation that flowers possessing specific combinations of floral traits appear to be visited by corresponding pollinator taxa, contributed to the idea that biotic pollination could explain the diversification of angiosperms. Pollination biologists during the mid-20th century suggested that suites of traits represent adaptive character syndromes aimed at attracting and using particular pollinators. Pollination syndromes are appealing because they seem to explain both floral diversification and the convergence of floral forms across angiosperms pollinated by similar pollinators. Shifts among functional pollinator groups (birds vs bees vs moths, etc.), are thought to have driven diversification in some plant families and genera (Grant & Grant, 1965; Goldblatt *et al.*, 1998; Johnson *et al.*, 1998; Fenster *et al.*, 2004). Such shifts

may have been facilitated by key innovations in flower morphology, such as bilateral symmetry (Sargent, 2004) and nectar concealment (Hodges, 1997). Diversification in bees and the plants they pollinate might also have been influenced by shifts in pollen host use; speciose groups of bees typically include pollen specialists (Müller, 1996; Wcislo & Cane, 1996; but cf. Sipes & Tepedino, 2005).

Diversification, however, has only rarely been the product of strict coevolution between plant and pollinator species pairs. The most thoroughly studied examples of tight coevolution are found in pollinating seed parasite systems (Cook & Rasplus, 2003; Pellmyr, 2003). Yet even the highly specialized fig–fig-wasp interaction sometimes involves more than one pollinating wasp species per fig (Machado *et al.*, 2005). More often, evolutionary changes and speciation in plants and pollinators occur in response to diffuse multispecies interactions (Fenster *et al.*, 2004).

Recent community-level surveys and analyses show that plant and pollinator assemblages (like those involved in most other mutualisms) are rather generalized: most plant species are visited by taxonomically diverse groups of pollinators, and most pollinator species visit several plant species (Herrera, 1996; Waser *et al.*, 1996). The lack of mutually dependent plant–pollinator relationships in these community surveys undermines a central assumption of the traditional view of pollinator-mediated floral evolution and pollination syndromes. This has generated a healthy discussion of the degree of specialization in pollination systems and its evolutionary implications (Ollerton, 1998; Waser, 1998; Johnson & Steiner, 2000; Fenster *et al.*, 2004), and has also prompted ecologists to search for community-scale properties that might reconcile empirical patterns with traditional views regarding floral evolution. One interesting finding is that most plant–pollinator interactions are asymmetrically specialized, with relatively rare plants and pollinators, as well as those with relatively few partners, interacting primarily with a core group of abundant generalist species (Bascompte *et al.*, 2003; Alarcón, 2004; Vázquez & Aizen, 2004, 2006; Jordano *et al.*, 2006). It is possible that, by studying the traits and behaviors of species with different levels of asymmetrical specialization, we might learn how floral evolution operates under various pollination environments.

Insect pollinators clearly exert strong selection on, and cause evolutionary change in, floral traits, as demonstrated by several contemporary studies (Fenster *et al.*, 2004). For example, bumble bee queens preferentially visit plants of the alpine sky pilot (*Polemonium viscosum*) that have large, wide corollas (Galen, 1989). When experimental plants with variable corolla shape were exposed to bumble bee pollination, the offspring resulting from these pollinations had larger and wider flowers than their parents. This intergenerational change in flower shape is one of the clearest examples of pollinator-mediated evolution in floral attributes (Galen, 1996).

In comparison with the extensive body of work on pollinator-mediated selection in plants, it is striking how little is known about plant-mediated selection on pollinator traits. It is exceedingly difficult to quantify fitness in mobile animals; in the absence of fitness measures, one cannot relate variation in specific pollinator traits to variation in pollinator fitness. Nevertheless, pollinators have clearly evolved characteristics that enhance their ability to extract rewards. For example, the long tongues of some butterflies, moths, and bees are adaptive for extracting nectar from flowers with long corollas (Nilsson, 1988). Evolution of complex morphological and behavioral traits involved in pollen collection and deposition has been well studied in the highly specialized yucca moths and fig wasps (Pellmyr & Krenn, 2002; Cook *et al.*, 2004). The structure of scopal hairs in oligolectic bees, those that obtain rewards from a restricted set of related plant species, differs according to the pollen characteristics of their host plants (Sipes & Tepedino, 2005). In South Africa, oil-collecting *Rediviva* bees use their forelegs to collect oils from floral spurs in *Diascia* (Scrophulariaceae). In several *Rediviva* populations, mean foreleg length correlates significantly with spur length of the *Diascia* populations they visit, suggesting that these bees can evolve in response to plant-mediated selection (Steiner & Whitehead, 1990, 1991).

Despite evidence that most plant–pollinator interactions are generalized and involve multiple interacting species, evolutionary studies of these interactions have typically focused on one plant species and one or a few pollinator species, reflecting a broader preoccupation with pairwise interactions among those who study mutualism (Stanton, 2003). Future research efforts on pollinator-mediated floral evolution must therefore consider the net evolutionary effects of interactions between multiple partners (Geber & Moeller, 2006). Patterns of selection imposed on floral traits by different pollinators may be the same (Gómez & Zamora, 2006), or they may differ. If they differ, the evolution of floral specialization will depend on whether there are fitness trade-offs involved in adapting to different pollinators, and on genetic correlations between traits best suited to one pollinator vs another (Aigner, 2001, 2004). Evolutionary studies of multispecies plant–pollinator interactions must also account for spatial and temporal variation in the species composition of plant and pollinator communities (Price *et al.*, 2005; Geber & Moeller, 2006). Finally, studies of floral evolution must be directed at measuring the influence of co-flowering plants on pollinator-mediated selection. For example, the pattern of selection by pollinators on corolla length in scarlet gilia (*Ipomopsis aggregata*) differs in the presence vs absence of Indian paintbrush (*Castilleja linariaefolia*) with which it competes for pollinators. When *C. linariaefolia* is present, *I. aggregata* flowers with longer corollas are favored (Caruso, 2000). Co-flowering plant species can also interact facilitatively when they attract or support larger pollinator populations compared with single-species plant populations. For example, *Clarkia xantiana* has

higher reproductive success in the presence than in the absence of other *Clarkia* species, because of a higher abundance of specialist *Clarkia* bees in multispecies *Clarkia* communities (Moeller, 2004). In addition, in the absence of congeners, pollinator-mediated selection on *C. xantiana* favors floral traits that promote self-pollination, and that therefore guarantee some measure of reproductive assurance when pollinators are scarce (Moeller & Geber, 2005).

Not all plants provide rewards to visitors, and not all flower visitors provide pollinator services in exchange for food rewards. These plants and flower visitors act as exploiters or cheaters in the partnership. Cheating is a nearly ubiquitous phenomenon in mutualisms (Bronstein, 2001; Yu, 2001; Sachs *et al.*, 2004). Just as beneficial interactions can impose selection on partners, cheating may impose selection both on the cheater to further the deception, and on the cheated partner to mitigate the costs of the interaction. Plant cheaters must rely on 'mistakes' made by flower visitors to unrewarding flowers (Renner, 2006). Given that many insects can learn to discriminate between unrewarding plants or species, cheating plants are likely to be most successful when they grow in close proximity to, but are less common than, rewarding plants (Laverty, 1992; Johnson *et al.*, 2003a). Rewardless species have also been shown to receive more pollinator visits if their flowers resemble those of rewarding neighbors in color or form (Johnson, 1994). Natural selection may therefore favor the convergence of flower phenotypes in rewardless species on the phenotype of profitable species (Johnson, 1994; Johnson *et al.*, 2003b).

Animal cheaters on pollination mutualisms are abundant and behaviorally diverse. They generally do not come from strictly parasitic lineages. Rather, they are opportunistic, exploiting flowers when it is energetically profitable to do so (Maloof & Inouye, 2000). Nectar thieves enter flowers, but fail to contact pollen while gathering nectar; nectar-robbers access nectar through holes they chew through corollas, or through holes made by other robbers, thus bypassing anthers and stigmas. As these cheaters generally do not transfer pollen, they are commonly assumed to be detrimental because subsequent, more beneficial visitors seem likely to be deterred or to make shorter visits to drained flowers. While such negative effects have been documented (Irwin, 2003), in other cases the effect of cheaters has been shown either to be neutral (when subsequent visitors do not avoid damaged flowers) or positive (e.g. when legitimate pollinators do visit robbed flowers but fly further after doing so, increasing the rate of outcrossing) (Maloof, 2001; Richardson, 2004). The effect of nectar robbing varies in time and space, as a function of the plant species and the identities and behaviors of pollinators and robbers (Irwin *et al.*, 2001; Irwin & Maloof, 2002). However, a meta-analysis suggests that, on average, nectar robbers have a weak but negative effect on female success (Irwin *et al.*, 2001). Where nectar robbers have strong negative effects on plant fitness, they may exert selection for shifts in flowering

time that reduce the temporal overlap with robbers (Irwin & Maloof, 2002), or for changes in floral traits that mitigate the negative effects of robbers (Maloof & Inouye, 2000). For example, in the alpine sky pilot, plants inhabiting high-elevation tundra have wide corollas and are visited almost exclusively by bumble bees. In contrast, plants at the timber line have narrow corollas and are often visited by nectar-thieving ants that damage pistils; ants are less damaging to flowers with narrow corollas (Galen & Cuba, 2001). Thus both beneficial bees and ant cheaters appear to have shaped the evolution of floral shape in this plant species.

It is unlikely that cheaters would drive plant or pollinator species to abandon mutualisms altogether. In fact, a growing body of theory predicts ecological and evolutionary stability of mutualisms even when heavily exploited by cheaters (Ferrière *et al.*, 2002; Bronstein *et al.*, 2003). Nevertheless, plant–insect pollination mutualisms have clearly been lost repeatedly over evolutionary time. Some plant species have opted out of animal-mediated pollination, while some pollinators have opted out of direct use of flower rewards.

In plants, loss (or partial loss) of biotic pollination takes two forms: a shift to abiotic pollination via wind or water, with wind pollination being more common; and a shift to uniparental mating via self-pollination or apomixis, with selfing being more common. The loss of animal pollination is expected to occur when pollinators are scarce, ineffective or unpredictable; where environmental conditions or plant traits are conducive to alternative pollination modes; or, in the case of uniparental mating, when the availability of suitable mates is low (Darwin, 1876; cf. Eckert *et al.*, 2006). Wind pollination, which has evolved independently in approx. 18% of plant families, is common in environments where obstruction of windborne pollen is low (moderate wind speeds, low humidity, open habitats; Culley *et al.*, 2002). Self-pollination and apomixis have evolved repeatedly from animal pollination in many plant families and genera. Species with uniparental mating often occur in isolated or low-density populations; at the geographic margins of animal-pollinated sister taxa; or as colonists of novel ranges (Stebbins, 1950; Baker, 1955, 1967; Asker & Jerling, 1992).

Evolutionary shifts can also be identified in flower-visiting insects, from complete dependence on floral rewards to reliance on other resources. For example, cheaters on obligately pollinating seed-parasite systems have arisen several times from nonpollinating lineages, and more rarely from mutualistic pollinators. In the fig–fig-wasp mutualism, most cheaters are not close relatives of the pollinating wasps (Agaonidae), but rather belong to other Chalcidoidea wasp families (Rasplus *et al.*, 1998; cf. Kerdelhue *et al.*, 1999). In the yucca–yucca-moth interaction, cheaters are typically close relatives of pollinating species (Segraves & Pellmyr, 2004), although not necessarily of the pollinator of the yucca species on which they cheat. Parasitism has also evolved in multiple lineages of bees (Superfamily Apoidea). These 'cuckoo bees' or cleptoparasites

lay their eggs in the nests of closely related pollinating bees, relying on the latter for pollen provisioning of larvae. The cleptoparasitic lifestyle has evolved multiple times, with parasitic taxa present in four of the seven bee families recognized by Michener (2000). Female bees belonging to these parasitic lineages are frequently recognizable by the absence of pollen-collecting structures, such as the scopa, and reduction in overall hairiness (Michener, 2000). The conditions favoring a parasitic lifestyle in these insects have received limited attention.

Although there is a long history of studies of insect pollination, much remains to be understood – from speciation and coevolution, to the diversification of insect and flower morphology, to the persistence of mutualisms in the face of cheating. This is especially true of the animals' perspective: we still lack a basic understanding of how selection operates on pollinators and how interactions with particular plant species affect their fitness.

IV. Protection of plants by ants

From the evolutionary perspective, the best understood plant defenses against herbivory are chemical in nature. However, diverse plants are known to engage instead (or in addition) in 'biological warfare': they attract and reward other animals, most commonly ants, which in turn deter or kill the herbivores. Ant–plant associations are extremely abundant, involving up to one-third of all woody species in a given habitat (Schupp & Feener, 1991). The only habitats in which reward-producing plant species are truly rare are those with few or no ant species (Keeler, 1980). These relationships were first described in the 19th century, although they were not widely accepted to be mutualistic until the 1970s, subsequent to rigorous experimental field studies of Janzen and others (Janzen, 1966, 1967; Bentley, 1977; reviewed by Bronstein, 1998). Since that time, a large literature has accumulated about their ecological features. However, they are still relatively unexplored from an evolutionary standpoint (but see valuable reviews by Davidson & McKey (1993); Heil & McKey (2003)).

Ant-protection associations range from facultative and generalized to obligate and highly specialized. It is important to distinguish between these at the outset, as they have rather different ecological features and evolutionary histories. In facultative, generalized associations, plants secrete small volumes of nectar from organs in various locations outside the flowers, termed extrafloral nectaries (EFN). The EFN are highly diverse in structure and ontogeny, and are found on an array of vegetative and reproductive parts, most commonly on developing structures including new leaves, flowers and fruits (Elias, 1983). They are easily accessible to plant visitors, and a variety of insects, including diverse ant species, feed there on a regular basis. Many, although not all, of these ants will attack other insects in the vicinity of the nectaries, including but not

restricted to the plants' herbivores. These ants generally exhibit low fidelity to the association; many different species are commonly present on a given plant over its lifetime and even at a single moment (Beattie, 1985). In the rarer specialized ant–plant associations, plants (myrmecophytes) offer substantially more valuable rewards, including shelter in the form of hollow stems and thorns, and protein- and lipid-rich food bodies. Certain myrmecophytic plants have been shown to absorb ant wastes deposited within these domatia, to the benefit of the plants (an interaction referred to as myrmecotrophy; Beattie, 1989; Treseder *et al.*, 1995). Myrmecophytic ants generally show strong fidelity to individual plants, nesting on them and deriving most or all of their diets from the resources they provide.

The earliest evidence for ant–plant associations is from EFN identified on 35-million-yr-old leaves of an extinct *Populus* species. Extinct ant species from this site have modern-day congeners that defend plants (Pemberton, 1992). Associations with ants are now extremely widespread across plants, and EFN are found in at least 332 genera belonging to at least 93 angiosperm families (more than a quarter of all plant families), as well as in 11 genera of ferns (Koptur, 1992). The EFN are most abundant in three advanced subclasses of the Magnoliopsida, Dilleniidae, Rosidae and Asteridae (Elias, 1983), and some families (such as the legumes) and genera are particularly rich in species bearing them (McKey, 1989; Schupp & Feener, 1991). They are found on plants exhibiting all life forms, but are especially common on vines (Blüthgen *et al.*, 2000). Specialized ant–plant associations are considerably rarer, but still are found in over 100 genera of tropical angiosperms (Davidson & McKey, 1993) and at least 20 plant families (O'Dowd, 1982). Domatia apparently modified for nutrient absorption from myrmecophytic ants are found in at least 200 plant species, most commonly in the Rubiaceae (Beattie, 1989). The majority of studies have been conducted on just three myrmecophytic genera, however: *Acacia* (Fabaceae); *Cecropia* (Moraceae); and *Macaranga* (Euphorbiaceae).

Ant–plant associations are also phylogenetically diverse when considered from the perspective of the ants. Davidson (1997) argues that most of the extraordinarily abundant ant species in tropical arboreal habitats are subsidized on insect and plant exudates, including extrafloral nectar. The specialized myrmecophytic ants belong disproportionately to certain taxa; they have evolved in five of 12 subfamilies in the Formicidae, and are absent only from some specialized and very small subfamilies.

The broad taxonomic distribution of EFN, their diverse ontogenies, and phylogenetic evidence all point to ant–plant associations having originated independently many times (at least 12 times in the legumes alone; McKey, 1989). Phylogenetic studies of ant–plant interactions are also beginning to shed light on transitions between specialized and more generalized relationships. In the genus *Macaranga*, in which

defensive mutualisms range across species from highly generalized to highly specialized (Fiala *et al.*, 1994), specialized myrmecophytism has evolved two to four times, and been lost one to three times (Blattner *et al.*, 2001; Davies *et al.*, 2001). In central American *Acacia* species, in contrast, myrmecophytism appears to have evolved only once (Heil *et al.*, 2004a). Heil & McKey (2003) conclude that more constant, long-lived and exclusive associations are permitted when ants are resident within plants; this has usually led to specialization of both partners, including increased rate of resource supply to ants by plants, and increased protective efficacy of the ants.

The major traits within ant–plant associations that have attracted attention from an evolutionary standpoint are the rewards that plants offer. In the more facultative ant–plant mutualisms, extrafloral nectar is the trait of interest. In one detailed experimental study, Rudgers (2004) demonstrated that predatory ants can act as agents of selection on EFN traits on wild cotton (*Gossypium thurberi*). When ant visitation was reduced, plants supported more herbivores, experienced greater leaf damage, and produced fewer flowers and seeds. Furthermore, fewer ants visited plants with experimentally reduced EFN, resulting in increased leaf damage and reduced seed production. In addition, natural variation in EFN frequency correlated positively with seed production. This study provided strong support that facultative, generalized ants can influence the evolution of EFN traits (cf. Agrawal & Rutter, 1998; Heil *et al.*, 2000, 2005; Wäckers & Bezemer, 2003). Plants involved in more specialized ant–plant mutualisms have clearly been under selection to produce relatively more nutrient-rich food bodies (Fiala & Maschwitz, 1992; Heil *et al.*, 1998, 2004b; Linsenmair *et al.*, 2001). Selection has also acted on a broader set of traits in these plants, including (a) preformed nesting sites (domatia) in hollow stems, petioles or leaf pouches; (b) mechanisms for quick acquisition of ant mutualists, such as olfactory cues, as growth and survival may be impossible without defense; and (c) in some cases the loss of alternative defenses, such as defensive chemicals (but see below). The distinction between traits of plants defended facultatively by communities of generalist ants and those defended obligately by specialist ants is not as clear-cut as was once thought, however. For example, some facultatively defended plants produce domatia (Maschwitz & Fiala, 1995) and/or food bodies (O'Dowd, 1982).

Much less is known about ant traits that may have been under selection in the context of these associations. Ants that visit extrafloral nectar-producing plants are simply those that feed on organisms that secrete fluids (including homopterans such as aphids, as well as lycaenid caterpillars) and that are willing to climb up plants to feed. Association with myrmecophytes involves a more identifiable group of repeatedly derived traits, including worker size (Meunier *et al.*, 1999); body shape (Brouat *et al.*, 2001a); and digestive chemistry (Heil *et al.*, 2005).

Growing evidence suggests that generalized ant–plant associations involve evolution primarily on the part of the plants, whereas in the more specialized myrmecophytic systems evolutionary processes are more often bilateral. Indeed, generalized associations form readily between native partners and introduced ones, as well as between pairs of introduced species (Koptur, 1979; Ness, 2003). In contrast, in myrmecophytic systems a number of studies have revealed fairly strong evidence for coevolution, although little for cospeciation (Janzen, 1966; Yu & Davidson, 1997; Quek *et al.*, 2004). One of the best pieces of evidence for coevolution is the 'lock-and-key' mechanism in *Leonardoxa* species (Fabaceae). The plant character is the prostoma, a small, unligified organ at the apex of the domatia in which myrmecophytic ants excavate an entrance hole. Brouat *et al.* (2001a) provide evidence for a close correspondence between the dimensions and shape of the myrmecophytic ants and the prostoma of the *Leonardoxa* species they inhabit, suggesting a history of pairwise reciprocal adaptation. Phylogenetic patterns of the ants and plants reveal a complex coevolutionary history in the *Leonardoxa* system, involving reticulate evolution of the plants, colonization of plants by multiple ant lineages, and local extinction of ant associates (Brouat *et al.*, 2001b; Debout *et al.*, 2003).

Three hypotheses have been discussed in relation to the origin and maintenance of ant–plant defensive mutualisms. First, the 'ant-limitation hypothesis' (Schupp & Feener, 1991) suggests that the origin and maintenance of ant defense is limited by aspects of the ant community, such as forager abundance, ant species richness, and the frequency of aggressive ant species that can effectively defend plants from enemies. Schupp & Feener (1991) have argued against this hypothesis, pointing out that tropical gap habitats with the highest diversity of EFN-bearing plants do not, in fact, have the most abundant or species-rich ant communities. Second, Becerra & Venable (1989) proposed that EFN may have evolved to distract ants away from tending destructive Homoptera. However, this 'distraction hypothesis' has been challenged by observations that, given a choice, ants generally prefer to tend Homoptera instead of EFN, rather than the reverse (Del-Claro & Oliveira, 1993). Others have contended that EFN may have evolved to distract ants away from the flowers (Wagner & Kay, 2002). Finally, the now-favored 'resource-limitation hypothesis' argues that the origin and maintenance of ant defense may reflect resource availability (Heil & McKey, 2003). Sugar- and lipid-based rewards will be energetically and metabolically cheap in carbon-rich habitats such as forest gaps, where leaves are flushed continuously and hence in need of persistent defense (McKey, 1989; Schupp & Feener, 1991).

These adaptive hypotheses for the origin and maintenance of ant defense generally take it as a given that plants benefit by ant attraction – that ant–plant associations are mutualisms. However, cheating and exploitation are rampant within these interactions. Certain ant species attracted to plant rewards

confer no benefit, and others are unequivocally detrimental some or all of the time. Many ant species that take food rewards and/or occupy domatia act relatively passively towards herbivores (Raine *et al.*, 2004; Tillberg, 2004); some of these freeloaders exclude effective mutualists from the plant (Raine *et al.*, 2004). Ants may also interfere with pollination: when they enter flowers in the course of their activities, they reduce pollen viability and/or deter pollinator visits (Wagner, 2000; Ness, 2006). Furthermore, ants may forage away from the plant parts primarily in need of defense (Yu & Davidson, 1997); tend Homopterans and other plant enemies on the plants they occupy (Gaume *et al.*, 1998); or clip reproductive tissue even while defending the vegetative parts (Yu & Pierce, 1998; Stanton *et al.*, 1999). Some reward-providing plants, such as bracken fern (Rashbrook *et al.*, 1992), seem never to benefit from any of the visitors to their EFN.

These observations raise the question of when ant associations will be maintained over evolutionary time, and when they will break down and be lost. With regard to the maintenance of mutualism, note that the outcomes of ant–plant associations are strongly context-dependent. When no enemies are present, no benefits of ant attendance should accrue. The costs of the mutualism (e.g. investment in reward production) will continue to accumulate, however. Thus the costs of ant occupancy may frequently outweigh its benefits. Mutualism, presumably, is maintained in situations where benefits exceed costs; the difference may be small but consistent, or rare but large. It seems increasingly clear that natural selection has acted to reduce the costs of these mutualisms to plants, thus shifting outcomes in the direction of net benefit. For example, although the cost of extrafloral nectar may be rather low (e.g. 1% of the energy costs of leaf production in *balsa*; O’Dowd, 1979), construction of protein- and lipid-rich food bodies in myrmecophytes entails significant nutrient investments, and they are produced in lower numbers in nutrient-stressed or shady conditions (Folgarait & Davidson, 1994, 1995; Heil *et al.*, 2001). Some ant-defended plants produce little or no reward until ants are present, herbivores attack, or herbivory-induced volatiles are detected (Letourneau, 1990; Agrawal & Rutter, 1998; Heil *et al.*, 2000; Linsenmair *et al.*, 2001; Wäckers & Bezemer, 2003). The nectaries themselves may also be inducible (Mondor & Addicott, 2003). Finally, some plants exhibit traits that specifically deter detrimental activities of their mutualist ants, while not deterring the ants themselves. One example involves adaptations that protect *Acacia* flowers from detrimental activities of myrmecophytic ants (Raine *et al.*, 2002). Flowers apparently produce a chemical that acts effectively to repel ants; this chemical is present, but in much lower levels, in *Acacia* species that are not ant-defended.

It seems likely, however, that there are circumstances in which the benefit of ant defense never exceeds its costs. The great evolutionary lability of these interactions suggests that ant defense is not only frequently gained, but also often lost. In a handful of cases, populations of an EFN-bearing species

lack functional nectaries, definitely suggesting loss. These populations tend to occur in isolated sites, notably certain islands (Janzen, 1973; Rickson, 1977; Keeler, 1984); they have been argued to have evolved under conditions of either reduced herbivore pressure or reduced native ant abundance. At one point it was believed that ant-defended plants commonly lacked chemical defenses (Rehr *et al.*, 1973), posing the dilemma of how plants could lose ant defense without incurring massive costs of herbivory. However, at least some chemical defense is retained in ant-defended species (Heil *et al.*, 2002), and expression of defensive chemistry and extrafloral nectar are uncorrelated in at least one plant family (Rudgers *et al.*, 2004). Continued expression of defensive chemistry is likely to facilitate the transition away from mutualism as a defense.

V. Ant-mediated seed dispersal

Seed dispersal is one of the most ecologically significant plant–animal mutualisms. Interest in its evolution has focused almost exclusively on dispersal of fleshy fruits by birds and mammals (Jordano, 1995; Tiffney, 2004; Bolmgren & Eriksson, 2005). However, ants are also important seed dispersers. The ecological significance of their actions has been examined in depth. Evolutionary aspects of seed dispersal by ants, in contrast, have been investigated only minimally (but cf. Giladi, 2006).

Ant-mediated seed dispersal (myrmecochory) has been recorded in over 3000 plant species and more than 80 plant families (Giladi, 2006). These make up a significant fraction of certain local floras (e.g. 26–35% of herbaceous species in forests in the eastern USA; Beattie & Culver, 1981). Seed-dispersing ants occur worldwide and all belong to the family Formicidae (Beattie, 1985). Myrmecochory increases in abundance from the poles to the Equator, paralleling the increased diversity of ants over that gradient, although there is some evidence for a peak in abundance at mid-latitudes (Beattie, 1985).

Several plant traits have undergone evolution in the context of seed dispersal by ants. Fruit ripening and the timing of seed release are commonly noted to be timed to the availability of mutualistic ants and to the relative rarity of seed predators (Ness & Bressmer, 2005). However, the signal adaptation of myrmecochorous seeds is the presence of an elaiosome, an external tissue attached to a seed that attracts ants and stimulates them to carry the seed back to the nest. There the elaiosomes are removed, then usually fed to the larvae; the seeds are discarded in an intact and viable state, either in an abandoned gallery of the nest or close to a nest entrance in a refuse pile along with other organic waste (Beattie, 1985).

Elaiosomes are outgrowths of three different types of ovule or seed tissue (Boesewinkel & Bouman, 1984). The varied development of elaiosomes indicates that the same functional structure has evolved independently on multiple occasions.

Their chemistry bears little resemblance to the chemistry of fleshy fruit. Elaiosomes are nitrogen-rich, with fatty acid compositions more similar to ants' insect prey than to other fruits (Hughes *et al.*, 1993). Given a choice among elaiosome-bearing plant species, ants prefer those with certain fatty acid profiles (Lanza *et al.*, 1992) and with high elaiosome-to-seed ratios (Hughes & Westoby, 1992). In some plant species, the elaiosome-bearing seeds are encased in fleshy fruits. Seed dispersal in these species is a multistage process: myrmecochory occurs after the fruit has been discarded by a vertebrate consumer (Böhning-Gaese *et al.*, 1999). Vander Wall & Longland (2004) argue that this is the stage of dispersal that leads to seed deposition in discrete, predictable, high-quality microsites.

Five hypotheses have been offered for the selective advantage to plants of ant-mediated seed dispersal: (i) seeds quickly removed to ant mounds are able to avoid consumption by predators; (ii) interspecific competition for seedling microsites is reduced by ant dispersal; (iii) seeds are moved significant distances away from unfavorable habitats directly under adults; (iv) seeds taken into ant nests are protected from fires, which are very common in some of the dry habitats in which myrmecochory is common; and (v) the ant nests to which seeds are moved are especially rich in some or all essential plant nutrients. There is at least some evidence for all these hypothesized advantages. They are not independent of each other, and their relative importance seems to vary across habitats (Giladi, 2006). Note that only the latter two are advantages unique to myrmecochory, among all forms of seed dispersal.

The advantages of myrmecochory to ants has received considerably less attention. Although the benefit has been assumed to be nutritional, the fact that oleic acid in elaiosomes actually functions to trigger ants' corpse-carrying behavior, rather than to feed them (Lanza *et al.*, 1992; Hughes *et al.*, 1994), suggests the intriguing possibility that ants do not necessarily profit from their interactions with myrmecochorous plants. However, elegant experimental work by Morales & Heithaus (1998) showed that, for the ant *Aphaenogaster rudis*, an elaiosome-rich diet enhanced reproductive output; more specifically, it led to the production of a higher proportion of reproductive females (see also Bono & Heithaus, 2002; Gammans *et al.*, 2005).

Myrmecochorous interactions are relatively generalized. Responses of ant species to elaiosome-bearing seeds are highly variable even within ant genera, and most of the ants in a given habitat do not, in fact, take seeds (Beattie, 1985). However, among the ant species that will take seeds, some are certainly better dispersers than others. Two guilds of ants have been recognized: one of poor-quality dispersers characterized by group-foraging granivores; the other of higher-quality dispersers characterized by solitary-foraging scavengers or omnivores attracted to the prey-like odors of the elaiosome (Hughes & Westoby, 1992; Hughes *et al.*, 1994; Giladi, 2006). Ness *et al.* (2004) showed that small ants move seeds shorter distances, partially explaining the poor quality of seed

dispersal that invasive ants, which are characteristically small, provide to native myrmecochorous plants. Certain seed-transporting species clearly confer no beneficial service at all (Gómez & Espalader, 1998; Zettler *et al.*, 2001). We are not aware of the existence of specialists and generalists among seed-dispersing ants, nor among myrmecochorous plants. However, efficient seed dispersal often involves very few of the ant species present in a given habitat, and the ants in that habitat clearly make choices among the available myrmecochorous seeds (reviewed by Giladi, 2006).

The wide taxonomic and biogeographical distribution, as well as the diverse ontogeny of the elaiosome, indicate that myrmecochory has arisen independently many times. Little is currently known about evolutionary transitions towards and away from myrmecochory. One of the only hypotheses offered to date is that mutualistic dispersal evolves from incidental, rare, but consistent benefits of granivory by ants (Levey & Byrne, 1993). Myrmecochory is common in certain well studied plant taxa currently under phylogenetic study. Thus, although it is too early to draw rigorous conclusions about the origins and loss of myrmecochory, it may be possible to do so in the near future.

VI. Discussion

The study of mutualism emerged from, and has long been rooted in, natural history. Probably as a consequence, research has tended to emphasize unique features of individual mutualisms, rather than searching for unifying patterns and processes (Bronstein, 1994). The goal of this review has been to take both approaches: to summarize current knowledge on the evolution of the three major forms of insect–plant mutualism, while also seeking generalities that cut across these details. In this section, we first revisit the five questions posed at the conclusion of Section II and summarize the current state of knowledge regarding each one. We then discuss the extent to which evolutionary models can contribute to a broader understanding of insect–plant mutualisms. Beyond attempting a synthesis of current knowledge, we point to areas in need of further research.

1. Evolutionary origins and maintenance of insect–plant mutualisms

Insect-mediated pollination, seed dispersal and protection mutualisms have each evolved multiple times, judging from their very wide but scattered taxonomic distributions, biogeographical distributions, and the diverse ontogenies of critical traits. There is strong evidence that each of these interactions arose via plants evolving mechanisms that took advantage of insects that were already foraging on plant tissue, or on the plant's surface. For example, insects were feeding on pollen long before the evolution of traits that attracted and rewarded them for these actions.

For a handful of particularly well studied plant–insect mutualisms, phylogenies have been interpreted to suggest the conditions under which mutualism has and has not arisen. Much more commonly, however, research in this area has proceeded by developing adaptive hypotheses for the conditions that favor and disfavor mutualism. Generally these hypotheses are based on ecological knowledge of the costs and benefits of the mutualism to each partner. Thus mutualisms have been hypothesized to originate more often in habitats where the relevant group of insects is particularly abundant, where alternative mutualists are particularly rare, where the benefit of mutualistic service is particularly high, or where its costs are particularly low. Given the apparent frequency with which each of these mutualisms has arisen, it is highly likely that no one adaptive hypothesis will explain the origin of that form of interaction. Rather, a diversity of conditions seems likely to select for the same ‘solution’ to a given ‘problem’.

Phylogenetic evidence, as well as taxonomic and biogeographical distributions, clearly suggest that all insect–plant mutualisms are not only frequently gained, but also frequently lost. Losses involve switches to mutualists other than insects (e.g. switches to birds as pollinators or seed dispersers), as well as shifts to abiotic alternatives to mutualism (wind pollination and self-pollination; chemical or physical defense; wind, water or gravity dispersal). It is too early to say which kinds of loss are most common, although at present there is extensive evidence for some and none at all for others. As in the case of mutualism gains, diverse explanations have been offered to account, after the fact, for mutualism losses. For example, very small, isolated, low-density populations appear frequently to lose both biotic pollination and biotic protection.

2. The evolution of mutualistic traits

Plant–insect mutualisms are united by one obvious feature: all involve a sedentary partner and a mobile one. (This feature also unites many mutualisms that do not involve plants and insects, such as protective relationships between anemones and anemonefish; nutritional relationships between corals and algae; and transportation relationships between beetles and fungi.) Natural selection can be expected to operate differently on the partners for this reason alone (see also Cushman & Beattie, 1991). Sedentary partners must exhibit traits that allow them to be located easily. In the case of plants, the major signals are visual and olfactory; these signals clearly evolve in the context of the mutualists’ major sensory modalities (Raguso, 2004). The sedentary partner also offers some form of reward that retains the attention of the visitors for the period in which their services are required. In the case of plants, these rewards are usually food substances matched to the nutritional needs of their mutualists. Thus nectar, which contains mostly sugars, is a ready source of energy that fuels the flight of pollinating insects and aggressive behaviors of ant defenders; myrmecophytic food bodies, elaiosomes and

pollen contain either lipids or other nitrogen-based compounds, and are gathered as food for larvae and sometimes for adults as well. Mobile partners within mutualisms also exhibit certain predictable traits. With the exception of some extreme specialists, they have the ability to move among alternative partners by making choices of who to visit, who to ignore, who to abandon, and when to abandon them. Their ability to make comparisons exerts selection on attraction and reward by the sedentary partner. The interactions among sedentary reward-providing mutualists, and partners that move among them and make choices, have been likened to a ‘biological marketplace’. A body of theory derived from economics has begun to develop that explores how such marketplaces function and evolve (Noë, 2001; Hoeksema & Schwartz, 2003).

This review has provided ample evidence that plants have undergone extensive trait evolution in the context of their mutualisms with insects. It is less clear whether insects have as well, because of the relative paucity of evolutionary and phylogenetic studies of traits in insects that enhance their benefit. At the very least, there is solid evidence for an asymmetry in the extent of evolutionary change that mutualistic plants and insects have undergone. This asymmetry is probably not independent of the previous one regarding evolutionary differences linked to mobility: mobile partners forage and make choices that lie within a behavioral repertoire also used by their relatives not involved in mutualisms, whereas sedentary partners have evolved suites of traits that take advantage of those behaviors for their own benefit. This asymmetry in trait evolution is more evident in the more generalized plant–insect mutualisms, but even many fairly specialized mutualisms exhibit it, at least to some degree.

One important consequence is that introduced insects often have the ability to invade native mutualisms with great facility, taking advantage of signals and rewards shaped over evolutionary time through selection exerted by native insects. The best known example involves introduced honeybees, but there are many others (Ness & Bronstein, 2004). Likewise, native insects can also take advantage of introduced plants. While it is clear that, in an ecological sense, invaders can significantly disrupt native mutualisms, there is a pressing need for work on the evolutionary consequences of such introductions (Bronstein *et al.*, 2004). More generally, what features of insect–plant mutualisms predict how they will respond evolutionarily to anthropogenic change? For example, have specialized mutualisms lost the evolutionary flexibility to respond to global shifts in climate?

3. Specialization and generalization

Another feature unifying insect–plant mutualisms is their wide range in levels of specialization: certain interactions are relatively specialized (e.g. one plant species has one or a very few insect mutualists), but most are widely generalized. On the plant side, more specialized mutualisms with insects

generally involve the provision of rewards that are nutritionally more valuable (qualitatively and/or quantitatively), as well as more protected from poorer mutualists. Specialization on the insect side appears to involve dietary adaptations that permit relatively complete reliance on commodities that the plant partners provide.

New research suggests that the degree of specificity within mutualistic networks is strikingly asymmetrical. One side of the interaction is considerably more specialized than the other, with the most specialized members of the network dependent on a nested core of generalists. Guimarães *et al.* (2006) recently analysed dependence in several pollination, seed-dispersal and ant–plant-protection networks, and concluded that all show similar patterns of asymmetry and nestedness (see also Bascompte *et al.*, 2006). Thompson (2005) contends that these similarities are probably caused by the actions of similar evolutionary processes, such as convergence and complementarity among interacting species.

In the two insect–plant mutualisms for which there is extensive phylogenetic work (insect pollination and ant protection), it is clear that switches between specialization and generalization have been frequent. In the case of protection mutualisms, these transitions have involved relatively few plant traits (e.g. gains and losses of domatia and lipid-rich food bodies), and phylogenetic studies of a few plant genera have proven extremely informative about the conditions that might foster them. The issue is considerably more complex in pollination mutualisms (Waser & Ollerton, 2006). A higher diversity of plant and insect traits play critical roles in these interactions; furthermore, the taxonomic distribution of potential partners is much wider. Evolution of increased generalization on the part of plants may involve the acquisition of more pollinating insect species or of vertebrate pollinators as well, which have considerably different sensory abilities and nutritional requirements.

4. Coevolution and cospeciation in mutualisms

We address this issue only briefly, as it has been reviewed at length by Thompson (2005) and others. There is phylogenetic evidence for cospeciation in only a handful of highly specialized insect–plant mutualisms (such as the fig–pollination mutualism; Machado *et al.*, 2005). Evidence for coevolution (e.g. trait-matching) is certainly more abundant. However, work in this area has been hampered by a relative lack of attention to the insect side of these interactions. As discussed above, it has been difficult to identify confidently traits and behaviors in insects that are not shared by close relatives that do not engage in mutualistic behaviors. This suggests the distinct possibility that evolution has been relatively one-sided in many of these mutualisms. However, an alternative interpretation is that we have not always been looking at the right insect traits. For example, it has been argued in the past that ants associated with specialized myrmecophytic plants

have undergone minimal evolution in the context of those mutualisms. Recently, however, Heil *et al.* (2005) have documented unique dietary adaptations in *Pseudomyrmex* ants that correspond to the unusual extrafloral nectar chemistry of their *Acacia* mutualists.

A shift to a more local view of the coevolutionary process, towards viewing coevolution as occurring within a complex geographical mosaic rather than across the range of a mutualism (Thompson, 2005), will probably greatly change our assessment of when, where and how coevolution is likely to occur within a given mutualism. Furthermore, the growing realization that coevolution can take place within broad multispecies networks must force a reassessment of the ubiquity of the coevolutionary process.

5. The ubiquity of cheating

A final feature shared by diverse plant–insect mutualisms is the ubiquity of cheating. Once again, there appears to be an asymmetry in this feature between the mobile and sedentary partners. Cheating does exist among plants, generally in the form of apparent rewards that are either not present or not delivered (Renner, 2006). However, as mobile mutualists have the opportunity to make choices, and abandonment carries detrimental consequences, the evolution of cheating in plants seems constrained to systems in which population densities are low, and one or very few visits are sufficient to obtain services from the partner (e.g. in rewardless orchids).

Conversely, cheating is extremely widespread among mobile, foraging insects, regardless of the form of mutualism. It commonly involves using an effective foraging strategy that does not result in benefits to the partner. That is, the food reward is collected successfully, but the partner is not transported (in pollination and seed-dispersal mutualisms) or defended (in protection mutualisms) in return. Foraging strategies that have detrimental effects are often not too different from those that confer benefits. In fact, mutualist individuals themselves are often the most damaging cheaters with which plants must cope (Bronstein, 2001). Beyond such ‘cheating from within’, the very presence of nutritional substances on sedentary partners favors entirely different groups of mobile organisms able to profit from them via behaviors quite different from those of the mutualists: hence ‘cheating from without’.

We have reviewed evidence from some insect–plant mutualisms for the existence of traits that either prevent cheating or reduce its negative effects. Interestingly, however, such traits are not as common as one might assume based on theoretical analyses (Bronstein, 2001), raising some intriguing questions about cheating that remain to be explored. For example, might cheaters routinely overcome mutualists’ defenses against them, potentially leading to coevolutionary races between cheaters and mutualists, even in cases where the mutualists themselves may not be coevolving? (R. Ferrière, M. Gauducon

and J.L.B., unpublished data). Alternatively, might the cost of being cheated, and the benefit of adopting a cheating strategy, simply not be very high?

6. A role for evolutionary theory

Evolutionary theories of mutualism began to develop in earnest only in the late 1980s. A variety of approaches have now been used, including population genetics models, both analytical and simulation models, game theory, economic theory, and adaptive dynamics. However, relatively few evolutionary questions about mutualism have yet been addressed theoretically. The majority of theoretical studies explore a single question: how mutualism can arise and persist in the light of investment costs and the apparent ease of cheating (Bull & Rice, 1991; Doebeli & Knowlton, 1998; Ferrière *et al.*, 2002; Hoeksema & Schwartz, 2003; Sachs *et al.*, 2004). These inquiries did not emerge from the growing base of empirical knowledge on mutualism. Rather, they belong to a larger body of work on the origin and stability of cooperation, defined broadly to include both within-species and between-species phenomena (Axelrod & Hamilton, 1981; Hammerstein, 2003). In parallel with developments in the theory of within-species cooperation, these models focus on the roles of transmission mode, spatial structure, partner choice, and sanctions in promoting and impeding the stability of mutualism.

Much of this body of theory has limited relevance to understanding mutualistic phenomena in nature, however. With a handful of exceptions (e.g. Law & Koptur, 1986), models of the evolutionary dynamics of mutualism focus on obligate, species-specific interactions. It is not that specificity is seen as inherently more interesting or more significant; rather, pairwise models are simply more tractable to construct and to analyse. However, as demonstrated in this review, generalization and asymmetrical dependence are ubiquitous within insect–plant mutualisms. Furthermore, much of the current body of evolutionary theory is directed specifically at exploring symbiotic mutualisms (e.g. Frank, 1995); it is difficult to apply to mutualisms involving free-living partners. Clearly, there is a pressing need for theory applicable to multispecies mutualisms between free-living partners (Stanton, 2003). Ecological theory has begun to fill this gap, but evolutionary theory has lagged behind.

It is important to emphasize that evolutionary models have revealed some fairly profound generalities about the mutualism that are beginning to change our overall understanding of these interactions. In particular, recent models utilizing a diversity of approaches and assumptions show that, despite initial conjectures, mutualism is not in fact evolutionarily fragile; rather, it is remarkably robust in the face of the apparent temptation to cheat. This is not an issue, however, that emerged out of empirical discoveries, nor has it driven further empirical research on the evolution of mutualisms.

Empiricists have taken it for granted that mutualisms arise repeatedly, diversify, and occasionally but not always go extinct. Rather, they have focused on the conditions that favor each of these processes.

Some important theoretical advances have been made on other central questions. There is a growing body of theory on conditions favoring and disfavoring coevolution within mutualisms (Kiestler *et al.*, 1984; Nuismer *et al.*, 1999; Thompson, 2005). Trait evolution has also been explored theoretically: for example, models have addressed the evolution of optimal rates of reward production (Sakai, 1993) and of traits with important functions in particular types of mutualism (Cohen & Shmida, 1993; Law *et al.*, 2001; Holland & DeAngelis, 2002). In addition, as mentioned previously, the distribution of specialization and generalization within community-wide mutualistic networks has been attracting great attention from theoreticians (e.g. Guimarães *et al.*, 2006; Bascompte *et al.*, 2006).

Theory has a potentially important, but not yet fulfilled, role in exploring many of the mysteries posed by empirical studies of mutualism (see also Hoeksema & Bruna, 2000). Fruitful avenues for theoretical research raised by this review might include these: within a given form of mutualism, do specialized or generalized associations show greater evolutionary stability? How do mutualistic networks arise, and what are the evolutionary implications of asymmetrical dependence? How does the presence of cheaters alter evolutionary trajectories of mutualisms? What are the comparative evolutionary effects of cheating behaviors of mutualistic species vs cheating behaviors of ‘freeloaders’ that never engage in mutualism? More generally, how does mutualism evolve in spatially and temporally patchy environments? Models are beginning to shed light on these questions (Hochberg *et al.*, 2000; Gomulkiewicz *et al.*, 2003), but much remains to be done.

7. Conclusion

In this review we have only scratched the surface of the features of plant–insect mutualisms that will influence how these interactions evolve, that is, how interactions that differ radically in natural history are under similar forms of selection, as well as what (beyond their natural history features) makes them quite different. Knowledge about plant–insect mutualisms is accumulating at a startling rate. We fully expect (and hope) that some of the generalizations we have made will soon be outdated, and the gaps we point to filled. Our aim has been to provide a template of current thinking about plant–insect mutualisms for interested readers to build on as this research field evolves.

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