

ECOLOGY AND EVOLUTION OF APHID-ANT INTERACTIONS

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Key Words mutualism, aphid-ant relationship, cost-benefit analysis

■ **Abstract** Aphids and ants are two abundant and highly successful insect groups, which often live in the same habitat and therefore are likely to interact with one another. Whether the outcome of such an interaction is a predator-prey or mutualistic one is dependent on what each partner has to offer relative to the needs of the other. Consequently, understanding why some aphids enter mutualistic interactions with ants is dependent on understanding the physiological, ecological, and evolutionary traits of both partners. This includes an appreciation of the spatial, temporal, and taxonomic context in which mutualistic interactions developed. In this review, we use aphid-ant interactions to illustrate the whole range of interactions from antagonistic to mutualistic as well as to identify the processes affecting the degree of association and in particular the context within which such interactions evolved. The constraints of establishing and maintaining beneficial interactions between aphids and ants is addressed from a cost-benefit perspective. Prospects for future research are identified to further the understanding of the patterns and processes associated with aphid-ant relationships.

INTRODUCTION

In many ecology textbooks, *mutualism* is defined as an interaction between two species that is beneficial for both species (Begon et al. 1999, Boucher et al. 1982, Krohne 1998). However, assuming that it is individuals that benefit, then mutualism is when organisms reciprocally and positively affect the individual fitness or per capita growth rate of their partners (Addicott 1985, Bartlett 1961). Or more simply, mutualism is a reciprocally beneficial relationship between organisms (Herre et al. 1999). There are several reviews of the ecology of mutualism (Boucher et al. 1982, Bronstein 1994b, Bronstein & Barbosa 2002, Buckley 1987a, Connor 1995, Hoeksema & Bruna 2000). These give general accounts of the conditions under which such beneficial associations might develop, e.g., the type of environment in which they are likely to evolve and the constraints. When dealing with mutualism, there is a tendency to describe general patterns across different taxonomic groups

and omit details and mechanisms that appear of little importance for the larger picture. Seemingly, there are many similarities in the biologies of the partners of ants (e.g., aphids, coccids, membracids, scale insects, and lycaenid butterflies), notably the production of honeydew/nectar, which makes it tempting to look for broad, general patterns (c.f. Delabie 2001) at the risk of ignoring mechanisms that shape different degrees of association. In this review, however, we focus exclusively on ant-aphid interactions, which were last reviewed some time ago (Buckley 1987a, Way 1963). These reviews are still cited in ecological textbooks as a paradigm for mutualistic associations between insects (e.g., Begon et al. 1999, Hölldobler & Wilson 1990). Over the past two decades, however, considerable progress has been made in gathering information on the physiological adaptations, the ecological context, and the evolutionary constraints acting on both partners when entering an association. This information challenges the widely held view that the interactions between these two groups of organisms are always positive. This information needs to be incorporated into any overview of the subject if one is to understand the costs and benefits of the associations between aphids and ants.

The many papers published on mutualistic relationships over the past two decades led to predictions about the conditions that favor the evolution of reduced antagonism and mutualism (Boucher et al. 1982, Bronstein 1994a, Bronstein 2001, Hoeksema & Bruna 2000, Holland et al. 2002, Stachowicz 2001). For example, it is suggested that facultative mutualism and those involving third partners should be more variable than obligate mutualism. In addition, mutualisms that depend on one or both partners being abundant are more likely to vary with conditions, obligate mutualism must include mechanisms limiting the abundance of partners, and highly specialized mutualisms should be rare. However, there is no general theory that predicts the outcome of species interactions ranging from mutualistic to antagonistic. This is possibly because there is no common currency for measuring the costs and benefits for both partners. However, there is a need to understand the physiological and ecological costs and benefits at the individual level to identify the structuring forces in the antagonism-mutualism continuum. Aphids and ants are characterized by distinctive population and genetic structures, which highlight the different temporal, spatial, and evolutionary aspects that are likely to affect these relationships.

The aim of this review is to use aphid-ant interactions to (a) illustrate the whole range of interactions from antagonistic to mutualistic, (b) identify the mechanisms regulating the degree of association, and, in particular, (c) identify the context in which such interactions evolved. The evolution and maintenance of beneficial interactions between aphids and ants is addressed from the perspective of both partners, and the research needed to further the understanding of the conflict of interests in aphid-ant interactions is highlighted.

FEATURES OF THE PARTNERS

In the next two sections we briefly summarize the main features of aphids and ants and the potential costs and benefits associated with myrmecophily.

Aphids

Aphids most likely evolved some 280 mya in the Carboniferous (Heie 1967), and there are now about 4000 species worldwide (Eastop 1973, Remaudière & Remaudière 1997). They characteristically have several parthenogenetic generations during summer, a single sexual generation in autumn, and overwinter as eggs. The parthenogenetic, iteroparous mode of reproduction associated with the telescoping of generations, in which aphid embryos start developing in their grandmother and develop to an advanced stage inside their mother (Dixon 1998, Kindlmann & Dixon 1989), results in rapid multiplication and facilitates the exploitation of short-lived resources. In addition, many species are highly polyphenic, with winged individuals specialized more for dispersal than reproduction and unwinged individuals more for reproduction than dispersal. That is, they show division of labor. Their prodigious rates of increase are unparalleled in other herbivorous insects. Aphids feed on phloem sap, which is typically rich in sugars but low in nitrogen (N). As a consequence, aphids need to ingest large volumes of phloem sap—most of which is excreted as honeydew (Dixon 2004, Stadler et al. 1998, Zoebelein 1954). Feeding on plant sap is a very old way of obtaining food and dates back to the Early Devonian (Labandeira 1997). There is a clear North-South gradient in species richness, with relatively few species in the tropics (Dixon et al. 1987). This geographic pattern is attributed to the small fat reserves, large investment in offspring, and high host-plant specificity of aphids. These life-history attributes greatly limit the amount of time aphids can spend searching for host plants. This in association with a high plant diversity in the tropics means that very few plants there are abundant enough to host aphids (Dixon 2004, Dixon et al. 1993a, Dixon et al. 1993b).

Ants

Ants have survived since the upper Cretaceous, some 100 mya, and now comprise some 8000 species (Hölldobler & Wilson 1990). They show division of labor and eusociality, which enables colonies to sustain high population densities for long periods of time (Hölldobler & Wilson 1990, Wilson 1987). Like an aphid colony, an ant colony is an almost exclusively female society. Central to the success of ant societies is that the members of each colony are divided into reproductive and nonreproductive worker castes. Workers are able to forage over vast areas relative to their size but operate from a fixed base (nest) to which they need to return. The nests of mound-building ants in temperate regions often last for many decades and have a strong influence on their immediate environment. For example, herbivore pressure on trees may be significantly reduced around ant nests, resulting in “green islands” (Laine & Niemela 1980) with higher survival rates of trees and a strong shift in herbivore community structure (Skinner & Whittaker 1981, Wellenstein 1980). Ants inhabit a broad geographic range with the highest species richness in the tropics, where they are the dominant insect group in terms of biomass (Fittkau & Klinge 1973, Wilson 1990). Not all ant taxa have developed trophobiotic relationships with aphids: Only workers of the subfamilies *Formicinae*

and *Dolichoderinae* and a few species in the genus *Myrmica* and *Tetramorium* of the *Myrmicinae* collect honeydew (Kunkel et al. 1985, Nixon 1951). Baltic amber fossils indicate that associations between ants and aphids date back at least to the early Oligocene (Wheeler 1914). However, mutualistic interactions with ants do not seem to be constrained to particular aphid taxa as, although not analyzed phylogenetically, the frequency of ant attendance does not vary strikingly between groups. This probably suggests multiple origins of myrmecophily (Bristow 1991, Stadler et al. 2003).

In view of their abundance and territoriality, their burrowing and mound construction, the relative stability of their populations, as well as their feeding habits and aggressiveness, ants are a group of insects that almost any other insect group is likely to encounter at some stage. The outcome of these encounters can be positive or negative.

Benefits and Costs

Before considering the interactions between ants and aphids, it is important to have some idea of the benefits and costs of the mutualism for both partners. Benefits for one partner may entail costs for the other. Therefore, the tension within these systems and the relative magnitude of the resulting conflict/shared interests determines whether a relationship is positive or negative. At the risk of oversimplification, ants are very active and many forage over great distances, so energy for foraging is likely to be a very important limiting factor. Aphids have to process very large quantities of phloem sap to sustain their very high growth rates, so honeydew is often likely to be abundant and available for fueling ant foraging. However, because phloem sap contains very little amino nitrogen and aphids are very good at assimilating most of it, honeydew is unlikely to be a source of N for ants. In addition to being a fuel for foraging, honeydew may also be stored and used to tide ants over periods of adverse conditions. A good example of this is the storing of coccid honeydew by honey-pot ants (Gullan & Kosztarab 1997). There is no example of this involving ants and aphids, but it could exist.

The cost for ants is that they need to monopolize, collect, transport, and pass honeydew to their nest mates, which involves morphological and behavioral adaptations. However, the biggest cost is likely to be that associated with being dependent on aphids for fuel for foraging. This is particularly so for obligate myrmecophily, involving one species of ant and aphid. Although the distribution of the aphid *Stomaphis quercus* (L.) on oak trees is limited to those that grow within the territories of the ant *Lasius fuliginosus* (Latreille) (Goidanich 1956), it is unknown whether the distribution and abundance of the ant is dependent on that of the aphid. The expectation, however, is that ants should rarely be dependent on a single aphid species because this would put them at great risk of extinction.

Aphids are soft bodied and have little defense against natural enemies other than avoidance. Therefore, it is likely that a major benefit of ant attendance for aphids is protection. In habitats where aphids are at particular risk of attack from

natural enemies, a high incidence of ant attendance is predicted. Most aphids that are ant attended are gregarious. Clearly, this is advantageous for ants because it results in the sources of energy being concentrated in a few places rather than scattered throughout their territory. However, in being gregarious, aphids become more attractive to natural enemies, which could put an upper limit on the size of ant-attended aphid colonies.

The cost for aphids appears to be mainly one of producing large quantities of high-quality honeydew to attract ants. It is well established that facultatively attended aphids increase their rate of honeydew production when attended by ants (Nixon 1951). Therefore, if unattended aphids feed at an optimum rate for the assimilation of amino nitrogen, then a faster rate is likely to adversely affect their feeding efficiency and consequently their rate of growth. If aphids are obligately ant attended, then another cost for aphids is the effect this has on their distribution. Good examples of this are the oak aphid, *S. quercus*, and the thyme aphid, *Aphis serpylli* Koc, both of which have markedly more restricted distributions than their host plants because they are dependent on ants being present in the habitat (Hopkins & Thacker 1999, Hopkins et al. 1998). This cost-benefit perspective is adopted in the remainder of the review.

PATTERNS IN APHID-ANT INTERACTIONS

Given the ecological success of both ants and aphids, that aphids excrete energy-rich honeydew, and that ants aggressively defend resources, it is difficult to understand why so few species of aphid have evolved a close relationship with ants. For example, only a quarter of the aphid species in the Rocky Mountain region are attended by ants (Bristow 1991), and in Central Europe, about one third are obligate myrmecophiles (Stadler & Dixon 1998b, Tizado et al. 1993). More than a dozen hypotheses have been proposed to account for the variability in aphid-ant relationships and the low proportion of attended species. First among them is the plant permissive hypothesis (Bristow 1991), which suggests that host-plant quality plays a critical role in determining the attractiveness of aphids for ants. Both variation in the quality of different hosts or different parts of the same host plant may affect the quality of honeydew, which is either more or less attractive to ants. However, this hypothesis ignores the fact that several species of aphids may feed on the same host plant or even plant organ but have very different degrees of associations with ants and assumes that the quality of phloem sap determines that of the honeydew. Recent studies have found that feeding on woody plant parts is positively associated with ant attendance, whereas mobility, feeding in isolation, and having winged adults are negatively associated with ant attendance (Dixon 1998, Stadler et al. 2003).

The literature provides little support for the idea that a single hypothesis can account for the diversity of aphid-ant relationships. Fitting aphid-ant relationships into a continuum from highly mutualistic to antagonistic and identifying the

physiological, ecological, and evolutionary constraints provide a conceptual framework for studying the opportunities and constraints shaping such relationships (Figure 1). Figure 1 also provides a road map for this review. The role of the evolutionary constraints has not been tested with the same rigor and is unlikely to be of the same importance, but these constraints may affect the direction of change in the mutualism/antagonism balance. A mutualistic relationship is expected if aphids and ants achieve higher population growth rates and larger colony sizes (Figure 1a). Aphids must be able to modify honeydew to make it more attractive to ants, which must be able to modify their foraging behavior so that they can effectively harvest this energy-rich resource.

Other ecological effects are well documented. For example, hygienic services like the collection of sugary excreta and protection from fungal infections (Figure 1b) are thought to favor mutualism. However, these are likely to be secondary because unattended aphids effectively dispose of their honeydew and are apparently not so prone to fungal infections associated with honeydew. The fragmentation of habitats and plant-related factors, such as abundance, wide distribution, and quality, are thought to facilitate mutualism because these attributes result in an increase in aphid abundance, which increases the probability of their being encountered by ants. Put another way, obligate mutualisms are unlikely to evolve between rare species. Lastly, morphological and behavioral adaptations in ants are likely to facilitate the successful establishment of mutualistic relationships (Figure 1c). Selection for an antagonistic relationship is likely if the costs, such as the production of high-quality honeydew and the absence of ant partners in many habitats or inaccessibility of suitable hosts, associated with ant attendance, are high (Figure 1d). If plants compete with aphids for the services of mutualists [e.g., via extrafloral nectaries (EFNs)] or if the chemical protection of the host plant affects the ants (e.g., honeydew containing secondary plant metabolites), an intimate relationship is less likely to develop (Figure 1f). Similarly, if the mortality due to natural enemies is low or if specialized predators or parasitoids exploit ant-attended aphids (Kaneko 2002, Völkl 1992) (Figure 1f), costs might outweigh benefits. These factors and associated mechanisms are addressed in more detail below.

It is difficult to assess the relative importance of these factors for aphid-ant relationships because of the poor understanding of their temporal dynamics or the interactions between factors. Very few studies last longer than 30 days (i.e., one aphid generation) even though the relative impact of the factors varies with time. For example, although protection is thought to be important, even obligate myrmecophiles, such as *Symydobius oblongus* (von Heyden) and *Metopeurum fuscoviride* Stroyan, are unattended on more than 25% of the occasions when surveyed during the course of a season (Stadler 2004, Stadler & Dixon 1999). Thus, short-term studies are unlikely to identify the dynamic aspects of the costs and benefits associated with ant attendance.

Features associated with:

Mutualism

Antagonism

- Physiological**
- a) • High growth rates—at least temporarily (El-Ziady & Kennedy 1956, Flatt & Weisser 2000, Stadler & Dixon 1999, Stadler et al. 2002)
 - Ability to make the sugar composition of honeydew more suitable for ants (Fischer & Shingleton 2001, Kiss 1981, Völkl et al. 1999, Yao & Akimoto 2001)
 - Honeydew is a waste product needing little further investment
 - Energy source for high activity tempo foragers (Davidson 1998, Oster & Wilson 1978)
- Ecological**
- b) • Hygienic services (Buckley 1987b, Nixon 1951)
 - Protection by ants (Addicott 1978a, Cushman & Addicott 1989, Katayama & Suzuki 2002, Morris 1992, Nixon 1951, Offenberg 2000, Sakata & Hashimoto 2000, Tilles & Wood 1982, Way 1963)
 - Habitat fragmentation (Braschler & Baur 2003, Braschler et al. 2003, Gotelli & Filson 2002b, Wilson et al. 2003)
 - Abundance of aphids
 - Distribution of aphids
 - High quality of host (Breton & Addicott 1992b, Bristow 1991)
 - Gregariousness (Stadler et al. 2003)
- Evolutionary**
- c) • Proventriculus for storing honeydew (Eisner 1957)
 - Extensible gaster further facilitates the storage of honeydew (Taylor 1978)
 - Overcome initial defense or aggressiveness (Doebeli & Knowlton 1998, Sakata 1994)
- d) • Cost of producing high-quality/large amounts of honeydew (Fischer & Shingleton 2001, Katayama & Suzuki 2002, Yao & Akimoto 2001, Yao & Akimoto 2002, Yao et al. 2000)- Changing nutritional requirements of ants during their life cycle e.g., need for less honeydew (Hölldobler & Wilson 1990, Katayama & Suzuki 2002, Pontin 1978, Rosengren & Sundström 1991, Sudd & Sudd 1985)

e) • Predation by ants (Cushman & Addicott 1989, Cushman & Whitham 1991, Engel et al. 2001, Katayama & Suzuki 2002, Offenberg 2001, Sakata 1994, Sakata 1995, Sakata & Hashimoto 2000, Yao & Akimoto 2001)- Competition for mutualists (Addicott 1978a, Cushman & Addicott 1989, Engel et al. 2001, Fischer et al. 2001, Offenberg 2001, Sakata & Hashimoto 2000)
- Fitness costs (Stadler 2004, Stadler & Dixon 1998a, Stadler et al. 2002)
- Low predictability of C resource
- Alternative sugar sources (e.g. EFNs) (Beerra 1989, Cushman & Addicott 1989, Dreisig 1988, Offenberg 2000, Offenberg 2001, Sakata 1995, Sakata & Hashimoto 2000)
- Chemical defense of plants affects honeydew and ants (Vreiling et al. 1991, Wink & Witte 1991)

f) • Low predator/parasitoid pressure (association costs) (Stadler et al. 2001)- Exploiters of mutualism (e.g. other aphids)
- Exploiters of mutualism (e.g. specialised parasitoids, predators) (Bartlett 1961, Bronstein 2001, Mackauer & Völkl 1993, Sloggett & Majerus 2003, Völkl 1992)

Figure 1 Factors that influence the strength and direction of the associations between aphids and ants. Temporal or spatial aspects of these factors are rarely documented.

PROCESSES SHAPING APHID-ANT INTERACTIONS

Next, we will focus on the adaptations aphids and ants developed to exploit each other and the constraints they encounter in doing so. The combination of physiological, morphological, and ecological boundary conditions ultimately determines whether the net outcome of a relationship is antagonistic or mutualistic.

Adaptations of Aphids and Ants

Papers on aphid-ant relationships often suggest that ant attendance has a positive effect on aphids, resulting in larger colonies (El-Ziady & Kennedy 1956, Flatt & Weisser 2000, Skinner & Whittaker 1981), lower mortality rates (Way 1963), and removal of sticky honeydew (Nixon 1951). However, such general statements do not account for the fact that different aphid species have developed associations with ants ranging from close (obligate) through occasional (facultative) to avoidance (unattended). Only recently have the benefits aphids are assumed to derive from ant attendance been questioned and critically examined. The results reveal a number of physiological costs associated with close associations. In particular, one needs to ask whether increases in feeding and excretion actually benefit aphids, in particular those that are not closely associated with ants (see, e.g., El-Ziady & Kennedy 1956). Aphids do not simply tap into the phloem elements of plants and passively regulate the flow of plant sap through their bodies, which is sometimes collected by ants. They actively modify the composition of the sap to avoid dehydration (Fisher et al. 1984, Rhodes et al. 1996, Rhodes et al. 1997), which may also make it more attractive to ants and could have significant metabolic costs. It is possible that osmoregulation is a preadaptation for forming an association with ants. For example, the aphid *Tuberculatus quercicola* (Matsumura) incurs significant costs when attended by *Formica yessensis* Forel because it produces smaller and less fecund adults than when unattended (Yao et al. 2000). Ant-attended aphids excrete smaller droplets of honeydew at a higher rate, and the honeydew contains significantly higher concentrations of amino acids (Yao & Akimoto 2002), sucrose, and trehalose (Yao & Akimoto 2001) than that of unattended aphids. Although the concentration of amino acids in honeydew is increased, possibly as a consequence of the effect of the increased flow of phloem sap on assimilation, its significance for ants needs to be established. It is suggested that in producing large quantities of honeydew aphids have less N for growth and reproduction (Stadler & Dixon 1998a). *Chaitophorus* spp. can even modify the sugar composition of their honeydew, with those that are more closely attended (*Chaitophorus popualibae*, *Chaitophorus populeti*) able to reduce the melezitose content when unattended (Fischer & Shingleton 2001). In contrast, *Chaitophorus tremulae*, which is less often associated with ants, does not show this response. That is, the production of large quantities of honeydew, which is attractive to ants, is likely to be costly for aphids because they have to feed faster and increase the rate of converting simple to complex sugars.

It is difficult to demonstrate the fitness cost for aphids. Contrary to the claim of El-Ziady & Kennedy (1956), *Aphis fabae cirsiacanthoides* Scop., feeding on *Cirsium arvense* (L.) Scop., incurs significantly higher costs when attended by *Lasius niger* L. It has a significantly lower mean relative growth rate, produces fewer offspring, takes longer to reach maturity, and invests less in gonads (Stadler & Dixon 1998a). The facultative myrmecophile species feeding on tansy (*Tanacetum vulgare* L.) also have significantly lower potential growth rates when attended by *L. niger* (Stadler et al. 2002). Therefore, there is increasing evidence that aphids can adapt their physiology in response to ant attendance, and this is costly. That is, there is a need to add a new dimension to the classical textbook paradigm of ant-aphid relationships.

Essential adaptations for ants involved in aphid-ant relationships are morphological changes to the proventriculus and gaster, which enable them to carry large quantities of honeydew. In the subfamilies *Formicinae* and *Dolichoderinae*, the development of a proventriculus enables them to gather large quantities of fluid rich in carbohydrate from plants or Homoptera (Davidson 1997, Davidson et al. 2004, Eisner 1957). This digestive organ is situated posterior to the crop and regulates the flow of food. The proventricular bulb pumps liquid from the crop into the midgut and prevents the posterior flow. Only in the *Dolichoderinae* and *Formicinae* does the proventriculus passively occlude the passage of food through the gut, which allows the associated musculature to be reduced (Eisner 1957). In this way ants are able to control the movement of honeydew from the crop, the “social stomach,” into the midgut, where it is digested. In addition, to store large quantities of honeydew and carry it to the nest, ants need the ability to expand and contract their gaster with changes in the volume of honeydew collected (Kunkel et al. 1985, Taylor 1978).

The Ecological Framework

If one is to understand mutualistic relationships, it is necessary to address the ecological context in which both partners interact. It is likely that ants evaluate the nutritive quality and associated mortality risks of food patches, i.e., the trade-off between colony growth and forager survival. The predictions of optimal foraging theory are generally well supported, when animals face simple decisions, such as maximizing net energy returns by choosing a particular prey (Stephens & Krebs 1986). It is now appreciated that foragers are more flexible and face more complex decisions in nature, which affect their lifetime reproductive success (Clark & Mangel 2000, Houston et al. 1988, Houston & McNamara 1988, Houston & McNamara 1999). Information on the environment and physiological condition of the organism making the decisions can be incorporated into optimal foraging models.

Ants do not simply collect honeydew but are also subject to predation risks and adjust their foraging activity accordingly (Carroll & Janzen 1973). For example, when food is offered to *Lasius pallitarsis* (Provancher) in patches where the risk

of predation by *Formica subnuda* Emery varies, *L. pallitarsis* spends less time foraging in the patches with *F. subnuda*, even though these patches contain high-quality resources (Nonacs & Dill 1991). Furthermore, the use of a high-quality patch depends on the magnitude of the difference in terms of growth between feeding in risky and safe patches: The greater the benefit of feeding in a risky patch, the more likely it is exploited. Thus, ant workers are capable of evaluating risks and rewards, and they forage in a way that maximizes colony fitness (Nonacs & Calabi 1992, Nonacs & Dill 1990). The trail marking by scouts, which recruit nest mates to an aphid colony, seems to be based on the rate at which they ingest honeydew (Mailleux et al. 2000). Thus, it is likely that the number of foragers recruited to a resource is related to the total production of honeydew or aphid colony size (de Biseau & Pasteels 1994, Mailleux et al. 2003, Völkl et al. 1999).

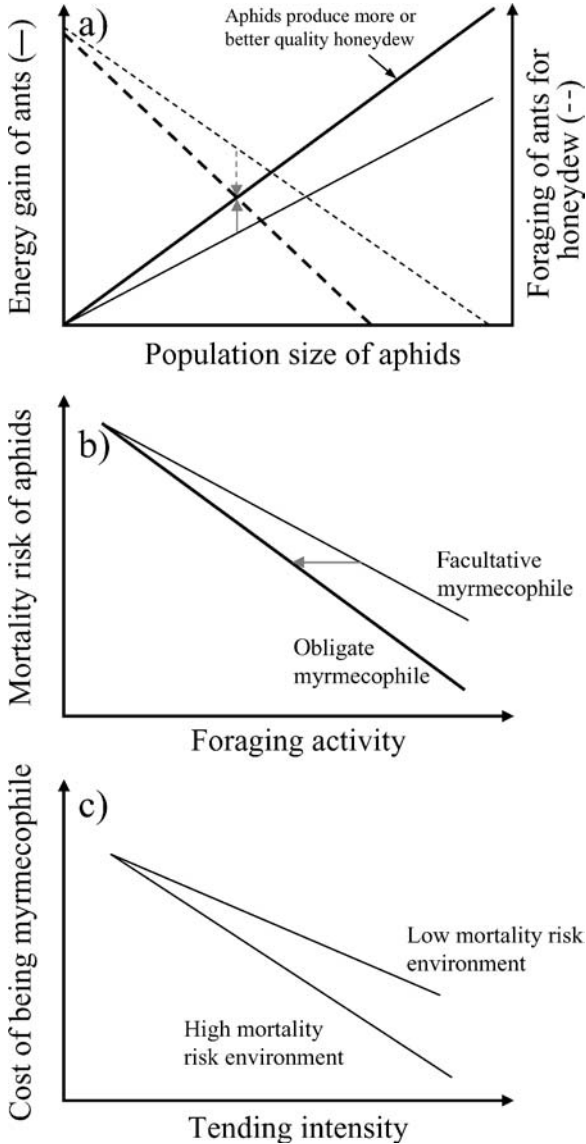
This simplistic view becomes more complicated if the spatial context in which aphid-ant relationships evolved is taken into consideration. There are numerous reports that aphid colonies close to ant nests experience higher attendance than those further away (Boucher et al. 1982, Bradley & Hinks 1968, Pontin 1978). However, even this tendency changes during the course of a season because aphids colonize trees further and further away from the main nest (Scheurer 1967). Aphids living in fragmented grassland are more frequently visited than those in unfragmented plots (Braschler et al. 2003). It is suggested that protection from predators may positively affect ant-attended colonies. However, unattended colonies are also more numerous in fragmented habitats, which indicates that fragmentation per se is more important than the services supplied by ants. Fragmentation is not only associated with an increase in aphid numbers but also a change in the composition of ant communities. For example, the polygynous ant *Formica aquilonia* Yarrow is more abundant in old forests and large fragments of forests and the monogynous *Formica lugubris* Zett. in young forests, small fragments of old-forest, and the edges of forests (Punttila 1996). Boreal ant communities, i.e., those in spruce-dominated forests, are influenced by succession more than the species of aphid they attend. There is good evidence that ant communities can affect the composition of aphid communities. In forest and grassland, apparent competition, the sharing of natural enemies (Bishop & Bristow 2001, Müller & Godfray 1999, Rott et al. 1998), or competition for mutualists is implicated in this (Addicott 1978a, Cushman & Addicott 1989).

Information on aphid ecology, mortality risks, ant foraging, recruitment behavior, and the spatial context, referred to above, is best summarized in a conceptual model, which predicts when and under what environmental conditions mutualistic relationships between aphids and ants are likely to evolve (Figure 2). It is reasonable to assume that with increase in aphid population size the energy supply for the ants will increase (Figure 2a). The energy gain is greater if the aphid species attended by the ants produce more or better quality honeydew. The more honeydew available per unit of foraging time/area the more likely ants will focus on the most productive colonies because fewer workers are required to collect the same

amount of energy. Less productive colonies further away from a nest are likely to be abandoned first. As a consequence of the decline in the foraging activity for honeydew, with fewer workers protecting distant aphid colonies, the mortality of aphids due to natural enemies might increase (Figure 2b). The risk to aphids of death caused by predators can be decreased through dispersal, leading to smaller colony sizes, which are too small to be attractive to natural enemies (Kindlmann & Dixon 1993), or through recruiting more ants by producing more attractive honeydew (Kiss 1981). This is likely to result in competition for mutualists, which may be the principal factor increasing the costs for myrmecophilic aphids (Addicott 1978a, Cushman & Addicott 1989, Offenberg 2001, Sakata & Hashimoto 2000). Competition between myrmecophilous aphids for mutualists is a “red queen game” as the need to produce attractive honeydew suggests that alternative resources should affect aphid-ant relationships, e.g., in situations where aphids feed on plants with EFNs or food bodies. However, the results are equivocal with some studies reporting no competition between EFNs and honeydew-producing Homoptera (Delclero & Oliveira 1993), whereas others do find negative interactions (Engel et al. 2001, Koptur 1991, Sakata & Hashimoto 2000). In addition, currently the effects of EFNs on aphid-ant interactions do not discriminate between different mechanisms or cause and effect in these associations (Offenberg 2000). In any case, closer associations with ants are likely to reduce the risk of mortality due to the activity of natural enemies (Figure 2b). Obligate myrmecophiles are probably more successful in attracting ants and benefit from being better protected than facultative myrmecophiles.

As noted above, the production of large quantities of honeydew entails metabolic costs. This is likely to be true for both obligate and facultative myrmecophiles. If this is correct, then there should be a negative correlation between the intensity of tending by ants and the cost of being a myrmecophile (Figure 2c). For a particular level of attendance, the overall costs should be higher in patches with a low mortality risk. This is because there is an investment in defense via ants, but the investment does not yield any interest in low mortality risk patches. Several recent studies have demonstrated that aphids are able to perceive mortality risks, e.g., *Acyrtosiphon pisum* Harris produces winged morphs in the presence of natural enemies such as ladybirds (*Coccinella septempunctata* L.) (Dixon & Agarwala 1999, Weisser et al. 1999), hoverfly larvae [*Episyrphus balteatus* (De Geer)], lacewing larvae [*Chrysoperla canea* (Stephens)] (Kunert & Weisser 2003), or parasitoids (*Aphidius ervi* Haliday) (Sloggett & Weisser 2002). This occurs either after contact with a predator or with chemical cues left by ladybirds. We hypothesize that ant-attended aphids do not respond in this way to the presence of ladybird larvae (Dixon & Agarwala 1999).

For aphids, the relationships between the different model parameters can be reduced to a simple ratio of the mortality risk (m) relative to the cost of being a myrmecophile (c). The expectation is that if $m/c < 1$ the aphids should not develop a relationship with ants, if $m/c \approx 1$ a facultative association is possible, and if $m/c > 1$ obligate myrmecophily is likely. This ratio reflects the trade-off between the



mortality suffered by a clonal population and the cost of producing more or better honeydew in response to a specific foraging activity and environment. The unit of measurement for these parameters must be related to the fitness of an aphid clone, which indicates the importance of using a common currency when measuring the effects of ant attendance. Currently, it is unknown whether the relationships shown in Figure 2a–c are linear.

Evolutionary Constraints

Once ants evolved ways of collecting and processing honeydew, it is likely they were able to forage larger areas and become more abundant. Oster & Wilson (1978) distinguish between “high tempo” and “low tempo” ants. They assume that a positive correlation exists between behavioral tempo, colony size, and polymorphism. Foraging over a large rather than a small area might impose a higher mortality risk, which may account for a higher turnover rate of workers. However, little attention was paid to the type of food collected, and they predicted that homopteran-tending ants would be low tempo foragers. This conflicts with the observed variation in foraging by ants associated with aphids, and diet analyses also show a more complex picture with a high variability in the food types used (Blüthgen et al. 2003). It is more likely that the remarkable range in worker activity is associated with the price of honeydew, which is dependent on the distance of the colony (gasoline station) from the ant’s nest and the time required to collect the honeydew. Ants that are able to build their nest, or parts of it, close to such resources should have a selective advantage over those that are restricted in where they can build their nests. The formation of subsidiary nests by *Formica rufa* L. leads to a network of intercommunicating nests with up to 200 meters between the main and peripheral nests (Gösswald 1941, Rosengren & Pamilo 1983). That is, polydomy could be the typical nest structure of species collecting large quantities of honeydew (Davidson 1997, Davidson 1998).

Another difficulty in the evolution of a mutualistic association is the initial response of aphids to ants. It is claimed that mutualism evolved out of a predacious/parasitic relationship, e.g., through the hosts’ ability to terminate exploitation by a predator/parasite (Johnstone & Bshary 2002). Others claim that individuals in populations with a mutualistic strategy survive environmental stress better than

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Figure 2 Expected associations between ant and aphid features in mutualistic relationships. (a) Population size of myrmecophiles is negatively correlated with the foraging activity of ants (*dashed lines*) and positively correlated with energy gain (*solid lines*). For a particular population size, those species of aphid that produce large quantities of honeydew are a better source of energy (*solid arrow*) because the ants spend less time foraging for honeydew (*dashed arrow*). (b) With decline in foraging activity, the mortality risk increases for ant-attended aphids. The expectation is that the rate of decline is higher for obligate myrmecophiles. Thus, to reduce this mortality risk, a facultative myrmecophile needs to increase the quality or quantity of honeydew it produces, which may lead to a closer relationship with ants. (c) Associated with the degree of myrmecophily and foraging activity, there are costs, which depend on the mortality risk associated with particular habitats. For a particular tending level, those patches with a low mortality risk are costly for myrmecophiles because their investment in defense (production of high-quality honeydew) exceeds the benefits afforded by protection when natural enemy pressure is low.

those with an antagonistic strategy (Stachowicz 2001). However, a major evolutionary challenge for the development of mutualism is likely to have been the ability of aphids to survive encounters with ants (Doebeli & Knowlton 1998), especially as they are aggressive and ecologically dominant. Aphids, however, are a poor food resource (e.g., Toft 1995) because of their high sugar content, and aphids are unlikely to be a preferred prey as long as alternative prey is available and ants do not become specialist predators of aphids [but see *Lasius flavus* (Pontin 1978)].

Mutualistic relationships also tend to be exploited by specialist predators and parasitoids or by cheaters (Bronstein 2001). For example, a number of coccinellid larvae are known to have evolved protective structures like waxy wool, chemical mimicry, or inconspicuous movements. The wax covered larvae of *Scymnus interruptus* (Goeze) and *Scymnus nigrinus* Kugelann survive attacks by *L. niger* and *Formica polyctena* more often than larvae without wax (Völkl & Vohland 1996) and reach higher densities in ant-attended colonies, indicating ants probably afford the larvae protection against their natural enemies. Similarly, the wax covered larvae of *Stator sordidus* Horn, *Hyperaspis congressus* (Bartlett 1961), and *Platynaspis luteorubra* Goeze (Völkl 1995) are reported to be protected. Larvae and adults of *Coccinella magnifica* Redtenbacher use behavioral and chemical defense to avoid attacks by *F. rufa* (Sloggett & Majerus 2003, Sloggett et al. 1998). Aphid parasitoids, such as *Lysiphlebus cardui* (Marshall), *Lysiphlebus hirticornis* Mackauer, *Paralipsis eicoae* Fr. Smith, and *Paralipsis enervis* (Nees), have evolved chemical and behavioral mimicry, which enable them to exploit ant-attended aphid colonies without being attacked (Mackauer & Völkl 1993, Takada & Hashimoto 1985, Völkl 1992, Völkl et al. 1996). It is, however, not clear how often such relationships have evolved, what the relative costs are for these specialist aphid predators and parasitoids, or what kind of selection pressure they exert on aphid-ant relationships.

In addition, aphid-ant relationships may also be exploited by other species of aphids. As indicated above, the association with ants does entail costs. Therefore, to obtain these attendance benefits without paying the cost would be beneficial for an aphid. Although conceivable, there is no direct evidence that aphids are able to exploit established aphid-ant relationships, for example, by benefiting from protection services on a shared host plant. The indirect evidence is that on the leaves of birch (*Betula pendula* Roth) the co-occurrence of *Betualphis brevipilosa* Börner with *Callipterinella calliptera* (Hartig), which is ant attended, is more frequent than expected by chance, whereas co-occurrence with the unattended *Euceraphis betula* (Koch) is random (Hajek & Dahlsten 1986). Therefore, not only interspecific competition for ants might act against the development of mutualistic relationships but also specialized natural enemies and opportunistic aphids.

When considering aphid-ant relationships, one needs to appreciate how selection might act. Aphid colonies largely consist of clones; ants are socially organized with a high genetic relatedness, and as a consequence, selection in both taxa does not operate on individuals but on the colony or genet to which an individual belongs. Therefore, a useful approach is to attempt to understand how a clone, rather

than an individual, should invest in defense and reproduction. An interesting case is aphid soldiers, which evolved in the closely related families Pemphigidae and Hormaphididae (Aoki 1977, Stern & Foster 1997). In a number of social aphid species, it is known that on both their primary and secondary host plants the aphids may have different means of protection. The tropical aphid *Cerataphis fransseni* (Hille Ris Lambers), for example, are attended by various species of ants on the secondary host but not on the primary host where this aphid produces galls (Stern et al. 1995). Similarly, *Pseudoregma sundanica* (van der Goot) has two defense strategies: It is obligately attended by ants, that is, it exploits their protection services and produces sterile soldiers. The level of investment in soldiers is adjusted in response to ant attendance, with soldier production and ant attendance being negatively correlated (Shingleton & Foster 2000). This response is rapid and leads to a significant change in caste structure. However, only if soldier production is directly and inversely proportional to the incidence of ant attendance are the costs the same. Investment in ants and/or soldiers might be just two alternative ways of defense, equally costly, but with different payoffs in different environments. Therefore, a major challenge is to identify costs and benefits at the level of a clone, even if only the fitness of individuals can be studied. Preliminary molecular evidence on phylogenetic patterns in aphid-ant relationships indicates that ant tending is an evolutionarily labile trait, which was evolved and lost several times. For example, ant attendance in the genus *Chaitophorus* evolved at least five times; that is, it is relatively "easy" for an aphid lineage to "gain and lose tending" (Shingleton & Stern 2003). A similar conclusion was drawn from a comparative analysis of ant attendance of 112 species of aphids and 103 species of lycaenids (butterflies) from Europe, using morphological and ecological traits, such as size, feeding site, colony structure, or host characteristics. Overall, in both insect groups, relationships with ants were only slightly (10%) associated with environmental and ecological traits. Most of the variation in the degree of ant attendance in aphids is explained at the subfamily level and least at the species level, whereas for the lycaenids most is explained at a higher taxonomic level, such as a tribe (Stadler et al. 2003). This suggests that aphids are more flexible in their associations with ants at the species level, entering and leaving associations with ants whenever it is advantageous. The most likely reason for the difference is that honeydew is a waste product, whereas lycaenids have to invest in morphological structures such as nectar glands, the structure and function of which are less easy to modify.

Little is known about the indirect costs of aphid-ant relationships. Indirect costs occur when aphids develop specific adaptations fostering a closer association with ants (e.g., aggregation behavior or reduction in defensive structures, such as siphunculi, or loss of defensive behavior), which become maladaptive when ants are not available. These are the "association costs." For example, aphids that feed on the woody parts of a tree need long stylets to reach the deeply located phloem elements. Because it takes longer to withdraw long than short stylets, the aphids are at greater risk of attack from natural enemies. This is likely to favor a closer relationship with ants to exploit their protective function (Dixon 1998, Shingleton

et al. 2005). As a consequence, host plants growing where an appropriate ant partner is not available cannot be exploited. A restriction in host availability is likely to lead to lower abundance and increased risk of local extinction. As the area where conditions are suitable for both partners is likely to be less than that potentially suitable for the aphid selection, pressures should operate against strong dependence on ants to minimize the association costs. That is, nonattendance and facultative myrmecophily rather than obligate associations should prevail, which is indeed the case for most aphids, coccids, and lycaenids (Bristow 1991, Pierce et al. 2002).

MUTUALISM IN A DYNAMIC CONTEXT

It is puzzling that some aphids are closely associated with ants, whereas closely related species and other species living on the same host plant are not. This is independent of whether the host is a tree, herbaceous plant, or grass. There are few if any exceptions to the general finding that on abundant, long-lived plants there are species of aphids that show obligate, facultative, or no association with ants. Because of the multiplicity of strategies, one must be extremely careful not to oversell particular hypotheses, such as the plant permissive hypothesis or competition for mutualists, resulting in statements that one strategy is superior to (or more successful than) another. Many of the factors that are thought to influence the relationships between aphids and ants (Figure 1) were revealed by experiments carried out in a constant environment. This could lead to erroneous conclusions. For example, the idea of competition for mutualists, although well documented, is supported by few field studies. That is, conclusions derived from laboratory experiments done under specific environmental conditions demonstrate just one of a range of possible outcomes and do not explain the coexistence of different species of aphids and their association with ants on a shared host plant. Below we describe some good examples that incorporate a dynamic approach to ant-aphid associations not apparent in the dichotomy of Figure 1.

One notable exception to the static approach is the pioneering work of John Addicott and coworkers who studied the fireweed-aphid-ant system in great detail. They conclusively demonstrated that the ecological framework, such as alternative sugar resources, affects the strength of competitive interactions with intra- and interspecific neighbors for the services of two species of ants (Addicott 1978a, Addicott 1985). In addition, they clearly demonstrated that the positive effect of ants on aphid population growth rates is density dependent. At low aphid densities, ant attendance reduced the probability of extinction, whereas it had either no effect or even increased the probability of a decline at high aphid densities (Breton & Addicott 1992a). The concept of ecological neighborhood (Addicott et al. 1987), which is the area of activity or influence of organisms within the temporal and spatial context, stresses the idea that the scales at which observations and experiments are made are important for the interpretation of the results. There is no single ecological neighborhood for any given organism, and it is important to address and

report the scales to facilitate comparisons between studies and between empirical and theoretical postulates. One example is given below.

The immediate environment of an aphid is its host plant and position on the plant. Plant quality changes during the course of a growing period, for example, with the age of the plant tissue the aphids feed on (Johnson et al. 2003), with growing conspecific or interspecific herbivore load, and via induced plant defense (Karban & Baldwin 1997). Although the effects of host plants on aphid-ant relationships might not be easy to identify (Breton & Addicott 1992b), the general expectation is that aphids do best on high-quality plants. As a consequence, not only is the local distribution of ants' nests in a habitat important for myrmecophiles (top-down effect) (see above) but also the distribution and seasonal changes in their host plants (bottom-up effects). Most plants consist of a mosaic of different tissues in different developmental stages (Gill et al. 1995). Therefore, it is important for an aphid to exploit the highest quality patches where their reproduction is highest. Feeding on host tissues of suboptimal quality, e.g., when confined to certain plant organs by attending ants, carries costs. This view emphasizes reproduction and fitness costs and benefits as determinants of the outcome of aphid-ant interactions. This is different from the plant permissive hypothesis because it favors a bottom-up control, which means that plant quality determines honeydew quality and thus the level of association in ant-aphid mutualisms.

Another study of the dynamic nature of ant-aphid associations combined field and laboratory experiments on the four co-occurring aphids on tansy, in which plant quality and access of ants were manipulated, to determine the relative fitness consequences for aphids showing different levels of associations with ants. In the absence of natural enemies and ants, the obligate myrmecophile, *M. fuscoviride* Stroyan, had the lowest potential growth rate on high-quality plants (supplemented with N), whereas the facultative myrmecophiles, *Aphis fabae* Scop. and *Brachycaudus cardui* (L.), and especially the unattended species, *Macrosiphoniella tanacetaria* (Kaltenb.), did significantly better. Low plant quality (no N addition) usually adversely affected the performance of the unattended species and facultative myrmecophiles, indicating the importance of high-quality plants for high aphid growth rates. Thus, a combination of host and degree of mutualism differentially affects the fitness of these aphids in different environments (Stadler et al. 2002). In the field, the realized population growth rates are less than the potential population growth rates because of fluctuations in abiotic conditions and predator pressure. On high-quality plants with ants, the aphid *M. fuscoviride* had the highest realized fitness, whereas on low-quality plants, the colonies became extinct probably because the small colonies that developed on these plants were not attractive to ants. Under these conditions, the mobile *M. tanacetaria* did better. In addition, the relative frequency of high- and low-quality plants and the presence of ants are likely to influence the outcome (Stadler 2004). This heterogeneity in patch quality might be the reason why *M. tanacetaria* is so mobile, with most colonies surviving for only 1–2 weeks (Massonnet et al. 2002). Therefore, it is suggested that a combination of top-down and bottom-up forces affect aphids within a season and determine the

advantage of mutualism. Different species experience different advantages and disadvantages from mutualistic relationships in a changing environment, which allows different degrees of association with ants and a simultaneous exploitation of a shared host species.

As indicated above, plant quality affects aphid-ant interactions in many ways. As a consequence, external influences on plant quality might also cascade through to ant-aphid mutualisms. For example, in addition to the N content of plant tissue (Mattson 1980), secondary plant compounds affect aphid performance (Montllor 1991, Pickett et al. 1992) and might also be expected to affect aphid-ant interactions. Evidence is slowly accumulating that this is indeed the case. For instance, several aphid species, such as *Macrosiphum albifrons* Essig and *Aphis genistae* Scop., are known to sequester quinolizidine alkaloids, reaching 4 mg/g fresh weight in *A. genistae* and 1.8 mg/g in *M. albifrons* (Wink & Witte 1991). It is suggested that these aphids are able to exploit the chemical defense compounds of plants for their own defense against natural enemies. *A. genistae* and *Aphis cytisorum* are facultatively associated with ants, and the honeydew collected by *L. niger* workers from colonies of *A. cytisorum* contain on average 45 $\mu\text{g/g}$ fresh weight of quinolizidine alkaloids (Szentesi & Wink 1991). However, it is unknown whether these secondary compounds affect the ants. The interactions between ragwort, *Senecio jacobaea* L., the aphid, *Aphis jacobaeae* Schrank, the moth, *Tyria jacobaeae* L., and ants are associated with variation in the pyrrolizidine alkaloid content of the host plant. In this system, aphids colonize plants with low-alkaloid concentrations and avoid those with high concentrations (Vrieling et al. 1991). Plants without aphids are often defoliated by *T. jacobaeae* because of the absence of ants. If not defoliated in the absence of ants, then they are likely to have a high pyrrolizidine alkaloid content, which protects them from the moth. It is suggested that the above interactions maintain the genetic variation in the alkaloid content of *S. jacobaea*. However, it is unknown whether ants actively select aphid colonies that produce honeydew with a low-alkaloid content.

For plants, the variation in availability of resources, particularly N, may determine their investment in secondary compounds and ultimately aphid-feeding behavior (Coley et al. 1985, Herms & Mattson 1992, Kainulainen et al. 1996). Application of fertilizers to plants often increases the performance of the aphids they host as the result of either direct effects (Grüber & Dixon 1988) and/or indirect effects, e.g., a concurrent increase in tending and patrolling by ants (Strauss 1987). In addition, the application of fertilizer often results in a decrease in the concentration of secondary compounds, such as phenolics (Kainulainen et al. 1996), but the effect of this on aphid-ant relationships is less clear. Soil invertebrates such as protozoa, collembola, and earthworms can also affect the N and secondary compound content of plants. For example, the soil biota act via the host plants on cereal aphids [*Sitobion avenae* (F.) and *Myzus persicae* (Sulzer)], but the effects are different for different groups of soil organisms. Protozoa and collembola, but not earthworms, significantly increase aphid performance (Bonkowski et al. 2001, Scheu et al. 1999). This indicates that indirect effects, such as the grazing of

bacteria by protozoa and fungi by collembola, might have a pronounced effect on nutrient availability, plant growth, and aphid performance. It is, however, not clear whether soil biota significantly affects mutualisms between aphids and ants, but it is conceivable. The conclusion is that factors that are patch specific (bottom-up) are likely to influence both partners and might affect the development of mutualistic relationships. It is increasingly recognized that multitrophic/multispecies effects on mutualistic interactions are important (Bronstein & Barbosa 2002), but the mechanisms shaping the strength of the interactions are difficult to identify, and the common patterns in different systems even more so. The take-home message is that those parts of a habitat in which aphids can achieve high growth rates and establish mutualistic relationships, especially close associations, with ants is probably considerably smaller than the potential habitat. Experimental and theoretical studies of aphid-ant associations are more likely to be successful if a patch-oriented perspective of coevolution (Thompson 1994) is adopted to explain the breadth of the associations between aphids and ants.

CONCLUSIONS AND FRONTIERS IN APHID-ANT INTERACTIONS

The study of aphid-ant interactions is hampered by many factors that influence the outcome of this relationship. For example, bottom-up effects like the distribution and abundance of the host plants of the aphids or community composition of soil invertebrates are likely to cascade through the system and either directly affect the growth rates of aphids or indirectly via plant nutrients or secondary plant compounds. In a similar way, top-down effects of natural enemies are likely to shape the strength of aphid-ant relationships. As a consequence, we should not expect a high degree of specialization in these interactions as most mutual associations are best characterized as temporary. This is probably true for many partners of ants. For example, even though there are spectacular instances of highly specialized associations between ants and aphids, coccids, membracids, and lycaenids, the majority are often facultative and unspecific (Pierce et al. 2002, Bristow 1991, Fiedler 1991, Delabie 2001), and the number of myrmecophilous species declines from the tropics to the temperate regions (Fiedler 1998).

Given their multitrophic nature, the outcome of these relationships needs to be followed for a complete season or several seasons to appreciate the full range of costs and benefits for both partners. Laboratory experiments done under constant conditions can only provide an indication of the constraints acting on both partners and need to be paralleled by field investigations whose duration is sufficiently long to encompass the life cycles of both partners. It is important to determine fitness costs and benefits in different environments. Although it is experimentally challenging to simultaneously determine intrinsic rates of increase, it is more rewarding to compare and understand the costs and benefits for different species in different environments.

Our current understanding of costs is still rather rudimentary. For example, at the physiological level, there is little or no information on the change in the composition of honeydew and associated adaptation costs for different generations of aphids in responding to ant attendance, when both colony size and quality of the host plants vary. Clearly, there is need to determine the extent to which foraging activity is associated with sugar:protein imbalances in the diet of ants, and their effect on aphid communities. In terms of ecology, there is a growing awareness that spatial variability affects the distribution and abundance of both partners and the effects of bottom-up and top-down forces (Blossey & Hunt-Joshi 2003, Edson 1985, Gotelli & Ellison 2002a, Morris 1985, Müller & Godfray 1999). This indicates that a more spatially explicit or metapopulation perspective may be more appropriate (Addicott 1978b, Albrecht & Gotelli 2001, Edson 1985). The relative importance of mutualistic, neutral, and antagonistic interactions between aphids and ants and their relative role in community structure and species diversity are beginning to be addressed (Wimp & Whitham 2001). Still further in the future, but no less important, is the need to address the effects of the mutualistic and antagonistic interactions of these two dominant groups of insects on nutrient cycling and ecosystem functioning (Loreau 1995, Stadler et al. 1998).

In the immediate future, there are a number of interesting questions that should be addressed, either experimentally or theoretically. For example, do the population dynamics of myrmecophiles and nonmyrmecophiles differ, and if so, in what way? How do costs and benefits vary with colony size and during the course of a season? How can costs and benefits be determined considering the different genetic structures of the clonal and socially organized partners? Are there differences in the dispersal rates/patterns of myrmecophiles and nonmyrmecophiles? How does patch size affect ant attendance, and what are the costs for ants in attending aphids? How does the spatial and temporal variability in plant phenology/quality affect the distribution and abundance of aphids showing different degrees of associations with ants? What is the relative importance, in a temporal and spatial context, of the factors depicted in Figure 1 for the outcome of mutualistic relationships? In what way do plant secondary compounds or the belowground community structure affect aphid-ant relationships?

The traditional view is that ants are in control of the interaction with aphids. However, many aphid species do not compete for the services of ants and appear to have a range of options to cope with ant partners that are an unpredictable and unreliable resource. Considering the different life cycles (e.g., parthenogenetic reproduction versus social organization) and the different selection pressures that are associated with these features, there is ample opportunity for both partners to exploit each other. For a clonal fast-reproducing organism, for example, there might be little cost involved if ants prey on a few individuals. However, tempo foragers (Oster & Wilson 1978) need to monopolize a source of energy within their foraging area to avoid conflicts with conspecifics or other ant species. Therefore, it is likely that adaptive changes in the physiology, behavior, and genetic structure of the partners results in an increase in their fitness. Aphid-ant relationships are easy to

manipulate and an ideal system for defining the driving forces in the ecology and evolution of antagonistic/mutualistic relationships.

ACKNOWLEDGMENTS

We would like to thank Aaron Ellison and Shin-ichi Akimoto for providing helpful comments on the manuscript. Financial support was given from the German Ministry for Research and Technology (Fördernummer: BMBF No. PT BEO 51-0339476D).

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