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Katherine E. McPhee

Eleanor Groden

Francis A. Drummond

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Ant–Homopteran Relationships: Relevance to an Ant Invasion in Maine

Katherine E. McPhee

Eleanor Groden

and

Francis A. Drummond

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MAINE AGRICULTURAL AND FOREST EXPERIMENT STATION
THE UNIVERSITY OF MAINE

Ant–Homopteran Relationships:
Relevance to an Ant Invasion
in Maine

Katherine E. McPhee
Graduate Student

Eleanor Groden
Professor

and

Francis A. Drummond
Professor

School of Biology and Ecology
University of Maine
Orono, ME 04469

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INTRODUCTION

The worldwide proliferation of invasive species and the impacts of these invasions have been the focus of numerous studies (Mack et al. 2000; Holway et al. 2002; Garnas 2005). Invasive species are expanding their ranges as commerce and transportation result in increasingly traversed geographic/political borders and disturbed habitats (Mack et al. 2000). The European red ant, *Myrmica rubra* (L.), a palearctic species with a native range stretching across northern Europe to western Siberia, has established colonies in several states and provinces in northeast North America (Grodén et al. 2005). *Myrmica rubra* was first reported in North America in 1908 at the Arnold Arboretum in Forest Hills, Massachusetts (Wheeler 1908). Later accounts suggest *M. rubra* was largely distributed throughout Maine via imported and transported nursery stock (Grodén et al. 2005).

The richness and diversity of native ant species on Mt. Desert Island, Maine, have been reduced in areas infested with *M. rubra* (Garnas 2005). In general, the success of invasive ant species has been attributed to interference and exploitative competition coupled with the ants' opportunistic diets (Holway et al. 2002). In field experiments on Mount Desert Island, Maine, *M. rubra* discovered and recruited to baits faster than native ants (Garnas 2005). This study also showed that *M. rubra* displaced most native ant species from food resources (Garnas 2005). This, together with *M. rubra*'s aggressive defense of invaded territories, has led to fewer native ants in infested areas. In the first chapter of his thesis, Garnas (2005) provides a comprehensive review of competition in ant communities and the role it appears to play in ant invasions.

Previous research on the ecology of *M. rubra* in Maine determined that several plant-feeding homopterans are more abundant in areas infested with *M. rubra* than in areas inhabited solely by native ants (Garnas 2005). These relationships between invasive ants and homopterans have been speculated to play a significant role in the success of invasive ants (Helms and Vinson 2002). The interactions between homopterans and *M. rubra* in Maine may have contributed to the ants' successful establishment by providing food resources for colony maintenance and growth. The purpose of this literature review is to investigate ant-homopteran relationships and discuss the possibility of homopterans indirectly aiding ant invasions.

MUTUALISTIC RELATIONSHIPS

Interspecific symbiotic relationships among insects are complex and diverse, ranging from predation and parasitism to mutualism. Mutualism is an interaction between species resulting in a net increase in the fitness of participating individuals of both species (Boucher et al. 1982). In his book on insect ecology, Price (1997: 215) argues that mutualisms are common in nature and are one of the “great forces in the ecology and evolution of species” affecting populations, communities, and ecosystems. Bronstein (1994) claims that the evolutionary trend in interspecific relationships has been a move towards mutualism and away from antagonism. In mutualistic relationships, the selection pressures are for improved benefits to each species in the relationship and a reduction of negative impacts (Price 1997). However, the outcomes of mutualistic interactions are dynamic and dependent on abiotic and biotic settings (Bronstein 1994). For example, when weather conditions are bad, ants are less likely to visit and tend myrmecophilous (ant-loving) homopterans (Way 1963). Existing mutualistic relationships can be analyzed as a set of costs and benefits, with the benefits outweighing the costs. Many mutualistic relationships can be found among insects: microbes aiding the absorption of nutrients in termites’ diets; pollinators consuming nectar and pollen while pollinating plants; oily elaiosomes on diaspore surfaces to encourage dispersal by ants; and the association of honeydew-secreting insects that provide nutrition for ants while the ants protect the homopterans from predators and parasitoids (Price 1997).

BASIS OF ANT–HOMOPTERAN MUTUALISMS

While some ants and Homoptera are mutualists, there is a spectrum of symbiotic relationships between these insects, ranging from predation to mutualism. The relationship often varies with the species involved and the needs of each partner species. In the Rocky Mountains of the United States, approximately 25% of aphid species are involved in mutualisms with ants (Bristow 1991). In Europe, one-third of aphid species are not attended by ants, and two-thirds are attended (Stadler 1997). Ants are opportunistic, omnivorous consumers who use and often monopolize available resources (Holldobler and Wilson 1990). Homopterans are plant feeders, ingesting phloem or xylem through their proboscis via a combination of sap pressure and cibarial muscles (Holldobler and Wilson 1994). Many Homoptera, such as aphids, excrete a carbohydrate-rich waste product, called honeydew, which is used

by ants, bees, and even human beings (Waldbauer 1996). While many ants forage for honeydew from the plant surfaces or ground where homopterans have deposited their feces, some ants solicit honeydew directly from homopterans, having evolved a more intimate, mutualistic relationship (Holldobler and Wilson 1994). In direct honeydew collection, ants often approach homopterans by antennating the homopteran's abdomen, thus stimulating the release of a droplet of honeydew that ants then ingest (Way 1963). Ants continue to collect the honeydew and return to the nest with distended abdomens to regurgitate the honeydew to nestmates (Holldobler and Wilson 1994). In Malaysia, honeydew derived from their myrmecophile mealybugs is the only source of nutrients for the ant *Dolichoderus cuspidatus* (Smith) (Holldobler and Wilson 1994). The majority of ant species, however, tends and/or attacks a wide range of homopterans (Buckley 1987b).

NATURE OF ANT-HOMOPTERAN MUTUALISMS

Ants and homopterans may be obligate or facultative mutualists (Stadler and Dixon 1999). Of the two-thirds of aphid species attended by ants in Europe, half are facultatively attended and half are obligatorily attended (Stadler 1997). In obligatory mutualism, one or both species cannot survive without the presence of the other species (Cushman and Beattie 1991). Obligate mutualisms are more commonly found in tropical ecosystems (Bristow 1984), though Stadler (1997) claims one-third of European aphid species are obligate mutualists with ants. The majority of associations between ants and aphids are facultative and nonspecific (Buckley 1987b). In facultative mutualism, each partner species can survive and reproduce without the presence of the other species (Cushman and Beattie 1991). Facultative mutualisms are also represented by situations where one homopteran species is attended by many ant species or one ant species uses the honeydew from a range of homopteran species (Katayama and Suzuki 2003).

Facultative mutualism is variable in space and time, and the intensity of the relationship is often density dependent (Stadler and Dixon 1998). For example, Reithel and Billick (2006) found the mutualism between membracids (treehoppers) and ants depended on the timing of plant phenology. The ant *Formica obscuripes* Forel tends the membracid *Publilia modesta* (Uhler) on *Wyethia* spp. plants (mulesear) and has a positive effect on membracid nymph number. However, *Wyethia* plants senesce before membracid nymphs reach adulthood, which prevents the benefits of ant tending from translating to adult numbers. Likewise, Breton and Addicott

(1992) found that the benefits of tending by the ant *Formica cinerea* Mayr of *Aphis varians* Patch on fireweed varied with the density of aphid population size. When *A. varians* populations were less than 30 aphids per plant, tended aphid populations grew significantly more than untended populations. However, when the mean starting densities of aphids were higher, ant tending had no significant effect on aphid population growth.

Changes in the relationship between ants and aphids, from mutualism to predation, have been found to be density dependent. Sakata (1994) found that when density of aphids per ant was high, *Lasius niger* L. would predate more often on myrmecophilous aphids, *Lachnus tropicalis* (Van der Goot) and *Myzocallis kuricola* (Matsumura), on chestnut trees. When density of aphids per ant was low, predation rates would decrease, and *L. niger* would preferentially tend aphids.

The intensity of the relationship between ants and homopterans is driven by the costs and benefits of the association. For example, Offenberg (2001) found *L. niger* ants increased their predatory behavior and decreased their tending and collection of *Aphis fabae* Scopoli honeydew when an alternative source of sugar (dilute honey) was available. Instead of maintaining a mutualistic relationship, the protein available through *A. fabae* prey had greater benefits when *L. niger* had an alternative source of carbohydrates. This finding suggests there is a conditional outcome between ants and aphids, with ants making the “best” nutritional choice for their greatest gain. Interestingly, when *Formica aserva* Forel workers are presented with either a natural enemy (*Coccinella septempunctata* Lin., seven-spotted ladybeetle) of their *Aphthargelia* sp. aphid mutualists or a competitor ant from a foreign colony, *F. aserva* attacked the competitor ant more often than the aphid predator (Phillips and Willis 2005). This is another example of the plasticity of facultative relationships between homopterans and ants.

BENEFIT OF HONEYDEW TO ANTS

The acquisition of carbohydrate-rich honeydew is one way ants benefit from their relationship with homopterans. Honeydew has been found to contribute significantly to the nutrition of attending ants (Way 1963; Fiedler and Maschwitz 1988). For the common wood ant of Europe (*Formica rufa* L.), honeydew is a major part of their diet (Holldobler and Wilson 1990). Skinner (1980) found that honeydew was very important to the wood ants' diet, as the number of workers foraging for honeydew exceeded the number of work-

ers involved in the collection of solid food. In studying California's carpenter ant, *Camponotus modoc* Wheeler, Tilles and Woods (1982) found that honeydew consisted of the greatest proportion of the ants' diet.

Between 0.2% and 1.8% of honeydew's dry weight consists of amino acids, while 90% to 95% consists of carbohydrates (Holldobler and Wilson 1990). Trehalose, the blood sugar of insects, makes up to 35% of honeydew (Holldobler and Wilson 1990). In addition, honeydew contains other organic acids, B vitamins, and minerals (Holldobler and Wilson 1994). Honeydew is an important food, as collected honeydew quantities can fulfill more than 50% of total colony energy intake for some ants (Skinner 1980).

Homopterans produce honeydew through their digestion of plant phloem or xylem and add further nutrients, such as specific amino acids and sugars, not found in the plant sap (Fischer and Shingleton 2001; Woodring et al. 2004). Honeydew composition also varies between different developmental stages of aphids (Fischer et al. 2002), between different species of aphids (Woodring et al. 2004), and between different host plants (Fischer and Shingleton 2001). The quality of honeydew produced by homopterans is a critical factor in determining the extent of ant attendance (Woodring et al. 2004). Ants preferentially tend aphids that produce honeydew with a higher concentration of a particular trisaccharide called melezitose (Fischer and Shingleton 2001; Fischer et al. 2002; Woodring et al. 2004). For example, while feeding on tansy and conifers, the aphid *Metopeurum fuscoviride* Stroyan produces honeydew that is 30% to 70% melezitose (Fischer and Shingleton 2001). Ants usually tend these aphids. In comparison, while feeding on tansy and tomato plants, the aphid *Macrosiphoniella tanacetaria* Kaltenbach produces honeydew that has no melezitose, and ants often do not tend these aphids (Fischer and Shingleton 2001). In their experiment, Fischer and Shingleton (2001) found that the aphids *Chaitophorus populeti* (Panzer) and *Chaitophorus populiabae* (Boyer de Fonscolombe), which produce honeydew that has higher melezitose levels than honeydew of the aphid *Chaitophorus tremulae* Koch, were preferentially tended by ants over *C. tremulae*. Tended aphids usually have honeydew that contains between 30% and 70% melezitose (Fischer and Shingleton 2001). Woodring et al. (2004) postulate that melezitose is a cue used by ants to find sugar-rich honeydew.

Ant tending can also have an impact on the amount and proportion of melezitose produced in honeydew. Fischer and Shingleton (2001) found *C. populeti* and *C. populiabae* had higher levels of melezitose in their honeydew when they were reared in the presence of *L. niger* than when reared in the absence of ants.

The quantity of honeydew is another critical factor determining ant attendance (Woodring et al. 2004). Fischer et al. (2001) found the aphid *M. fuscoviride* Stroyan produced four times the amount of honeydew compared with *Brachycaudus cardui* (L.) and *A. fabae*. As a result, *L. niger* preferentially tended *M. fuscoviride*. Fischer et al. (2002) also found that older nymphs and adult *M. fuscoviride* produced more honeydew and received more attention from *L. niger* than first and second instar nymphs.

The use of honeydew differs among ant species. For example, *L. niger* feeds primarily on honeydew (Buckley 1987a), whereas *Formica integroides subnitens* Creighton is a honeydew-collecting ant species that is primarily predaceous (Way 1963). Regardless of the predaceous status of an ant species, however, honeydew is always an important part of the ant diet (Carroll and Janzen 1973; Skinner 1980).

Another benefit for ants is the acquisition of homopterans as prey. Although 60% to 100% of ants' aphid prey is made up of non-myrmecophilous aphids (Novgorodova 2005), ants also prey upon attended aphids when there is surplus honeydew (Offenberg 2001) and aphids (Way 1963). Ants also attack injured aphids (Nault et al. 1976) and prey upon accidental killings (Way 1963).

Ant attendance varies with weather and the nutritional demands of the colony (Fischer et al. 2001). Fewer ants will forage in windy or wet conditions unless food is scarce (Way 1963). *Lasius niger* increase their attendance of aphids before swarming of this species' gynes and males and exhibit a significant decrease in honeydew demands after swarming (Fischer et al. 2001). While studying the feeding habits of *F. rufa* in England, Skinner (1980) found that aphid prey and honeydew were brought into nests in the greatest quantities during the spring and early summer. Likewise, Porter and Tschinkel (1987) found *Solenopsis invicta* Buren in Florida ignored protein baits and relied on carbohydrate baits during the winter months when no brood was produced.

Sugar-laden honeydew is primarily used to meet the energy requirements of workers (Skinner 1980). As an energy source, workers can use honeydew to carry out all tasks required for colony maintenance, such as foraging for prey, defense, and caring for brood, queens, and aphid colonies (Carroll and Janzen 1973; Skinner 1980). Larvae also need carbohydrates for proper growth (Way 1963). However, honeydew is an incomplete diet (Offenberg 2001), and protein is required for queens to oviposit, proper larval development, and colony growth (Skinner 1980; Offenberg 2001). Aphids, however, help ants to meet their protein demands by fuel-

ing the workers; therefore, aphids benefit ants in both ant colony maintenance and colony growth.

In this relationship, time and energy spent in collecting honeydew and defending aphids are the major costs to ants (Buckley 1987b). Ants also risk exposure to potential predators and parasitoids while tending Homoptera (Pierce et al. 1987). However, it is hypothesized that the benefits outweigh the costs of attendance. For example, through honeydew consumption, weaver ants, *Polyrachis simplex* Mayr, gain five to 10 times the energy they expend in guarding *C. populialbae* (Boyer de Fonscolombe) (Buckley 1987b).

BENEFITS OF ANT TENDING FOR HOMOPTERANS

Many scientists have studied the benefits and costs to homopterans provided by myrmecophilous relationships. These studies have shown that homopterans receive a number of benefits through mutualistic relationships with ants, ranging from protection from predators and parasitoids (Way 1963; Buckley 1987a; Bach 1991; Yao et al. 2000; Fischer et al. 2001), larger colony growth and size (Stechmann et al. 1996; Bishop and Bristow 2003; Renault et al. 2005), increased survival time of colonies (Bristow 1984; Yao et al. 2000), increased reproduction (Bach 1991; Stechmann et al. 1996), faster development (Flatt and Weisser 2000), increased feeding rates (Banks and Nixon 1958), increased production of honeydew (Way 1963; Katayama and Suzuki 2002; Woodring et al. 2004), and improved sanitary conditions (Buckley 1987a).

Studies have also shown that survivorship of myrmecophilous homopteran colonies is dependent upon ant attendance. Bishop and Bristow (2003) demonstrated the increased survival of colonies of the aphid *Cinara banksiana* Pepper and Tissot in the presence of the tending ant *Formica exsectoides* Forel. When ants were excluded from colonies via the pest barrier tanglefoot, there was a noticeable decline in population size and a greater colony extinction rate than with tended colonies. Bach (1991) found green scale, *Coccus viridis* (Green), populations had greater densities when tended by *Pheidole megacephala* (Fabr.) ants. Likewise, Shingleton and Foster (2000) found that excluding ants from colonies of *Pseudoregma sundanica* (Van der Goot) led to decline and extinction of aphid populations. Studies have also shown that ant attendance enhances the aggregation and density of homopterans (McNeil et al. 1977; Bach 1991; Renault et al. 2005; Daane et al. 2007).

Breton and Addicott (1992) found a density-dependent effect on ant-homopteran mutualism. The benefits that *F. cinerea* Wheeler

provided for *A. varians* Patch varied with the density of the aphid colonies; ant tending significantly increased small populations, but decreasing benefits were associated with larger aphid populations. At higher aphid populations, there was less direct contact between the ant and aphid, which may have resulted in decreased benefits (Breton and Addicott 1992). Likewise, Morales (2000) studied the relationship between the treehoppers *Publilia concava* (Say) and tending *Formica* sp. Treehopper survivorship was proportional to the density of ants and the duration of ant tending. Therefore, when treehopper densities were low, duration of tending per treehopper was higher; treehoppers received maximum benefits from ant tending.

The effects of ant attendance have also been studied on individual homopterans, such as with the aphid *M. fuscoviride* Stroyan. In the presence of the ant *L. niger*, these aphids lived longer, matured earlier, and reproduced at a higher rate than *M. fuscoviride* aphids not tended by *L. niger* (Flatt and Weisser 2000). Likewise, in the presence of *Myrmica lobicornis* Emery and *Myrmica americana* Weber, the membracid *Publilia reticulata* Van Duzee achieved greater size and shorter development times (Bristow 1984). While Rauch et al. (2002) initially hypothesized that increased aphid fitness was due to tended aphids spending more time penetrating into plant vascular sieve elements and thus receiving a higher percentage of nutrients, they disproved this hypothesis with electrical penetration graph techniques. They instead suggested that increased fitness of tended aphids could be attributed to easier excretion of honeydew with ant assistance, processing nutrients more efficiently, and/or increasing the rate of sap intake.

While the predation pressure on homopteran colonies can vary between seasons (Bristow 1984), the success of ant-tended homopteran colonies has largely been attributed to the protection ants provide against predators and parasitoids (Tilles and Wood 1982; Phillips and Willis 2005). In field experiments, tended aphids are attacked less heavily by predators than are unattended control aphids (Fischer et al. 2001). In the Brazilian savannah, Fernandes et al. (2005) found that treehopper populations on *Byrsonima crassifolia* (Linnaeus) declined as predators and parasitoids frequently attacked them when ants were excluded. When surveying forests in Quebec, McNeil et al. (1977) found less parasitism of aphids when ants were present. Muller and Godfray (1999) found that predators attacked all non-tended aphid species in a meadow in southern England.

Studies have shown that ants preferentially attack both predators and parasitoids that approach their tended homopterans (Way

1963; Nault et al. 1976). For example, *F. aserva* attacked aphid-predatory ladybird beetles placed on the aphid-colonized plants, but did not attack non-aphid-predatory muscid flies (Phillips and Willis 2005). In predator introduction experiments, *P. megacephala* (Fabr.) removed coccinellid larvae on *Pluchea indica* (L.) plants with the green scale, *C. viridis* (Green) (Bach 1991). Also, *C. viridis* tended by ants had lower rates of parasitism (Bach 1991). Studies have also shown that tending ants prevent adult predator oviposition, attack and drive off larvae, and eat predators' eggs (El Ziady and Kennedy 1956; Tilles and Wood 1982). Ant workers also attack some aphid parasitoids (Volkl 1992), chase scale parasitoids (Liere and Perfecto 2008), and thus reduce parasitism of scale insects (Bartlett 1961). Ants may also remove parasitized aphids that do not behave normally (Tilles and Woods 1982).

In some cases, the protection provided by ants negatively affects attempted biological control of homopteran pest species. Stechmann et al. (1996) found that ants severely interfered with the parasitism of the banana aphid, *Pentalonia nigronervosa* Coq, by the parasitoids *Lysiphlebus testaceipes* (Cresson) and *Aphidius colemani* Viereck. These parasitoids were released in the South Pacific to control the banana aphid. With ant attendance, however, the amount of parasitism of aphids was reduced because attending ants attacked the parasitoids. Likewise, Vinson and Scarborough (1991) found that *S. invicta* reduced the emergence of the parasitoid *L. testaceipes* Cresson from the corn leaf aphid, *Rhopalosiphum maidis* (Fitch). The authors concluded that *S. invicta* could interfere with biological control of aphids through reduced parasitism and reduced parasitoid survival during development.

Different ant species also exhibit different levels of homopteran protection. Novgorodova (2005) tested the reaction of eight species of ant to potential aphid predators. When *C. septempunctata* (lady beetle) adults and larvae were placed near tended aphids, *Formica cunicularia glauca* Ruzsky and *Formica fusca* L. did not protect the aphids. *Camponotus saxatilis* Ruzsky and *L. niger* protected aphids against lady beetle adults, but not against larvae. The other four ant species (*Formica polycenta* Forester, *Formica aquilonia* Yarrow, *Formica pratensis* Retzus, and *Lasius fuliginosus* Latreille) actively guarded the aphids against both adults and larval predators.

The protection of aphids from predators has been implicated as the main benefit in the evolution of ant-aphid mutualism. Aphids that feed on petioles, branches, and trunks of host plants have longer mouthparts than leaf-feeding aphids (Shingleton et al. 2005) in order to reach the more deeply located plant phloem.

Aphids with longer mouthparts take a significantly longer time to withdraw their mouthparts and escape predators and parasitoids than aphids with shorter mouthparts (Shingleton et al. 2005). Most aphids that feed on woody plant parts have longer stylets and are obligate mutualists with ants (Stadler and Dixon 1999). Of the 13 aphid species studied by Shingleton et al. (2005), tended aphids had longer mouthparts than untended species. Shingleton et al. (2005) suggest that the need for better protection from predators drove the evolution of a mutualism between aphids with longer mouthparts and ants, with aphids evolving traits to better attract ants, such as increased honeydew quality, quantity, and production.

Many scientists have linked the increase in fitness of tended homopteran to an increase in honeydew production as a demonstration of improved nutritional intake and feeding rates (Bristow 1984). Banks and Nixon (1958) found *L. niger* directly stimulated an increase in the feeding and excretion rates of *A. fabae*. Katayama and Suzuki (2002) recorded a twofold increase in honeydew production in *Aphis craccivora* Koch when *L. niger* was present.

In addition to increasing the survivorship and size of homopteran colonies, studies have also shown that ant attendance affects the reproductive rate of homopterans and the composition of aphid colonies. While aphid reproduction rate is affected by the nutritional value and age of plant tissue (Banks and Nixon 1958), ants also play a role in aphid reproduction. Some aphids produce more offspring in the presence of ants (Fischer et al. 2001), as do scale insects (Bishop and Bristow 2003). Tilles and Wood (1982) found that aphids attended by *C. modoc* ants were more likely to survive to oviparae (reproducing adult female). Tended aphids also produce lower proportions of alates (Tilles and Wood 1982). Some view the reduction in alate production as a benefit to aphid colonies (Tilles and Wood 1982). Dispersal to new host plants is intrinsically risky for aphids—suitable host plants may not be found, competitive aphids may already be in residence, and there is the risk of predation and parasitism. Aphids may reduce the risk of potential hazards to colony members by reducing the number of alates produced (Tilles and Wood 1982). This is probably only true if ants relocate tended aphids onto new host plants since production of alates is also a response to crowding and deteriorating resources.

Another effect of ant attendance on aphid colony composition was found among the obligate myrmecophilous aphid *Pseudoregma sundanica* (Van der Goot) (Shingleton and Foster 2000). In the absence of ants, these aphids increased the production of soldier aphids for defense of the colony. An increase in the level of ant

tending decreased the number of soldier aphids produced. These findings suggest that ants are a preferred defense as soldier aphids are more costly to the aphid colonies because they may not survive to reproduce (Shingleton and Foster 2000).

Studies have also shown that the presence of ant semiochemicals changes the behavior of tended aphids. *Aphis fabae* moved more slowly when placed in dishes with *L. niger* semiochemicals on filter paper (Oliver et al. 2007). Their movement was also significantly reduced in the presence of *L. niger* ants (Oliver et al. 2007).

Ants also provide shelters and modified parental care for some of their tended homopteran species. These shelters can protect the aphids from predation and harsh weather conditions (Way 1963; Carroll and Janzen 1973). For example, in England, Pontin (1978) found that *Lasius flavus* (Fabr.) built subterranean cavities for 13 myrmecophilous aphid species. In some cases, the ants even take the aphids into their nests to overwinter (Way 1963). For example, the ant *Lasius neoniger* Emery transports aphid eggs, *Anuraphis maidi-radialis* (Forbes), into its nest to overwinter, and in the spring, the ants transport the nymphs back to the roots of nearby plants (Holldobler and Wilson 1994). If the *L. neoniger* ants decide to relocate, they will take some aphid eggs with them (Holldobler and Wilson 1994). Likewise, *L. fuliginosus* (Latreille) has been found to transport fundatrices of *Stomaphis quercus* (L.) from overwintering sites at the base of oak trees to upper branches (Way 1963). In Maine, Drummond and Groden (unpublished data) have observed *M. rubra* providing shelter to aphids in their nests prior to the onset of winter.

Ants also benefit their tended homopteran species through the removal of interspecific competitors (Kaplan and Eubanks 2002). For example, ants are known to remove and kill the larvae of *Tyria jacobaeae* moths, which compete with aphids for host plant resources (Muller and Godfray 1999).

Finally, ant attendance has been linked to increased sanitary conditions for homopterans with the removal of honeydew (Bartlett 1961; Buckley 1987a; Bach 1991; Muller and Godfray 1999), which decreases the risk of fungal attack. In the exclusion of ants, Flatt and Weisser (2000) found some of the aphids in their study were infected by a fungus prior to their death, whereas tended aphids were not infected. Likewise, when 12 tending ant species were excluded from *Croton floribundus* Spreng. shrubs hosting the whitefly *Aleurothrixus aepim* (Goeldi), fungal infection as a result of honeydew build-up was three times more frequent than control groups with ant access (Queiroz and Oliveira 2001).

COSTS OF ANT TENDING FOR HOMOPTERANS

While homopterans gain direct benefits from ant attendance, there are also inherent costs. Stadler and Dixon (1999) postulate that the low percentage of ant-tended aphids is indicative of the high cost of forming a relationship with ants. In addition, not all homopterans experience every benefit possible from ant attendance. Stadler and Dixon (1998) found that *A. fabae* tended by *L. niger* suffered from prolonged development time, delayed offspring production, smaller gonads, and fewer well-developed embryos. Yao et al. (2000) found that *Tuberculatus quercicola* (Matsumura) aphid colonies that were continually cared for by the ant *Formica yessensis* Forel were significantly smaller in body size and number of embryos produced than colonies that were raised in the absence of both ants and natural enemies. Yao et al. (2000) postulate that aphids sequester more resources in the production of honeydew to maintain ant guards, resulting in negative effects towards body growth and reproduction. Stadler and Dixon (1998) propose the idea that the increased feeding rate of aphids when tended by ants may reduce the efficiency of assimilation of nutrients, resulting in costs to their fitness.

Studies have also shown that ant attendance negatively affects homopterans through predation and parasitism. Although ants protect their aphid partners from predators and parasitoids, there is evidence that some parasitoids have developed abilities to exploit the mutualistic relationship between ants and aphids. The monophagous parasitoid *Lysiphlebus hirticornis* Mackauer is able to avoid ant aggression and parasitize tended aphids (Fischer et al. 2001). Likewise, in experiments with *Lysiphlebus cardui* (Marshall), female parasitoids actively sought ant-tended aphid colonies for oviposition and were not attacked by ant guards (Völkl 1992). Ant attendance of parasitized aphids reduced incidences of hyperparasitism by 30% (Völkl 1992). The exploitation of the ant-aphid relationship provides *L. hirticornis* and *L. cardui* with an “enemy-free space,” protecting *L. hirticornis* and *L. cardui* eggs from hyperparasitism. However, while some aphids are parasitized, Fischer et al. (2001) found the parasitism had a less dramatic effect on aphid colony size and persistence than the effects of predation in the absence of ant guards. The benefits of ant attendance outweigh the costs of parasitism.

Similarly, *Azteca instabilis* F. Smith is ineffective at guarding the green scale, *C. viridis* (Green), from predation by *Azya orbigera* Mulsant larvae (Liere and Perfecto 2008). Ant tending led to high densities of *C. viridis* and ultimately created an enemy-free space with a lack of predator competition for *A. orbigera*.

Delayed dispersal rates for homopterans have also been linked to ant attendance and could be a potential cost of tending (Kindlmann et al. 2007). Based on 22 years of data in France in ant-attended aphid species, long-distance dispersal occurs significantly later than for unattended species. A delay in dispersal could lead to reduced potential of finding high-quality plant hosts during the summer, thereby leading to a lower rate of increase in aphid populations (Kindlmann et al. 2007).

Besides affecting the fitness of homopteran populations and ant colonies, the mutualism between homopterans and ants affects homopteran behavior, host plant fitness, the biological control of pest species, and invasive ant ecology.

MYRMECOPHILOUS AND NON-MYRMECOPHILOUS APHIDS

Myrmecophilous and non-myrmecophilous aphids have morphological and behavioral differences. Myrmecophilous aphids usually have poorly developed cornicles, reduced cauda, and a thin coating of wax filaments (Holldobler and Wilson 1990). Myrmecophilous aphids also have an increased number of anal setae and more setae on dorsal and tibiae appendages (Holldobler and Wilson 1990). Non-myrmecophilous aphids are usually cryptic in coloring and form diffuse colonies (Dixon 1973). In contrast, myrmecophilous aphids are usually conspicuous in coloring (at least to human beings) and form large aggregated colonies (Dixon 1973).

The excretion of honeydew also differs among myrmecophilous and non-myrmecophilous aphids. Non-myrmecophilous aphids will kick droplets away with hind legs or expel the honeydew through contractions of the anus and abdomen (Way 1963; Holldobler and Wilson 1990). Myrmecophilous aphids, however, slowly excrete honeydew, presumably to help ants to collect it more easily (Holldobler and Wilson 1990).

The alarm behavior of myrmecophilous aphids also differs from the alarm behavior of non-myrmecophilous aphids (Nault et al. 1976). Non-myrmecophilous aphids respond to predation attacks by secreting sticky droplets from their cornicles to impede attackers, and by falling, jumping, or walking away to escape (Nault et al. 1976). The droplets released from their cornicles also serve as an alarm pheromone to alert other members of the colony (Dixon 1973). Myrmecophilous aphids, however, disperse less readily in response to alarm pheromone (Nault et al. 1976). Even in the absence of ants, myrmecophilous aphids do not exhibit escape behavior when attacked

by predacious lady beetle larvae (Katayama and Suzuki 2003). This difference in alarm behavior may contribute to the maintenance of a mutualistic relationship with ants (Nault et al. 1976). When non-myrmecophilous aphids did respond to alarm pheromone by dispersing, ants were triggered to respond with attack (Nault et al. 1976). An inactive response may protect myrmecophilous aphids from a predation response by their ant guards. Ants also respond to aphid alarm pheromone by turning towards the source, rising up, and attacking (Nault et al. 1976).

ANT-HOMOPTERAN MUTUALISM EFFECTS ON PLANTS

The relationship between ants and homopterans also has implications for plant communities. As an indirect result of ants protecting homopteran colonies, some plants gain protection from other herbivorous insects (Carroll and Janzen 1973) along with possible protection from sooty molds growing from honeydew build-up (Bach 1991). However, many of the world's major plant pests are homopterans that vector plant viruses and attack plant tissues (Buckley 1987b). Aphids have been implicated in plant death, reduced plant growth, and lower levels of chlorophyll in leaves (Dixon 1973). Renault et al. (2005) found that *Camponotus* sp. increased the densities of *Aphis coreopsidis* (Thomas) on hairy beggarticks plants, *Bidens pilosa* L. The increase in aphid densities resulted in a reduction in the number of viable seeds produced by *B. pilosa*, thereby reducing the fitness of the plant. Similarly, studies have shown that *S. invicta* increases the survival and density of cotton aphid, *Aphis gossypii* Glover, colonies through predator interference (Kaplan and Eubanks 2002). Cotton aphids can vector more than 50 plant viruses (Kaplan and Eubanks 2002). For example, the cotton aphid was implicated in a multi-virus tomato epidemic in Alabama, which resulted in a 100% yield loss (Kaplan and Eubanks 2002).

In contrast, Messina (1981) found indirect positive effects for host plant fitness due to ants tending membracids. After a series of plant surveys, Messina discovered that goldenrod plants, *Solidago altissima* L., with membracids, *Publilia concava*, and tending ants, *Formica* spp., had lower rates of defoliation by the beetles, *Trirhabda virgata* LeConte and *Trirhabda borealis* Blake. Plants that escaped defoliation showed greater mean height growth and seed production than neighboring plants without tending ants.

ANT–HOMOPTERAN MUTUALISM AND ANT INVASIONS

Ant–homopteran relationships can also play a role in invasive ant ecology. Invasive ant species cause many major problems in introduced areas (Williams 1994). Invasive ants are typified by a number of characteristics: high abundance, polygynous social structure, expansive super colonies, generally small-sized workers, aggressive nature, attraction to high-carbohydrate resources, flexible and opportunistic diets, and quick recruitment (McGlynn 1999; Holway et al. 2002; Lach 2003; Garnas 2005). Because of these characteristics, invasive ants are adept at displacing native ant fauna and changing composition of insect communities.

Holway et al. (2002) ascribe the dominance of invasive ant species in invaded sites to the combined effects of interference and exploitative competition. For example, in one study in California, *Linepithema humile*, the invasive Argentine ant, exploited resources by finding and recruiting to bait faster, in higher numbers, and more consistently than native ants (Human and Gordon 1996). *Linepithema humile* also foraged for longer periods of the day. When encountering each other at baits, *L. humile* displaced native ants 60% of the time, effectively interfering with native ant foraging (Human and Gordon 1996). Likewise in New Caledonia, the little fire ant, *Wasmannia auropunctata*, occupied 100% of the baits in invaded areas after two hours. In comparison, native ants only occupied 44.6% after two hours (LeBreton et al. 2005). Native ants also only nested in 48.9% to 64.5% of two native tree species whereas *W. auropunctata* nested in 92.6% to 98.3% of these native trees (Le Breton et al. 2005). In Maine, the invasive red ant *M. rubra* has significantly displaced native ants, reducing species richness and diversity (Garnas 2005). In baiting experiments, *M. rubra* discovered and recruited more quickly to baits than native ants and effectively dominated and displaced most native ants at baits (Garnas 2005).

At sites of invasion in Texas, the red imported fire ant, *S. invicta*, has devastated native ant fauna, reducing species richness by 70% and total abundance by 90% (Porter and Savignano 1990). The species richness of non-ant arthropods also fell by 30% and total abundance by 75% (Porter and Savignano 1990). *Solenopsis invicta* has also reduced arboreal arthropod abundance in a Texan forest (Kaspari 2000). *Linepithema humile* similarly decimates native ant fauna. In northern California, *L. humile* coexists with only one native ant species, *Prenolepis imparis*, at sites of invasion (Holway

1998). The invasive range of *L. humile* is continuing to increase at the expense of native ant taxa in northern California (Sanders et al. 2001). In the unique setting of a closed greenhouse called Biosphere 2 in Arizona, the invasive crazy ant, *Paratrechina longicornis* (Latreille), has reduced native ant richness and abundance, as well as reducing arthropod diversity resulting in a decline of cockroaches, katydids, and homopterans (Wetterer et al. 1999).

Homopterans are often tended by invasive ants. Some invasive ants are capable of providing the benefits of tending to homopterans: increased abundances (Kaplan and Eubanks 2002; Le Breton et al. 2005; Coppler et al. 2007; Daane et al. 2007; Wetterer 2007), protection against natural enemies (Markin 1970; Vinson and Scarborough 1991; Michaud and Browning 1999; Kaplan and Eubanks 2005), improved hygienic conditions (Markin 1970), shelter construction (Helms and Vinson 2002), and transportation to healthy plants (Vinson and Scarborough 1991). Similarly to native ants, invasive ants can sometimes provide enemy-free space for some homopteran natural enemies (Reilly and Sterling 1983; Daane et al. 2007). In some cases, however, tending by invasive ants increases homopteran abundances more than tending by native ants. For example, *W. auropunctata* significantly increased populations of native mealybugs more than native ants in New Caledonia (Le Breton et al. 2005). Similarly in Maine, increased populations of homopterans are found in areas invaded by the European red ant, *M. rubra* (Garnas 2005).

Kaplan and Eubanks (2002) also found *S. invicta* preferentially forages on aphid-infested plants. This mutualistic relationship between fire ants and aphids was a key interaction that alters the community structure of arthropod communities (Kaplan and Eubanks 2005). The presence of aphids on cotton plants attracted fire ants onto the canopy of cotton plants. Through tending of the aphids, ants significantly decreased the population of herbivores and aphid-predators on cotton plants. Similarly to *S. invicta*, *L. humile* also changes foraging patterns when *Aphis fabae solanella* Theobald are present on black nightshade, *Solanum nigrum* L. (Grover et al. 2008). The presence of aphids on plants increased the foliage foraging of the ants, which in turn increased the encounters between the ants and the aphid predator, the lacewing *Chrysoperla rufilabris* (Burmeister). By foraging higher in plants, *L. humile* may potentially alter the communities of foliar arthropods, other than natural enemies of aphids.

The increased activity and abundances of invasive worker ants over native worker ants could be affecting ecological balance and

relationships in both natural and agroecosystems. Lach (2007) found that *L. humile* ants were more likely to be present on *Protea nitida* Mill. wagon trees and their inflorescences when the membracids *Beaufortiana* sp. were present than when native ants were. Because of the increased presence on inflorescences, *L. humile* ants reduced potential pollinator abundance and arthropod taxa (Lach 2007). Aside from decreasing pollinator visitation, invasive ants are also raising risks for agricultural crop health. Tending *P. megacephala* (Fabricius) ants increase abundances of mealybugs on pineapple and sugarcane. When *P. megacephala* ants are removed from a pineapple field, pineapple wilt disease can be brought under control (Beardsley et al. 1982). Likewise, *P. megacephala* tends banana aphids and increases banana bunchy top virus vectored by aphids (Stechmann et al. 1996). A variety of aphid species that feed on tomato are capable of reducing the yield and fruit quality of tomatoes (Coppler et al. 2007). They are also the primary vectors of many damaging plant viruses (Coppler et al. 2007). *Solenopsis invicta* increases abundances of tomato aphids in agricultural fields (Coppler et al. 2007). Another exotic pest ant species, *W. auropunctata*, is a significant agricultural pest on tropical islands. Not only does this ant sting workers, cause blindness in domestic and native mammals, but it also enhances populations of aphids and other plant pests (Wetterer 2003). Similarly, the presence of the invasive *L. humile* ants has led to the eruption of homopterans in agricultural systems (Holway 1998). For example, *L. humile* increases abundances of the obscure mealybug, *Pseudococcus viburni*, in California vineyards. The obscure mealybug causes economic injury by damaging fruits through the accumulation of honeydew, which fouls the fruit and is associated with an increase in fungal pathogens, as well as by transmitting viruses (Daane et al. 2007).

In contrast, some studies have revealed the beneficial aspects of invasive species (Sterling et al 1979; Hu and Frank 1996; Vogt et al. 2001; Wetterer 2007). For example, in an Oklahoma peanut field, *S. invicta* collected seven times more pest arthropods than beneficial insects, including the rednecked peanutworm, *Stegasta bosqueella* (Chambers). *Pheidole megacephala* also preys on pest species in agricultural fields, including sugarcane stem borer, *Chilo sacchariphagus* Bojer, and banana weevil, *Cosmopolites sordidus* (Germar) (Wetterer 2007).

The tending of homopterans is probably important to the establishment and spread of invasive ant species (Helms and Vinson 2002), increasing likelihood of dominance of invasive ants. In a study of *S. invicta*, half of the ants' energetic requirements

were satisfied with collected honeydew (Helms and Vinson 2002). Tillberg et al. (2007) found that *L. humile* that settled after the initial invasion front in California have shifted their diets to chief reliance on plant-based resources, especially honeydew-producing homopterans. Tillberg et al. (2007) hypothesize this dietary shift away from carnivory could be a result of resource depletion after the invasion. One of the characteristics of successfully invasive ant species is dietary plasticity and opportunism. If resources are stressed and limited after invasive fronts move through an area, the relationship between ants and homopterans could be vitally important for maintaining a large abundance of invasive ants. Even when resources are not depleted or stressed, the energy supplied by homopterans could contribute to the spread of invasive ant species. There is also substantial evidence that invasive ant species are often associated with invasive Homoptera, with each species occurring at large densities (Helms and Vinson 2002).

CONCLUSION

Mutualisms between ants and aphids vary with abiotic and biotic conditions, including the species involved and the needs of each partner. For example, more aggressive ant species protect more aphids from parasitism and hyperparasitism than less aggressive ant species (Kaneko 2003). Different species of ants do not provide equal benefits to all species of Homoptera; one species of ant may better benefit a particular homopteran over another (Bristow 1984). Aphids are seemingly more vulnerable in this relationship than their ant tenders as ant behavior can vacillate between mutualism and exploitation; ants have been found to turn predacious with availability of higher quality and quantity of honeydew, excess honeydew, and larger aphid colonies (Offenberg 2001). The mutualism between ants and aphids is extremely dynamic, with resounding impacts on population, community, and ecosystem levels.

By successfully dominating food resources, and in some cases increasing homopteran abundance, invasive ants may gain significant energy for colony maintenance, expansion, and dominance in invaded territories. *Myrmica rubra* populations in Maine may have succeeded in displacing native ant fauna by dominating and increasing these homopteran-based food resources (McPhee 2008). As *M. rubra* effectively tends and protects homopteran populations, they may increase their potential for dominance in the landscape.

LITERATURE CITED

- Bach, C.E. 1991. Direct and indirect interactions between ants (*Pheidole megacephala*), scales (*Coccus viridis*) and plants (*Pluchea indica*). *Oecologia* 87:233–239.
- Banks, C.J., and H.L. Nixon. 1958. Effects of the ant, *Lasius niger* L., on the feeding and excretion of the bean aphid, *Aphis fabae* Scop. *J. Exp. Biol.* 35(4): 703–711.
- Bartlett, B.R. 1961. The influence of ants upon parasites, predators, and scale insects. *Ann. Entomol. Soc. Am.* 54(4): 543–551.
- Beardsley, J.W., T.H. Su, F.L. McEwen, and D. Gerling. 1982. Field investigations on the interrelationships of the big-headed ant, the gray pineapple mealybug, and the pineapple mealybug wilt disease in Hawaii. *Proc. Hawaii. Entomol. Soc.* 24(1): 51–68.
- Bishop, D.B., and C.M. Bristow. 2003. Effects of the presence of the Allegheny mound ant (Hymenoptera: Formicidae) in providing enemy-free space to myrmecophilous aphid and soft scale populations. *Ann. Entomol. Soc. Am.* 96(3): 202–210.
- Boucher, D.H., S. James, and K.H. Keeler. 1982. The ecology of mutualism. *Ann. Rev. Ecol. Syst.* 13:315–347.
- Breton, L.M., and J.F. Addicott. 1992. Density-dependent mutualism in an aphid-ant interaction. *Ecology* 73(6): 2175–2180.
- Bristow, C.M. 1984. Differential benefits from ant attendance to two species of Homoptera on New York ironweed. *J. Animal Ecol.* 53:715–726.
- Bristow, C.M. 1991. Why are so few aphids ant-tended? *Ant-Plant Interactions*, ed. C.R. Huxley and D.F. Cutler. Oxford University Press, Oxford. 102–119.
- Bronstein, J.L. 1994. Conditional outcomes in mutualistic interactions. *Trends Ecol. Evol.* 9:214–217.
- Buckley, R. 1987a. Ant-plant-homopteran interactions. *Adv. Ecol. Res.* 16:53–85.
- Buckley, R. 1987b. Interactions involving plants, homoptera, and ants. *Ann. Rev. Ecol. Syst.* 18:111–135.
- Carroll, C.R., and D.H. Janzen. 1973. Ecology of foraging by ants. *Ann. Rev. Ecol. Syst.* 4:231–251.
- Coppler, L.B., J.F. Murphy, and M.D. Eubanks. 2007. Red imported fire ants (Hymenoptera: Formicidae) increase the abundance of aphids in tomato. *Fla. Entomol.* 90(3): 419–425.
- Cushman, J.H., and A.J. Beattie. 1991. Mutualisms: assessing the benefits to hosts and visitors. *Trends Ecol. Evol.* 6(6): 193–195.
- Daane, K.M., K.R. Sime, J. Fallon, and M.L. Cooper. 2007. Impacts of Argentine ants on mealybugs and their natural enemies in California's coastal vineyards. *Ecol. Entomol.* 32:583–596.
- Dixon, A.F.G. 1973. *Biology of Aphids*. Edward Arnold Limited, London.
- El Ziady, S., and J.S. Kennedy. 1956. Beneficial effects of the common garden ant, *Lasius niger* L., on the black bean aphid, *Aphis fabae* Scopoli. *Proc. R. Soc. Lond. (A)* 31:61–65.

- Fernandes, G.W., M. Fagundes, M.K. Barcelos Greco, M.S. Barbeitos, and J.C. Santos. 2005. Ants and their effects on an insect herbivore community associated with the inflorescences of *Byrsonima crassifolia* (Linnaeus) H.B.K. (Malpighiaceae). *Rev. Brasil. Entomol.* 49(2): 264–269.
- Fiedler, K., and U. Maschwitz. 1988. Functional analysis of the myrmecophilous relationships between ants (Hymenoptera: Formicidae) and lycaenids (Lepidoptera: Lycaenidae). *Oecologia* 75:204–206.
- Fischer, M.K., K.H. Hoffman, and W. Volkl. 2001. Competition for mutualists in an ant-homopteran interaction mediated by hierarchies of ant attendance. *Oikos* 92(3): 531–541.
- Fischer, M.K. and A.W. Shingleton. 2001. Host plant and ants influence the honeydew sugar composition of aphids. *Funct. Ecol.* 15:544–550.
- Fischer, M.K., W. Volkl, R. Schopf, and K.H. Hoffman. 2002. Age-specific patterns in honeydew production and honeydew composition in the aphid *Metopeurum fuscoviride*: implications for ant attendance. *J. Insect Physiol.* 48:319–326.
- Flatt, T., and W.W. Weisser. 2000. The effects of mutualistic ants on aphid life history traits. *Ecology* 81(12): 3522–3529.
- Garnas, J. 2005. European fire ants on Mount Desert Island, Maine: population structure, mechanisms of competition and community impacts of *Myrmica rubra* L. (Hymenoptera: Formicidae). M.S. thesis, University of Maine, Orono.
- Groden, E., F.A. Drummond, J. Garnas, and A. Franceour. 2005. Distribution of an invasive ant, *Myrmica rubra* (Hymenoptera: Formicidae), in Maine. *J. Econ. Entomol.* 98(6): 1774–1784.
- Grover, C.D., K.C. Dayton, S.B. Menke, and D.A. Holway. 2008. Effects of aphids on foliar foraging by Argentine ants and the resulting effects on other arthropods. *Ecol. Entomol.* 33:101–106.
- Helms, K.R., and S.B. Vinson. 2002. Widespread association of the invasive ant *Solenopsis invicta* with an invasive mealybug. *Ecology* 83(9): 2425–2438.
- Holldobler, B., and E.O. Wilson. 1990. *The Ants*. The Belknap Press of Harvard University Press, Cambridge, MA.
- Holldobler, B., and E.O. Wilson. 1994. *Journey to the Ants*. The Belknap Press of Harvard University Press, Cambridge, MA.
- Holway, D.A. 1998. Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. *Oecologia* 116:252–258.
- Holway, D.A., L. Lach, A.V. Suarez, N.D. Tsutsui, and T.J. Case. 2002. The causes and consequences of ant invasions. *Ann. Rev. Ecol. Syst.* 31:181–223.
- Hu, G.Y., and J.H. Frank. 1996. Effect of red imported fire ant (Hymenoptera: Formicidae) on dung-inhabiting arthropods in Florida. *Environ. Entomol.* 25(6): 1290–1296.

- Human, K.G., and D.M. Gordon. 1996. Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia* 105(3): 405–412.
- Kaneko, S. 2003. Different impacts of two species of aphid-attending ants with different aggressiveness on the number of emerging adults of the aphid's primary parasitoid and hyperparasitoids. *Ecol. Res.* 18:199–212.
- Kaplan, I., and M.D. Eubanks. 2002. Disruption of the cotton aphid (Homoptera: Aphididae)—natural enemy dynamics by red imported fire ants (Hymenoptera: Formicidae). *Environ. Entomol.* 31(6): 1175–1183.
- Kaplan, I., and M.D. Eubanks. 2005. Aphids alter the community-wide impact of fire ants. *Ecology* 86(6): 1640–1649.
- Kaspary, M. 2000. Do imported fire ants impact canopy arthropods? Evidence from simple arboreal pitfall traps. *Southwest. Nat.* 45(2): 118–122.
- Katayama, N., and N. Suzuki. 2002. Cost and benefit of ant attendance for *Aphis craccivora* (Hemiptera: Aphididae) with reference to aphid colony size. *Can. Entomol.* 134(2): 241–249.
- Katayama, N., and N. Suzuki. 2003. Bodyguard effects for aphids of *Aphis craccivora* Koch (Homoptera: Aphididae) as related to the activity of two ant species, *Tetramorium caespitum* Linnaeus (Hymenoptera: Formicidae) and *Lasius niger* L. (Hymenoptera: Formicidae). *J. Appl. Entomol. Zoo.* 38(3): 427–433.
- Kindlmann, P., M. Hulle, and B. Stadler. 2007. Timing of dispersal: effect of ants on aphids. *Oecologia* 152:625–631.
- Lach, L. 2003. Invasive ants: unwanted partners in ant-plant interactions? *Ann. Miss. Bot. Gard.* 90(1): 91–108.
- Lach, L. 2007. A mutualism with a native membracid facilitates pollinator displacement by Argentine ants. *Ecology* 88(8): 1994–2004.
- Le Breton, J., H. Jourdan, J. Chazeau, J. Orivel, and A. Dejean. 2005. Niche opportunity and ant invasion: the case of *Wasmannia auropunctata* in a New Caledonian rain forest. *J. Trop. Ecol.* 21:93–98.
- Liere, H., and I. Perfecto. 2008. Cheating on a mutualism: indirect benefits of ant attendance to a coccidophagous coccinellid. *Environ. Entomol.* 37(1): 143–149.
- Mack, R.N., D. Simberloff, W.M. Lonsdale, H. Evans, M. Clout, and F.A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. App.* 10(3): 689–710.
- Markin, G.P. 1970. Foraging behavior of the Argentine ant in a California citrus grove. *J. Econ. Entomol.* 63(3): 740–744.
- McGlynn, T.P. 1999. The worldwide transfer of ants: geographical distribution and ecological invasions. *J. Biogeogr.* 26:535–548.
- McNeil, J.N., J. Delisle, and R.J. Finnegan. 1977. Inventory of aphids on seven conifer species in association with the introduced red wood

- ant, *Formica lugubris* (Hymenoptera: Formicidae). *Can. Entomol.* 109:1199–1202.
- McPhee, K. 2008. Interactions between Homoptera and the European red ant, *Myrmica rubra* (L.) (Hymenoptera: Formicidae), on Mount Desert Island, Maine. M.S. thesis, University of Maine, Orono.
- Messina, F.J. 1981. Plant protection as a consequence of an ant-membracid mutualism: interactions on goldenrod (*Solidago* sp.). *Ecology* 62(6): 1433–1440.
- Michaud, J.P., and H.W. Browning. 1999. Seasonal abundance of the brown citrus aphid, *Toxoptera citricida*, (Homoptera: Aphididae) and its natural enemies in Puerto Rico. *Fla. Entomol.* 82(3): 424–447.
- Morales, M.A. 2000. Survivorship of an ant-tended membracid as a function of ant recruitment. *Oikos* 90(3): 469–476.
- Muller, C.B., and H.C.J. Godfray. 1999. Predators and mutualists influence the exclusion of aphid species from natural communities. *Oecologia* 119:120–125.
- Nault, L.R., M.R. Montgomery, and W.S. Bowers. 1976. Ant-aphid association: role of aphid alarm pheromone. *Science* 192:1349–1351.
- Novgorodova, T.A. 2005. Ant-aphid interactions in multispecies ant communities: some ecological and ethological aspects. *Eur. J. Entomol.* 102(3): 495–501.
- Offenberg, J. 2001. Balancing between mutualism and exploitation: the symbiotic interaction between *Lasius* ants and aphids. *Behav. Ecol. Sociobiol.* 49(4): 304–310.
- Oliver, T.H., A. Mashanova, S.R. Leather, J.M. Cook, and V.A.A. Jansen. 2007. Ant semiochemicals limit apterous aphid dispersal. *Proc. R. Soc. Biol. Sci.* 274(1629): 3127–3131.
- Phillips, I.D., and C.K.R. Willis. 2005. Defensive behavior of ants in a mutualistic relationship with aphids. *Behav. Ecol. Sociobiol.* 59:321–325.
- Pierce, N.E., R.L. Kitching, R.C. Buckley, M.F.J. Taylor, and K.F. Benbow. 1987. The costs and benefits of cooperation between the Australian lycaenid butterfly, *Jalmenus evagoras*, and its attendant ants. *Behav. Ecol. Sociobiol.* 21:237–248.
- Pontin, A.J. 1978. The numbers and distribution of subterranean aphids and their exploitation by the ant *Lasius flavus* (Fabr.). *Ecol. Entomol.* 3:203–207.
- Porter, S.D., and D.A. Savignano. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology* 71(6): 2095–2106.
- Porter, S.D., and W.R. Tschinkel. 1987. Foraging in *Solenopsis invicta* (Hymenoptera: Formicidae): effects of weather and season. *Environ. Entomol.* 16(3): 802–808.
- Price, P.W. 1997. *Insect Ecology*, 3rd ed. John Wiley & Sons, Inc, New York. 213–238.

- Queiroz, J.M., and P.S. Oliveira. 2001. Tending ants protect honeydew-producing whiteflies (Homoptera: Aleyrodidae). *Environ. Entomol.* 30(2): 295–297.
- Quinn, G.P., and M.J. Keough. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, New York.
- Rauch, G., J. Simon, B. Chaubert, L. Haack, T. Flatt, and W.W. Weisser. 2002. The influence of ant-attendance on aphid behaviour investigated with the electrical penetration graph technique. *Entomol. Exp. Appl.* 102:13–20.
- Reilly, J.J., and W.L. Sterling. 1983. Interspecific association between the red imported fire ant (Hymenoptera: Formicidae), aphids, and some predaceous insects in a cotton agroecosystem. *Environ. Entomol.* 12:541–545.
- Reithel, J.S., and I. Billick. 2006. Bottom-up mediation of an ant-membracid mutualism: effects from different host plants. *Evol. Ecol.* 20:27–38.
- Renault, C.K., L.M. Buffa, and M.A. Delfino. 2005. An aphid-ant interaction: effects on different trophic levels. *Ecol. Res.* 20:71–74.
- Sakata, H. 1994. How an ant decides to prey on or to attend aphids. *Res. Pop. Ecol.* 36(1): 45–51.
- Sanders, N.J., K.E. Barton, and D.M. Gordon. 2001. Long-term dynamics of the distribution of the invasive Argentine ant, *Linepithema humile*, and native ant taxa in northern California. *Oecologia* 127:123–130.
- Shingleton, A.W., and W.A. Foster. 2000. Ant tending influences soldier production in a social aphid. *Proc. R. Soc. Lond. (B)* 267:1863–1868.
- Shingleton, A.W., D.L. Stern, and W.A. Foster. 2005. The origin of mutualism: a morphological trait promoting the evolution of ant-aphid mutualisms. *Evolution* 59(4): 921–926.
- Skinner, G.J. 1980. The feeding habits of the wood-ant *Formica rufa* (Hymenoptera: Formicidae), in limestone woodland in north-west England. *J. Animal Ecol.* 49:417–433.
- Stadler, B. 1997. The relative importance of host plants, natural enemies and ants in the evolution of life-history characters in aphids. *Vertical Food Web Interactions*, ed. K. Dettner, G. Bauer, and W. Völk. Springer Verlag, Berlin. 241–256.
- Stadler, B., and A.F.G. Dixon. 1998. Costs of ant attendance for aphids. *J. Animal Ecol.* 67:454–459.
- Stadler, B., and A.F.G. Dixon. 1999. Ant attendance in aphids: why different degrees of myrmecophily? *Ecol. Entomol.* 24:363–369.
- Stechmann, D.H., W. Volkl, and P. Stery. 1996. Ant-attendance as a critical factor in the biological control of the banana aphid *Pentalonia nigronervosa* Coq. (Hom. Aphididae) in Oceania. *J. Appl. Entomol.* 120:119–123.
- Sterling, W.L., D. Jones, and D.A. Dean. 1979. Failure of red imported fire ant to reduce entomophagous insect and spider abundance in a cotton agroecosystem. *Environ. Entomol.* 8(6): 976–981.

- Tillberg, C.V., D.A. Holway, E.G. LeBrun, and A.V. Suarez. 2007. Trophic ecology of invasive Argentine ants in their native and introduced ranges. *Proc. Natl. Acad. Sci.* 104(52): 20856–20861.
- Tilles, D.A., and D.L. Woods. 1982. The influence of the carpenter ant (*Camponotus modoc*) (Hymenoptera: Formicidae) attendance on the development and survival of aphids (*Cinara* spp.) (Homoptera: Aphididae) in a giant sequoia forest. *Can. Entomol.* 114:1133–1142.
- Vinson, S.B., and T.A. Scarborough. 1991. Interactions between *Solenopsis invicta* (Hymenoptera: Formicidae), *Rhopalosiphum maidis* (Homoptera: Aphididae), and the parasitoid *Lysiphlebus testaceipes* Cresson (Hymenoptera: Aphidiidae). *Ann. Entomol. Soc. Am.* 84(2): 158–164.
- Vogt, J.T., R.A. Grantham, W.A. Smith, and D.C. Arnold. 2001. Prey of the red imported fire ant (Hymenoptera: Formicidae) in Oklahoma peanuts. *Environ. Entomol.* 30(1): 123–128.
- Volkl, W. 1992. Aphids or their parasitoids: who actually benefits from ant-attendance? *J. Animal Ecol.* 61(2): 273–281.
- Waldbauer, G. 1996. *Insects Through the Seasons*. Harvard University Press, Cambridge, MA. 197–198.
- Way, M.J. 1963. Mutualism between ants and honeydew-producing homoptera. *Ann. Rev. Entomol.* 63(8): 307–344.
- Wetterer, J. 2003. The little fire ant, *Wasmannia auropunctata*: distribution, impact, and control. *Sociobiology* 42(1): 1–41.
- Wetterer, J.K. 2007. Biology and impact of pacific island invasive species. 3. The African big-headed ant, *Pheidole megagephala* (Hymenoptera: Formicidae). *Pac. Sci.* 61(4): 437–456.
- Wetterer, J.K., S.E. Miller, D.E. Wheeler, C.A. Olson, D.A. Polhemus, M. Pitts, I.W. Ashton, A.G. Himler, M.M. Yospin, K.R. Helms, E.L. Harken, J. Gallaher, C.E. Dunning, M. Nelson, J. Litsinger, A. Southern, and T.L. Burgess. 1999. Ecological dominance by *Paratechina longicornis* (Hymenoptera: Formicidae), an invasive tramp ant, in biosphere 2. *Fla. Entomol.* 82(3): 381–388.
- Wheeler, W.M. 1908. A European ant (*Myrmica laevinodis*) introduced into Massachusetts. *J. Econ. Entomol.* 1:336–339.
- Williams, D.F., ed. 1994. *Exotic Ants: Biology, Impact, and Control of Introduced Species*. Westview Press, Boulder, CO.
- Woodring, J., R. Wiedermann, M.K. Fischer, K.H. Hoffmann, and W. Volkl. 2004. Honeydew amino acids in relation to sugars and their role in the establishment of ant-attendance hierarchy in eight species of aphids feeding on tansy (*Tanacetum vulgare*). *Physiol. Entomol.* 29(4): 311–319.
- Yao, I., H. Shibao, and S. Akimato. 2000. Costs and benefits of ant attendance to the drepanosiphid aphid *Tuberculatus quercicola*. *Oikos* 89(1): 3–10.



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