

Review

Ecological consequences of interactions between ants and honeydew-producing insects

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Interactions between ants and honeydew-producing hemipteran insects are abundant and widespread in arthropod food webs, yet their ecological consequences are very poorly known. Ant–hemipteran interactions have potentially broad ecological effects, because the presence of honeydew-producing hemipterans dramatically alters the abundance and predatory behaviour of ants on plants. We review several studies that investigate the consequences of ant–hemipteran interactions as ‘keystone interactions’ on arthropod communities and their host plants. Ant–hemipteran interactions have mostly negative effects on the local abundance and species richness of several guilds of herbivores and predators. In contrast, out of the 30 studies that document the effects of ant–hemipteran interactions on plants, the majority (73%) shows that plants actually benefit indirectly from these interactions. In these studies, increased predation or harassment of other, more damaging, herbivores by hemipteran-tending ants resulted in decreased plant damage and/or increased plant growth and reproduction. The ecological consequences of mutualistic interactions between honeydew-producing hemipterans and invasive ants relative to native ants have rarely been studied, but they may be of particular importance owing to the greater abundance, aggressiveness and extreme omnivory of invasive ants. We argue that ant–hemipteran interactions are largely overlooked and underappreciated interspecific interactions that have strong and pervasive effects on the communities in which they are embedded.

Keywords: ants; hemipterans; mutualism; indirect effects; tritrophic interactions; conditionality

1. INTRODUCTION

Mutualism, defined as a reciprocally beneficial interaction between individuals of two species, is increasingly recognized as a common and important ecological interaction (Boucher *et al.* 1982; Bronstein 1994a; Stachowicz 2001). Perhaps one of the most familiar examples is the food-for-protection mutualism between ants (Hymenoptera: Formicidae) and honeydew-producing insects in the hemipteran suborders Sternorrhyncha (specifically aphids, whiteflies, scales and mealy bugs) and Auchenorrhyncha (specifically treehoppers and leafhoppers; formerly grouped together as the single order/suborder ‘Homoptera’). Honeydew is a sugary excretion of carbohydrates, amino acids and water derived from plant phloem upon which many hemipterans feed (Way 1963). Ants are attracted to honeydew as a predictable, renewable food resource and, consequently, ‘tend’ honeydew-producing hemipterans, protecting them from predators and parasitoids (Way 1963; Buckley 1987).

Ant–hemipteran mutualisms are very common, if not well appreciated, interactions in terrestrial communities from temperate to tropical latitudes (Buckley 1987; Hölldobler & Wilson 1990; Delabie 2001). Ants tend honeydew-producing hemipterans on an extremely wide range of plants, including grasses (e.g. Moya-Raygoza & Nault 2000), forbs (e.g. Messina 1981; Renault *et al.* 2005), vines, shrubs and trees (e.g. Floate & Whitham

1994; Rico-Gray & Castro 1996; Way *et al.* 1999). In a study of the ant community in the Amazonian rainforest canopy, Blüthgen *et al.* (2000) recorded ant–hemipteran associations on 20 out of 24 tree genera (in 15 tree families) and on 41 out of 66 individual trees surveyed. The interactions between ants and honeydew-producing hemipterans are also very common in managed (e.g. agricultural) habitats in addition to being widespread in natural habitats from grasslands to forests (Buckley 1987; Way & Khoo 1992).

The mutualistic interactions between ants and honeydew-producing insects have been a popular subject of investigation for over 100 years, and the literature is replete with studies that have focused on the benefits of the interaction to both partners, particularly the protection of hemipterans by tending ants (Hölldobler & Wilson 1990). However, more recent work challenges the long-held assumption that tending ants always benefit their hemipteran partners (reviewed in Stadler & Dixon 2005). For example, some aphid species alter their feeding behaviour and the composition of their honeydew (e.g. by increasing the concentrations of amino acids) at the expense of their own growth and fecundity in the presence of tending ants (Stadler & Dixon 1998; Yao *et al.* 2000; Yao & Akimoto 2002). Thus, while most ant–hemipteran interactions are assumed to be mutualistic, they may not always be so.

Despite the long-standing interest in the mutualistic aspects of ant–hemipteran interactions, the broader community-level consequences of these interactions, particularly their potential effects of trophic interactions on food webs, arthropod community structure and host

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plant fitness, have received comparatively little scrutiny. Predatory species of ants are important constituents of arthropod food webs owing to their active and catholic feeding habits, efficiency in recruiting to and subduing prey and sheer abundance (Hölldobler & Wilson 1990). The mutualistic interactions between ants and honeydew-producing hemipterans may dramatically increase the effects of ants as predators, however, because the presence of hemipterans alters ant behaviour such that ants become more aggressive and attack insects that they might otherwise ignore, including other predators as well as other (non-honeydew-producing) herbivores (Way 1963). Further, hemipteran honeydew supports entire colonies of arboreal ants, allowing them to maintain much greater densities than could be supported by scavenging and predation alone (Davidson 1997; Blüthgen *et al.* 2000; Davidson *et al.* 2003), and attracts ground-dwelling ants onto plant foliage, increasing the likelihood that they would encounter arthropods in plant-based food webs (Way & Khoo 1992; Del-Claro & Oliveira 1999; Kenne *et al.* 2003; Kaplan & Eubanks 2005).

Since the strength of interactions between ants and other species in the local arthropod community may be enhanced in the presence of honeydew-producing hemipterans, hemipteran-tending ants may also indirectly affect plant fitness. Increased ant predation of other herbivores (including hemipteran insects that do not feed from plant phloem or produce honeydew) may benefit plants if those herbivores impose a greater cost to plant growth and reproduction than do the ant-tended hemipterans (Buckley 1987; Way & Khoo 1992; Delabie 2001). In contrast, by protecting hemipterans from predators and parasitoids, and by stimulating hemipteran feeding rate, fecundity and dispersal, tending ants may exacerbate the negative effects of honeydew-producing hemipterans on plants, including stunted growth, reduced leaf area and the introduction of plant pathogens, all of which can decrease plant fitness (Way 1963; Beattie 1985; Buckley 1987; Delabie 2001). Thus, the consequences of ant–hemipteran interactions on plant fitness should represent a trade-off between the indirect benefit of increased ant suppression of other herbivores and the direct cost of herbivory by ant-tended hemipterans (Carroll & Janzen 1973; Buckley 1987; Lach 2003; figure 1*a,b*).

Here, we review the published literature on the ecological consequences of ant–hemipteran interactions. Our goal is to highlight mutualistic interactions between ants and honeydew-producing hemipterans as ‘keystone interactions’ that have broad, yet underappreciated effects on (i) the abundance and distribution of species in arthropod communities and (ii) host plant fitness. The ecological consequences of ant–hemipteran interactions have been discussed by several other authors (e.g. Beattie 1985; Buckley 1987; Way & Khoo 1992; Lach 2003), but our review provides the first comprehensive summary and synthesis of all published data. The two important points that we emphasize are how relatively few studies have actually quantified the effects of ant–hemipteran interactions and how specific design problems common to the majority of the studies weaken their conclusions. We also emphasize the extreme paucity of information regarding the ecological consequences of the interactions between honeydew-producing hemipterans and invasive ant species.

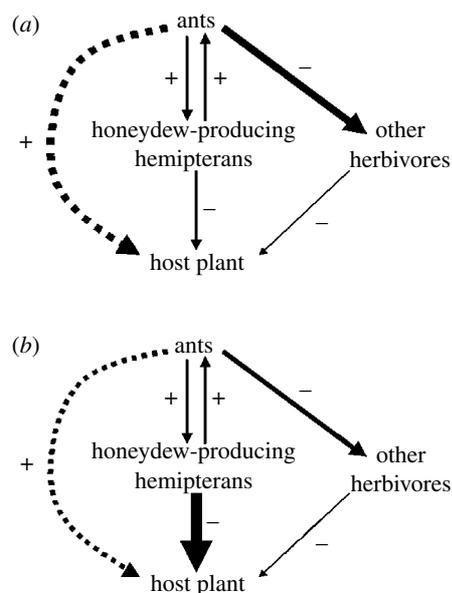


Figure 1. Potential consequences of the interactions between honeydew-producing hemipterans and ants on plants. Arrows indicate the direction of effects, positive (+) and negative (-), and arrow width indicates the relative magnitude of effects. Solid arrows indicate direct effects, whereas dashed arrows indicate indirect effects. Ant–hemipteran interactions may provide a net benefit to plants (a) if the indirect positive effect of increased ant suppression of other (non-honeydew-producing) herbivores outweighs the direct negative effect of hemipterans on plants. In contrast, ant–hemipteran interactions may harm plants (b) if the direct negative effect of hemipterans on plants outweighs the indirect positive effect of increased ant suppression of other herbivores. Note that honeydew-producing hemipterans and other (non-honeydew-producing) herbivores may also interact indirectly via effects on host plant quality (effects not shown).

2. LITERATURE SEARCH AND DATA SELECTION

We broadly searched the ecological literature for studies investigating the effects of ant–hemipteran interactions on arthropod communities and their host plants using standard search engines (Agricola, Biological Abstracts, Science Citation Index). We supplemented our web-based searches by perusing lists of references in relevant published studies. We included studies (both correlative and experimental) that either explicitly tested for the effects of ant–hemipteran interactions or tested more generally for the effects of ants shown to have a positive association with honeydew-producing hemipterans. More explicit selection criteria are described in §§3 and 4.

3. EFFECTS OF ANT–HEMIPTERAN INTERACTIONS ON COMMUNITY STRUCTURE AND SPECIES DIVERSITY

Most previous studies of the ecological effects of ant–hemipteran interactions have focused on a few key taxa of interest and do not examine the effects of the interaction on the community as a whole. That hemipteran-tending ants reduce the survival, abundance and alter the spatial distribution of specific natural enemies of hemipterans on plants, for example, is extensively documented (e.g. Bradley 1973; Cushman & Whitham 1989; Tedders *et al.* 1990; Stechmann *et al.* 1996; Del-Claro & Oliveira 2000; Kaplan & Eubanks 2002; Renault *et al.* 2005). Far fewer studies have focused on the

effects of ant–hemipteran interactions on other (non-honeydew-producing) herbivores sharing the same host plant, but, in most cases, hemipteran-tending ants significantly reduce their survival and abundance as well (e.g. Nickerson *et al.* 1977; Messina 1981; Ito & Higashi 1991; Floate & Whitham 1994; Suzuki *et al.* 2004; Kaplan & Eubanks 2005).

The species-specific differences among herbivores in their vulnerability to ant predation, however, can lead to changes in the overall structure of the herbivore guild in the presence of hemipteran-tending ants (Fowler & MacGarvin 1985; Mahdi & Whittaker 1993; Oliveira & Del-Claro 2005). For example, in an experimental study of the effects of the ant *Formica lugubris* on the community of herbivorous insects in birch (*Betula pubescens*), Fowler & MacGarvin (1985) found that the abundance of the ant-tended aphid, *Symydobius oblongus*, increased by 8200% on branches with ants compared with branches from which ants had been excluded. In contrast, species richness of sucking herbivores that did not produce honeydew was reduced by 28%, species richness of leaf-chewing caterpillars was reduced by 69% and total herbivore species richness was reduced by 28% on branches with ants. In a separate survey, species richness of leaf-chewing beetles was 61% lower on the trees with aphid-tending ants. In contrast, species richness of leaf-mining caterpillars, a guild of herbivores that was not vulnerable to ant predation, was actually 44% greater on the trees with aphid-tending ants, presumably because the ants indirectly protected the concealed caterpillars from other predators (Fowler & MacGarvin 1985). Mahdi & Whittaker (1993) documented similar changes in the guild structure of herbivorous insects in a separate study on birch involving another aphid-tending ant, *Formica rufa*.

Ant–hemipteran interactions can also alter the structure of ant communities on plants. Defence of exclusive foraging territories in tropical tree canopies by particularly abundant and aggressive hemipteran-tending ants reduces the density and diversity of other ants, resulting in ‘mosaic’ distributions of ‘dominant’ and ‘sub-dominant’ arboreal ant species (Blüthgen *et al.* 2000, 2004; Dejean & Corbara 2003). The unique assemblages of dominant and sub-dominant ants among the trees caused at least in part by the availability of hemipteran honeydew probably result in spatially variable effects of those ants on arboreal arthropod communities and on herbivore damage and plant fitness (Blüthgen *et al.* 2004; cf. Horvitz & Schemske 1984; Dejean *et al.* 1997a,b). To our knowledge, this has been documented in only one study. In the presence of a honeydew-producing tetti-gometrid species, tending ants *Camponotus brutus* effectively excluded several other, normally dominant, ant species that tend scale insects on fig trees (*Ficus vallis-choudae*) in Cameroon (Dejean *et al.* 1997a). As a consequence, *C. brutus* protected figs and their hymenopteran pollinators on tetti-gometrid-infested trees from predation by the scale-tending ants. However, on the trees without aggregations of tetti-gometrids, *C. brutus* was relegated to the role of a sub-dominant ant species by the scale-tending ants, thus affording no indirect protection to fig trees and their pollinators (Dejean *et al.* 1997a).

Only two studies have investigated the effects of ant–hemipteran interactions on the entire arthropod community in which they are embedded. Wimp & Whitham

(2001) manipulated the presence and absence of the ant-tended aphid *Chaitophorus populicola* on cottonwood (*Populus* sp.) trees to test specifically for community-level effects of an ant–hemipteran mutualism. On the trees from which aphids were removed, tending ants *Formica propinqua* abandoned the trees resulting in a 76% increase in herbivore abundance and a 76% increase in the abundance of generalist predators. Moreover, total arthropod abundance increased by 80% and total species richness increased by 57% on the trees from which aphids were removed. Likewise, a mutualistic interaction between cotton aphids (*Aphis gossypii*) and red imported fire ants (*Solenopsis invicta*) strongly affected the abundance and distribution of other arthropods in cotton (*Gossypium hirsutum*; Eubanks 2001; Eubanks *et al.* 2002; Kaplan & Eubanks 2002, 2005). In large-scale field manipulations of fire ant densities, the interaction between *S. invicta* and *A. gossypii* negatively affected the abundance of 27–33% of herbivore taxa and 40–47% of predator taxa (Kaplan & Eubanks 2005).

The studies described previously provide compelling evidence that ant–hemipteran interactions can act as ‘keystone interactions’ that dramatically change the structure of arthropod communities on plants. In the presence of honeydew-producing hemipterans, tending ants altered the abundance and distribution of specialist and generalist predators and parasitoids, and multiple species of herbivores in several feeding guilds, resulting in the changes to local species diversity. Though poorly documented, such community-level consequences of ant–hemipteran interactions are probably quite common, particularly for the interactions involving abundant and aggressive ant species. The importance of mutualistic interactions to community structure and diversity has been historically downplayed, however, relative to the effects of competition and predation.

4. EFFECTS OF ANT–HEMIPTERAN INTERACTIONS ON HOST PLANT DAMAGE AND PLANT FITNESS

Given both the ecological and the economic significance of honeydew-producing hemipterans as plant pests, and the widespread distribution and abundance of both honeydew-producing hemipterans and ants in terrestrial communities, surprisingly few studies have investigated explicitly the consequences of ant–hemipteran interactions on plant fitness. This is not to say that the subject has not received a great deal of attention in the literature, leading to what we think is a general misconception that indirect benefits of ant–hemipteran interactions to plants are well documented. Repeated assertions that hemipteran-tending ants indirectly benefit host plants in multiple review papers (e.g. Beattie 1985; Buckley 1987; Way & Khoo 1992; Lach 2003) and in an abundance of papers investigating the effects of ants on plants in general belie the fact that relatively few studies provide a quantitative supporting evidence.

Our search of the literature revealed 22 studies in which a stated goal was to investigate specifically the effects of the interactions between ants and honeydew-producing hemipterans on plants. Equivalent effects could be inferred from eight additional studies of the general effects of ants on plants and associated herbivores, including honeydew-producing hemipterans. These 30 studies (summarized in table 1) examined the

Table 1. Summary of 30 studies that either explicitly tested for the effects of ant-hemipteran interactions on plants or tested more generally for the effects of ants on plants and associated herbivores, including honeydew-producing hemipterans. (Effects of ant-hemipteran interactions on plants are quantified as the per cent change in plant damage and/or plant fitness associated with the presence of the interaction. Asterisks indicate statistically significant changes in plant damage and plant fitness. 1, Banks & Macaulay (1967); 2, Buckley (1983); 3, Fritz (1983); 4, Rico-Gray & Thien (1989); 5, Rosengren & Sundström (1991); 6, Rico-Gray & Castro (1996); 7, Sipura (2002); 8, Renault *et al.* (2005); 9, Cooper (2005); 10, Jutsum *et al.* (1981); 11, Messina (1981); 12, Skinner & Whittaker (1981); 13, Whittaker & Warrington (1985); 14, Bach (1991); 15, Compton & Robertson (1988); 16, Ito & Higashi (1991); 17, Khoo & Ho (1992); 18, Lohr (1992); 19, Floate & Whitham (1994); 20, Dejean *et al.* (1997a); 21, Karhu (1998); 22, Moya-Raygoza & Nault (2000); 23, Van Mele & Cuc (2001); 24, Suzuki *et al.* (2004); 25, Crutsinger & Sanders (2005); 26, Moreira & Del-Claro (2005) and Del-Claro (2005) and Del-Claro (2005); 27, Oliveira & Del-Claro (2006); 28, Styrsky & Eubanks (in preparation).)

ant species (status ^a)	hemipteran species	system	host plant	method ^b	% change in plant damage ^c	% change in plant fitness	citation
negative effects of ant-hemipteran associations on plants (i.e. increased plant damage and/or decreased plant fitness)							
<i>Lasius niger</i> (N) Formicidae	<i>Aphis fabae</i> Stern.: Aphidoidea	managed: field crop	<i>Vicia faba</i> Leguminosae	exp(1)	—	–26% ^c (no. of seed pods) –53% ^c (no. of seeds) –38% ^c (seed mass)	1
<i>Iridomyrmex</i> sp. (N) Dolichoderinae	<i>Sextus virescens</i> Auchen. ^d : Membracidae	natural: woodland	<i>Acacia decurrens</i> Leguminosae	exp(3)	—	significant decrease in plant growth and seed number (no data provided)	2
<i>Formica subsericea</i> (N) Formicidae	<i>Vandusca arguata</i> Auchen.: Membracidae	natural: woodland	<i>Robinia pseudoacacia</i> Leguminosae	corr	–1 to +15%*	–10 to +10% (radial growth)	3
<i>Crematogaster brevispinosa</i> (N) Myrmicinae	<i>Planococcus citri</i> Stern.: Coccoidea	natural: coastal dune	<i>Schomburgkia tibicinis</i> Orchidaceae	exp(1)	+38%*	–55%* (no. of flowers) –78%* (no. of fruits)	4
<i>Formica aquilonia</i> (N) Formicidae	<i>Cinara</i> sp. Stern.: Aphidoidea	natural: woodland	<i>Pinus sylvestris</i> Pinaceae	corr	—	–19%* (radial growth)	5
<i>Camponotus planatus</i> (N) Formicidae	unidentified aphid sp. Stern.: Aphidoidea	natural: coastal dune	<i>Paulinia fuscescens</i> Sapindaceae	exp(1)	—	–7* to –23%* (% flowers with seeds) –46* to –60%* (no. of seeds/flower)	6
<i>Formica aquilonia</i> (N) Formicidae	<i>Pterocomma salicis</i> Stern.: Aphidoidea	natural: woodland	<i>Salix myrsinifolia</i> Salicaceae	exp(3)	–5%	–5% (shoot length) +3% (radial growth)	7
<i>Myrmica rubra</i> (N) Myrmicinae	<i>Pterocomma salicis</i> Stern.: Aphidoidea	natural: woodland	<i>Salix myrsinifolia</i> Salicaceae	exp(3)	< –1%	–24% (shoot length) +6% (radial growth)	7
<i>Camponotus</i> sp. (N) Formicidae	<i>Aphis coreopsidis</i> Stern.: Aphidoidea	natural: grassland	<i>Bidens pilosa</i> Asteraceae	exp(1)	—	–24%* (seed viability)	8
<i>Solenopsis invicta</i> (I) Myrmicinae	unidentified aphid spp. Stern.: Aphidoidea	managed: vegetable crop	<i>Lycopersicon esculentum</i> Solanaceae	exp(1)	+65%* (level of infection by aphid-vectored virus)	–24% (no. of seeds)	9
positive effects of ant-hemipteran associations on plants (i.e. decreased plant damage and/or increased plant fitness)							
<i>Azteca</i> sp. (N) Aneuretinae	<i>Coccus viridis</i> Stern.: Coccoidea	managed: orchard	<i>Citrus reticulata</i> Rutaceae	exp(1)	–28%*	—	10
<i>Formica</i> sp. (N) Formicidae	<i>Publilia concava</i> Auchen.: Membracidae	natural: old field	<i>Solidago altissima</i> Asteraceae	corr	—	+135%* (plant growth) +569%* (no. of seeds)	11
<i>Formica rufa</i> (N) Formicidae	<i>Periphyllus testudinaceus</i> Stern.: Aphidoidea	natural: woodland	<i>Acer pseudoplatanus</i> Aceraceae	exp(1)	–7%*	—	12

(Continued.)

Table 1. (Continued.)

ant species (status ^a)	hemipteran species	system	host plant	method ^b	% change in plant damage ^c	% change in plant fitness	citation
<i>Formica rufa</i> (N) Formicinae	<i>Periphyllus testudinaceus</i> Stern.: Aphidoidea	natural: woodland	<i>Acer pseudoplatanus</i> Aceraceae	corr exp(1)	-3 to -13%* —	+20* to +34% (% viable seeds) +14%* (seedling growth) +116* to +216%* (radial growth)	13
<i>Pheidole megacephala</i> (I) Myrmicinae	<i>Coccis viridis</i> Stern.: Coccoidea	natural: coral rubble	<i>Pluchea indica</i> Asteraceae	exp(1)	-16%*	—	14
<i>Pheidole megacephala</i> (N), Myrmicinae	<i>Hilda patruelis</i> Auchen.: Tetrigometridae	natural: woodland	<i>Ficus sur</i> Moraceae	exp(1)	—	+58 to +234%* (no. of undamaged seeds) +80 to +2150%* (emergence of pollen-carrying fig wasps)	15
<i>Anoplolepis custodiens</i> (N), Formicinae							
<i>Formica yessensis</i> (N) Formicinae	<i>Tuberculatus quercicola</i> Stern.: Aphidoidea	natural: chaparral	<i>Quercus dentata</i> Fagaceae	corr exp(1)	— -4%*	+76%* (no. of viable seeds)	16
<i>Dolichoderus thoracicus</i> (N), Dolichoderinae	<i>Cataenococcus hispidus</i> Stern.: Coccoidea	managed: plantation	<i>Theobroma cacao</i> Sterculiaceae	exp(1)	—	+32* to +40%* (no. of undamaged pods)	17
<i>Anoplolepis custodiens</i> (N), Formicinae	<i>Cerataphis variabilis</i> Stern.: Aphidoidea	managed: plantation	<i>Cocos nucifera</i> Areaceae	corr	—	+59 to +76% ^c (no. of nut sets per palm) +63% ^c (% undamaged nuts)	18
<i>Formica</i> sp. (N) Formicinae	<i>Chaetophorus populicola</i> Stern.: Aphidoidea	natural: woodland	<i>Populus fremontii</i> Salicaceae	exp(2)	-8%*	—	19
<i>Camponotus brutus</i> (N) Formicinae	<i>Hilda undata</i> Auchen.: Tetrigometridae	natural: woodland	<i>Ficus vallis-chondae</i> Moraceae	corr	—	+88* to +90%* (% undamaged fruits)	20
<i>Formica aquilonia</i> (N) Formicinae	<i>Symydobius oblongus</i> Stern.: Aphidoidea	natural: woodland	<i>Betula pubescens</i> Betulaceae	exp(1)	-11%*	—	21
<i>Brachymyrmex obscurior</i> (N), Formicinae	<i>Dalbulus quinquevittatus</i> Auchen.: Cicadellidae	natural: grassland	two <i>Tripsacum</i> species Poaceae	exp(1)	—	0 to +13% (no. of leaves)	22
<i>Dolichoderus thoracicus</i> (N), Dolichoderinae	<i>Planococcus lilacinus</i> Stern.: Coccoidea	managed: plantation	<i>Mamilkara zapota</i> Sapotaceae	exp(1)	—	+18* to +23%* (% undamaged fruits)	23
<i>Formica aquilonia</i> (N) Formicinae	<i>Pterocomma salicis</i> Stern.: Aphidoidea	natural: woodland	<i>Salix phylicifolia</i> Salicaceae	exp(3)	-26%*	+54%* (shoot length) +89%* (radial growth)	7
<i>Myrmica rubra</i> (N) Myrmicinae	<i>Pterocomma salicis</i> Stern.: Aphidoidea	natural: woodland	<i>Salix phylicifolia</i> Salicaceae	exp(3)	-4%	+9% (shoot length) +29% (radial growth)	7
<i>Lasius japonicus</i> (N) Formicinae	complex of three aphid species ^f Stern.: Aphidoidea	natural: grassland	<i>Vicia angustifolia</i> Leguminosae	corr	—	significant increase in seed number (no data provided)	24
<i>Formica obscuripes</i> (N) Formicinae	unidentified <i>Aphis</i> sp. Stern.: Aphidoidea	natural: coastal dune	<i>Salix hookeriana</i> Salicaceae	corr	-30%*	—	25

(Continued.)

Table 1. (Continued.)

ant species (status) ^a	hemipteran species	system	host plant	method ^b	% change in plant damage ^c	% change in plant fitness	citation
complex of 10 species ^d (N)	<i>Enchenopa brasiliensis</i> Auchen.: Membracidae	natural: cerrado	<i>Solanum lycocarpum</i> Solanaceae	exp(1)	-4* to -23%*	—	26
complex of five species ^h (N)	<i>Guyaquila xiphias</i> Auchen.: Membracidae	natural: cerrado	<i>Didymopanax vinosum</i> Araliaceae	exp(1)	-28* to -55%* (damage to leaves and apical meristems)	—	27
<i>Solenopsis invicta</i> (I) Myrmicinae	<i>Aphis gossypii</i> Stern.: Aphidoidea	managed: field crop	<i>Gossypium hirsutum</i> Malvaceae	exp(2)	-5%*	+16%* (no. of cotton bolls) +25%* (no. of cotton seeds) +10%* (seed-cotton mass)	28

^a Status of ant as native (N) or invasive (I) species at study site.

^b Studies categorized as either correlative, 'corr', or experimental, 'exp'. Experimental studies are further classified by the manipulation employed: (i) ant exclusion alone, (ii) hemipteran exclusion alone, and (iii) both ant and hemipteran exclusion in a crossed design. The significance of this difference in methodology is discussed in the text.

^c Quantified as leaf damage, except where noted.

^d Stern., suborder Sternorrhyncha; Auchen., suborder Auchenorrhyncha.

^e Statistical analyses not provided.

^f *Aphis craccivora*, *Acyrtosiphon pisum* and *Megoura crassicauda*.

^g *Camponotus blandus*, *C. crassus*, *C. ruffipes*, *C. sp.* (Formicidae); *Crematogaster* sp., *Pheidole* sp. (Myrmicinae); *Ectatoma quadridens* (Ponerinae); two *Pseudomyrmex* spp. (Pseudomyrmecinae); and an unknown species of Dolichoderinae.

^h *Camponotus crassus*, *C. renggeri*, *C. ruffipes* (Formicidae); *Cephalotes pusillus* (Myrmicinae); and *Ectatomma edentatum* (Ponerinae).

effects of ant-hemipteran interactions on plants by either (i) comparing plants on which honeydew-producing hemipterans and/or tending ants were naturally present or absent (correlative studies) or (ii) comparing plants on which the presence/absence of honeydew-producing hemipterans and/or tending ants was manipulated (experimental studies). We did not include in our review any studies (of which there are many) that provided only an anecdotal evidence of the effects of ant-hemipteran interactions on plants, or any studies that were not designed with a meaningful control treatment (e.g. Room 1972; Bach 1991; Fernandes *et al.* 2005) or that did not demonstrate a positive correlation between hemipteran density and ant density on plants (e.g. Way *et al.* 1999; Perry *et al.* 2004).

We think it is important to note that out of the 30 studies reviewed here, 21 studies (70%) utilized either ant-exclusion manipulations ($n=19$ studies) or natural variation in the presence and absence of ants on plants ($n=2$ studies; table 1). A major limitation of manipulative and natural experiments of this type is that they do not specifically test the effect of the interaction *per se* between ants and hemipterans on plants (i.e. whether ants have stronger effects as predators in the presence of honeydew-producing hemipterans). Ants forage for arthropod prey on many plants even in the absence of honeydew-producing hemipterans (Hölldobler & Wilson 1990). For example, wood ant (*F. rufa*) foraging activity has been recorded on sycamore trees (*Acer pseudoplatanus*) prior to colonization of the trees by the honeydew-producing aphid *Periphyllus testudinaceus* (Skinner 1980). Similarly, wood ant predation of leafhoppers (Cicadellidae) and a non-honeydew-producing aphid species on sycamore trees has occurred at times when wood ants did not actively tend *P. testudinaceus* (Whittaker 1991). The interpretation of results from the studies that purport to demonstrate the beneficial effects of the interactions between wood ants and honeydew-producing hemipterans on the trees (table 1), therefore, is somewhat compromised. Indeed, in any system in which ants forage on plants in the absence of honeydew-producing hemipterans, studies relying on the presence/absence of ants to investigate the effects of ant-hemipteran interactions on plants cannot rigorously distinguish whether ant predation is independent of or truly facilitated by honeydew-producing hemipterans.

In contrast, seven studies (23%) reviewed in table 1 either manipulated the density of honeydew-producing hemipterans (hemipterans excluded from plants or added to plants where there were none previously; $n=2$ studies) or utilized natural variation in the presence and absence of honeydew-producing hemipterans on plants ($n=5$ studies). These types of manipulative and natural experiments probably provide more realistic tests of the effects of ant-hemipteran interactions on plants, because ant behaviour changes in response to the presence of honeydew-producing hemipterans rather than vice versa (see Floate & Whitham 1994). Better still are the experiments that manipulate both ants and honeydew-producing hemipterans in a crossed design, because they allow a comparison of the effects of the ants alone and the hemipterans alone with the effects of the ant-hemipteran interaction specifically. Only two studies (7%) have utilized a crossed design (table 1). Thus, even though 30 studies are included in this section of the review, only four

experimental studies rigorously tested for the effects of ant–hemipteran interactions on plants.

(a) *Net negative effects*

Despite the abundant evidence that tending ants can cause outbreaks of honeydew-producing hemipterans (Beattie 1985; Buckley 1987; Holway *et al.* 2002) and that honeydew-producing hemipterans can impose tremendous costs on plant fitness via consumption of plant sap and transmission of plant pathogens (Carter 1962; Buckley 1987; Delabie 2001), negative effects of mutualistic interactions between ants and hemipterans on plant fitness have rarely been demonstrated ($n=9$ studies; table 1). Whether negative effects of ant–hemipteran interactions are truly uncommon in nature or whether they have simply been assumed and, thus, not quantified remains unclear. Banks & Macaulay (1967) reported that the aphid *Aphis fabae* was 30–50% more abundant on the faba bean (*Vicia faba*) when tended by the ant *Lasius niger*, resulting in significantly fewer pods and seeds per plant relative to plants with *A. fabae* not tended by ants. Similarly, in a study of the effects of an ant–aphid mutualism on the fitness of the forb *Bidens pilosa*, Renault *et al.* (2005) reported that the aphid *Aphis coreopsidis* was 34% more abundant in the presence of tending *Camponotus* ants than in their absence. Consequently, plants hosting ant-tended aphids produced significantly fewer viable seeds than did plants from which ants were excluded. In the only study that documented the effect of an ant–hemipteran mutualism on the transmission of a plant pathogen, the presence of *S. invicta* caused a 240% increase in aphid abundance on tomato (*Lycopersicon esculentum*), resulting in a significant increase in the level of infection of plants by the aphid-vectoring *Cucumber mosaic virus* (Cooper 2005).

(b) *Net positive effects*

Studies documenting net positive effects of ant–hemipteran interactions on plants are more numerous ($n=22$; table 1). In these studies, ant–hemipteran interactions benefited plants as a consequence of increased ant predation or harassment of other, more damaging, insects, resulting in decreased plant damage by those insects and/or increased plant fitness. However, the majority of these studies ($n=14$, 64%) used ant-exclusion manipulations to test for the effects of ant–hemipteran interactions on plants, an experimental design that hinders distinction between the effects of ant–hemipteran interaction specifically versus the effects of the ants alone (see above). For example, Skinner & Whittaker (1981) showed that leaf damage by lepidopteran larvae was significantly reduced on sycamore trees on which wood ants (*F. rufa*) tended the aphid *P. testudinaceus* compared with trees from which wood ants were experimentally excluded. In later ant-exclusion experiments in the same system, Whittaker & Warrington (1985) showed that the radial growth of sycamore trees was two to three times greater in the presence of the ant–aphid interaction, presumably as a consequence of herbivore suppression by the aphid-tending ants.

Other studies ($n=5$) utilized natural variation in the presence and absence of honeydew-producing hemipterans to test for the effects of ant–hemipteran interactions on plant fitness. Treehopper-tending ants (*Formica* spp.) on

Solidago altissima, for example, deterred feeding by the larvae of two species of leaf beetle (Messina 1981). Increased plant protection by ants in the presence of treehoppers resulted in increased plant growth and seed production relative to neighbouring plants on which treehoppers were naturally absent. Only two studies experimentally tested for the effects of ant–hemipteran interactions on plant fitness by manipulating the hemipteran densities. For example, Floate & Whitham (1994) manipulated the aphid densities to test whether a facultative mutualism between the aphid *C. populicola* and a *Formica* ant species indirectly protected cottonwood (*Populus fremontii* and hybrids) foliage from beetle herbivory. The addition of aphids to trees dramatically increased ant abundance, which translated into a 95% reduction in the abundance of beetle larvae and significantly less beetle damage to leaves.

We think it noteworthy that five of the studies that documented a net positive effect were conducted in managed systems (table 1), demonstrating that ant–hemipteran interactions may be exploited for biological control of more damaging pests on agriculturally important plants. In fact, arboreal ants attracted to hemipteran honeydew have long been utilized to control non-honeydew-producing herbivore pests in several tree crops (Way & Khoo 1992). For example, growers manipulate colonies of *Dolichoderus* ants in cocoa (*Theobroma cacao*) and sapodilla (*Manilkara zapota*) plantations in Southeast Asia, because the mealy bug-tending ants protect cocoa pods and sapodilla fruits from damage by mirids (Heteroptera; Khoo & Ho 1992) and pyralid larvae (Lepidoptera; Van Mele & Cuc 2001) without any direct yield loss caused by the mealy bugs. However, far less is known about the net effects of ant–hemipteran interactions on herbaceous crop plants in more ephemeral systems, such as row and vegetable crops. Protection by tending ants can lead to hemipteran outbreaks in agricultural monocultures of herbaceous plants, resulting in a significantly reduced yield caused by phloem loss (e.g. Banks & Macaulay 1967) and transmission of plant pathogens (e.g. Cooper 2005). If the honeydew-producing hemipterans do not vector plant pathogens to particular crop plants, and if those plants show a high tolerance to hemipteran herbivory, the ant–hemipteran interactions may still benefit plant yield. For example, in cotton, we have shown experimentally that *A. gossypii* attract ground-foraging *S. invicta* onto plants, resulting in increased ant predation of an important cotton herbivore, the beet armyworm caterpillar (*Spodoptera exigua*). Cotton plants hosting the ant–aphid interaction suffered less caterpillar damage to leaves and bolls (cotton fruit) and, consequently, produced significantly more bolls and seedcotton relative to plants from which *A. gossypii* were excluded (Styrsky 2006; Styrsky & Eubanks in preparation). We encourage additional studies of the effects of ant–hemipteran mutualisms on other annual cropping systems to further evaluate their utility for increased biological control of non-honeydew-producing herbivores (Eubanks & Styrsky in press).

(c) *Search for general patterns*

We summarized the effects of ant–hemipteran interactions on plants in each study by calculating the per cent change in plant damage and/or plant fitness associated with the

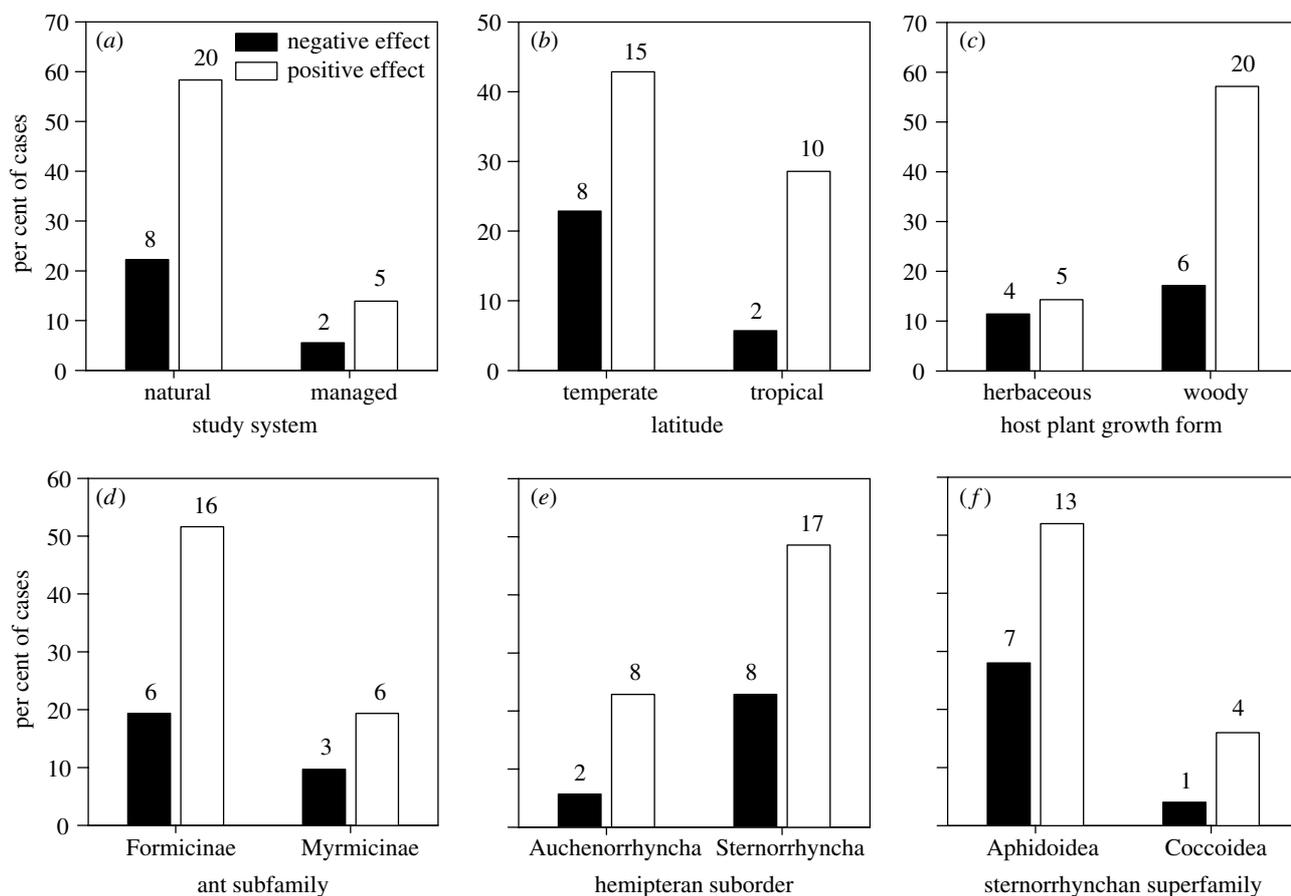


Figure 2. Percentage of studies that documented positive effects versus negative effects of ant–hemipteran interactions on plant fitness relative to (a) study system (natural or managed), (b) latitude (temperate or tropical), (c) host plant growth form (herbaceous or woody), (d) ant subfamily (Formicinae or Myrmicinae), (e) hemipteran suborder (Auchenorrhyncha or Sternorrhyncha) and (f) Sternorrhynchan superfamily (Aphidoidea or Coccoidea). Numbers above columns indicate the total number of studies in each category. See text for further details.

presence of the interactions relative to their absence (table 1). The effects ranged along a continuum from strong negative effects to strong positive effects. Plant damage was most often quantified as leaf damage by non-honeydew-producing herbivores. Plant fitness was quantified using a wide variety of traits that were related to both plant growth and reproduction, thus precluding the calculation of any representative average value. The ant–hemipteran interactions were studied on plants in 18 plant families in both natural and managed systems in temperate and tropical habitats and involved ant species in six subfamilies and honeydew-producing hemipterans in two suborders (Sternorrhyncha and Auchenorrhyncha) and in two superfamilies within the Sternorrhyncha (Aphidoidea and Coccoidea). Given this variety in study systems, we attempted to discern the general patterns in the effects of ant–hemipteran interactions on plants based on several ecological factors. Specifically, we asked whether the frequency of negative and positive effects varied between natural and managed systems, temperate and tropical habitats, woody and herbaceous plants, ant subfamilies, hemipteran suborders, and aphids and scales/mealy bugs. We also asked whether the frequency of negative and positive effects varied between correlative and experimental studies.

Study systems using agricultural host plants were categorized as ‘managed’ systems, whereas those using non-agricultural host plants in either natural or disturbed

habitats (e.g. cattle pastures, second-growth woodlands) were categorized as ‘natural’ systems. Habitats were categorized as ‘temperate’ or ‘tropical’ based on the latitude of the study sites with respect to the tropics of Cancer and Capricorn. The frequency of negative and positive effects of ant–hemipteran interactions on plants neither varied between natural and managed systems (Fisher’s exact test: $p=1.0$; figure 2a) nor between temperate and tropical habitats ($p=0.43$; figure 2b). Ant–hemipteran interactions tended to benefit woody host plants more frequently than harming them, relative to herbaceous host plants (figure 2c). However, statistically, the frequency of negative and positive effects did not vary between woody and herbaceous plants ($p=0.39$).

Although ant species from six subfamilies participated in the ant–hemipteran interactions reviewed here, the majority (89%) were from Formicinae and Myrmicinae. These two ant subfamilies, along with Dolichoderinae, are characterized by a majority of species that tend honeydew-producing hemipterans (Hölldobler & Wilson 1990). Ant–hemipteran interactions involving formicine ants were equally as likely to benefit plants as were interactions involving myrmicine ants ($p=1.0$; figure 2d). Likewise, the frequency of negative and positive effects did not vary between hemipteran suborders Sternorrhyncha (aphids, scales and mealy bugs) and Auchenorrhyncha (treehoppers and planthoppers; $p=0.69$; figure 2e) or between Sternorrhynchan superfamilies Aphidoidea (aphids) and

Coccoidea (scales and mealy bugs; $p=1.0$; figure 2f). Finally, the frequency of negative and positive effects of ant–hemipteran interactions on plants did not vary between correlative (22% negative and 78% positive) and experimental (31% negative and 69% positive) study designs ($p=1.0$).

The lack of association between the frequency of negative and positive effects of ant–hemipteran interactions on plants and the ecological variables tested above should be treated with caution. The limited amount of published data probably compromised the power of our analyses, further emphasizing the need for additional studies of the effects of ant–hemipteran interactions on plant fitness. More importantly, despite broad diversity in the geographical locations, habitats, and plant, ant and hemipteran species studied, the ant–hemipteran interactions had strong effects on plants in most studies, suggesting that ant–hemipteran interactions are important components of ecological communities.

5. CONDITIONALITY IN THE EFFECTS OF ANT–HEMIPTERAN MUTUALISMS ON PLANTS

Conditionality in the outcome of mutualistic interactions between both ants and hemipterans and ants and plants has widely been noted (Buckley 1987; Cushman & Addicott 1991; Bronstein 1994b). Since the net effects of ant–hemipteran interactions on plants represent a trade-off between the direct cost of feeding by hemipterans and the indirect benefit of ant suppression of other (non-honeydew-producing) herbivores, any biotic or abiotic factor that influences the magnitude of the cost or benefit may alter the consequence of the interaction on the plant (Lach 2003). Such conditionality has been often suggested but rarely tested. Factors that could mediate the effects of ant–hemipteran interactions on plant fitness include: (i) the proximity of ant colonies to host plants (because distance may affect the numerical response of ants to honeydew-producing hemipterans; Karhu 1998; Wimp & Whitham 2001), (ii) the strength and persistence of the interactions between particular ant species and honeydew-producing hemipterans (Buckley 1987; Del-Claro & Oliveira 2000), (iii) the proximity and abundance of other plants hosting honeydew-producing hemipterans that may distract tending ants (Cushman & Whitham 1991), (iv) the abundance and efficacy of other arthropod predators, and the effects of tending ants on those predators (Fritz 1983), (v) the abundance and relative cost to plant fitness of insects in other herbivore guilds (Messina 1981; Fritz 1983; Styrsky 2006), (vi) the indirect interactions between honeydew-producing and non-honeydew-producing insect herbivores mediated by host plants (Stout *et al.* 1998; Rodriguez-Saona *et al.* 2005), (vii) the host plant tolerance of and resistance to other (non-honeydew-producing) herbivores (Sipura 2002; see also Vrieling *et al.* 1991), (viii) the variation in plant vulnerability to hemipteran and non-hemipteran herbivory associated with plant phenology (Rosenheim *et al.* 1997), (ix) the availability and quality of plant extrafloral nectar (Buckley 1983), (x) the effects of plant genotype on plant quality (Floate & Whitham 1994), and (xi) the effects of other biotic (e.g. pathogen infection) and abiotic factors (e.g. nitrogen availability, shade) on host plant quality (Cushman 1991).

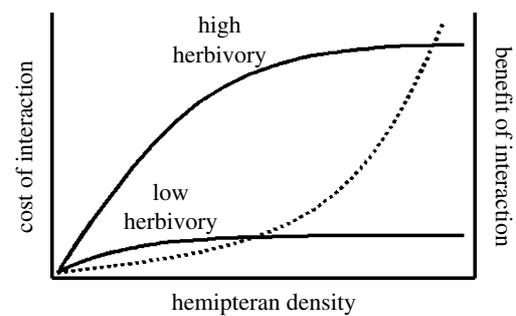


Figure 3. Conditionality in the consequences of a mutualistic interaction between ants and honeydew-producing hemipterans on a host plant based on the intensity of herbivory by other herbivores (including hemipteran insects that do not feed from plant phloem or produce honeydew). The cost of the interaction to the plant (in terms of loss of caused by honeydew-producing hemipteran damage to plants) is shown as the dotted curve and increases with an increasing density of honeydew-producing hemipterans. The benefit of the ant–hemipteran interaction to the plant (in terms of increased plant fitness caused by ant suppression of plant damage by other herbivores) is shown as the two solid curves. At a high level of herbivory by non-tended herbivores, the benefit of the ant–hemipteran interaction to the plant is predicted to outweigh the cost at all but extremely high levels of honeydew-producing hemipteran density. However, at a low level of herbivory by non-tended herbivores, the mutualism either provides only a slight fitness benefit (at lower hemipteran densities) or results in a net loss of fitness (at higher hemipteran densities).

As suggested by Messina (1981) and Fritz (1983), the consequences of an ant–hemipteran interaction on a particular host plant may vary simply with the intensity of herbivory by other (non-honeydew-producing) herbivores (figure 3). We tested this hypothesis in an experiment in which we manipulated the presence and absence of the aphid *A. gossypii* and the densities of *S. exigua* caterpillars (low and high) on cotton plants in a field that was naturally infested by the invasive ant, *S. invicta*. As described earlier, *S. invicta* workers were more abundant on plants with *A. gossypii*, resulting in increased predation of caterpillars. The fitness benefit of reduced caterpillar damage to plants varied with caterpillar density, however, such that plant protection by the aphid-tending *S. invicta* resulted in a 32% increase in bolls (relative to plants without aphids) at high caterpillar density versus just a 3% increase in bolls at low caterpillar density (Styrsky 2006; Styrsky & Eubanks in preparation). Thus, the indirect benefit of ant suppression of caterpillars substantially outweighed the direct cost of *A. gossypii* only when caterpillars were abundant.

Only one other study has investigated the conditionality in the ecological consequences of ant–hemipteran interactions on plants. Sipura (2002) manipulated the presence and absence of the ant, *Formica aquilonia*, on shoots of two willow species with and without aggregations of the aphid, *Pterocomma salicis*, to test the effect of the ant–aphid mutualism on willow herbivory and growth. The two willow species differed in the salicylate concentration in the foliage, a trait that confers resistance to leaf-chewing herbivores. Leaf damage was significantly reduced and shoot length and radial growth were significantly enhanced in the

presence of the mutualism only in the willow species with a low concentration of salicylate (*Salix phylicifolia*) and, thus, low resistance to herbivores. In contrast, the ant–aphid interaction had a negligible effect on the growth in the willow species with high resistance (*Salix myrsinifolia*), suggesting neither an indirect benefit to the plant of ant predation of other herbivores nor a direct cost of aphid herbivory.

6. ECOLOGICAL CONSEQUENCES OF ANT–HEMIPTERAN INTERACTIONS INVOLVING NATIVE ANTS VERSUS INVASIVE ANTS

The degree of protection provided by tending ants to honeydew-producing hemipterans varies among native ant species, primarily owing to the differences among species in aggressiveness and territoriality (Bristow 1984; Buckley & Gullan 1991; Kaneko 2003; Novgorodova 2005). Given that more aggressive ant species with more strongly defended territories provide greater protection to honeydew-producing hemipterans, these ant species may be expected to have stronger direct and indirect effects on community structure and host plant fitness. We are unaware of any studies that have compared the effects of ant–hemipteran interactions involving different native ant species on arthropod community structure, but a few studies suggest that more aggressive ant species have stronger indirect effects on plants. For example, Sipura (2002) compared the effects of the interactions between aphids and two native ant species on the herbivory and growth of two willow species and found that only the more aggressive ant species had measurable effects on plant growth.

Invasive ants, that subset of unintentionally introduced ant species which establish populations in natural (undisturbed by human activity) areas, are particularly notorious for their extreme abundance and aggressiveness, two traits at least partly responsible for their pervasive negative ecological effects in invaded habitats (Holway *et al.* 2002). Invasive ants are also very attracted to hemipteran honeydew and rapidly recruit in large numbers to hemipteran aggregations from which they may exclude the native tending ants (Holway *et al.* 2002; Lach 2003; Ness & Bronstein 2004). Indeed, exploitation of hemipteran honeydew and plant extrafloral nectar is hypothesized to contribute to the ecological dominance of invasive ants (Holway *et al.* 2002). Although invasive ants can cause local declines in arthropod abundance and diversity (Holway *et al.* 2002), only one study has investigated the direct and indirect effects of ant–hemipteran interactions involving invasive ant species on interspecific interactions within arthropod food webs (Kaplan & Eubanks 2005; see §3).

Additionally, few data exist which evaluate the consequences of ant–hemipteran interactions involving invasive ants on plants (table 1). Invasive ants are exceptional tenders and frequently cause local hemipteran outbreaks (Holway *et al.* 2002; Ness & Bronstein 2004). However, owing to their abundance, aggression and territoriality, invasive ants may provide comparatively greater protection to plants from other herbivores than do native ants (Holway *et al.* 2002; Lach 2003; but see Rapp & Salum 1995). For example, Way *et al.* (1999) observed that defoliation of the pine *Pinus pinaster* by the

larvae of the pine processionary moth (*Thaumetopoea pityocampa*) was slight to negligible in trees patrolled by the invasive Argentine ant (*Linepithema humile*), but was moderate to severe in trees patrolled by several native ant species. The authors suggested that aggregations of honeydew-producing aphids facilitated protection of pines by *L. humile*, but they did not specifically test whether ant predation was actually greater in the presence of aphids than in their absence. Facultative mutualisms between the invasive ant *S. invicta* and aphids in tomato can harm plants by increasing the severity of infection by a plant virus (Cooper 2005), but can benefit plant reproduction in cotton by increasing ant suppression of more damaging herbivores (Styrsky 2006; Styrsky & Eubanks in preparation). Whether the effects of *S. invicta* in these systems differ from those by native aphid-tending ants is unknown.

7. WHY SO LITTLE INFORMATION ON SUCH UBIQUITOUS AND POTENTIALLY IMPORTANT INTERACTIONS?

Despite their ubiquity in terrestrial communities, mutualistic interactions between ants and honeydew-producing hemipterans have received relatively little attention in terms of their effects on food web dynamics and tritrophic interactions involving their host plants. This dearth of information regarding the ecological consequences of ant–hemipteran interactions potentially represents a major void in our understanding of the dynamics of complex trophic interactions in arthropod communities. Our review of the literature shows that ant–hemipteran interactions can broadly affect the local abundance and distribution of specialist and generalist predators and parasitoids, as well as herbivores in several feeding guilds. In addition, though some evidence shows that ant–hemipteran interactions result in a net decrease in the fitness of their host plants, a majority of studies document an indirect positive effect in which hemipteran-tending ants protect host plants from other, more damaging, herbivores. Since the broad ecological effects of hemipteran-tending ants as predators are precipitated by their interaction with hemipterans (i.e. ant effects would not be as strong in the absence of honeydew-producing hemipterans), ant–hemipteran interactions may represent ‘keystone interactions’ in many communities.

Why, then, have the ecological consequences of ant–hemipteran mutualisms been so little studied? We suggest that in many systems, the effects of mutualistic interactions between ants and honeydew-producing hemipterans, either positive or negative, are often assumed without ever being quantified. A mutualistic interaction between the invasive ant *Pheidole megacephala* and the grey pineapple mealy bug (*Dysmicoccus neobrevipes*), for instance, is thought to severely damage pineapple trees in Hawaii, because the mealy bug vectors a devastating phytopathogen (Beardsley *et al.* 1982). Whether the interaction *per se* actually reduces plant fitness (i.e. whether ant-tending exacerbates the negative effects of the mealy bugs), however, has not been tested. Similarly, Way *et al.* (1999) surmise that the protection of pine trees by the ant *L. humile* is partly a consequence of ant attendance on aphids, but they never specifically test this hypothesis. In observational studies such as these (of

which there are many), the assumed consequences of the ant–hemipteran interactions may very well be real, but the lack of empirical data precludes any definitive conclusions or generalizations.

We also argue that the ecological effects of ants and their interactions with other arthropods are simply ignored. Ants may be noted as abundant predators, particularly in annual agricultural systems, but the consequences of their interactions with other arthropods are often not quantified. Several ant species, for example, tend the recently introduced aphid *Aphis glycines* in soybean (*Glycine max*) in North America (Ragsdale *et al.* 2004; Styrsky & Eubanks in preparation), but no effort has been made to determine the consequences of these interactions to the abundance and distribution of other natural enemies and herbivores, or to soybean yield. The ecological consequences of ant–hemipteran interactions are also often dismissed, because they are assumed to be too local or too ephemeral to affect community structure or plant fitness. However, Wimp & Whitham (2001) showed that the local effects of an ant–aphid interaction on the abundance and distribution of arthropods on individual trees also influenced arthropod abundance and diversity throughout the surrounding plant community. Further, populations of some honeydew-producing hemipteran taxa (e.g. aphids) may indeed be ephemeral, but even short-term ant–hemipteran associations can have dramatic community-level consequences, as demonstrated by Floate & Whitham (1994) and Kaplan & Eubanks (2005; see §3). Ephemeral ant–hemipteran interactions may even induce long-term changes in host plant quality that affect other herbivores and their interactions with natural enemies later in the season (cf. Van Zandt & Agrawal 2004).

8. CONCLUSIONS

Whether because they are assumed, ignored, dismissed or simply overlooked, the ecological consequences of ant–hemipteran interactions and their importance in arthropod communities remain poorly understood. Interactions between ants and honeydew-producing hemipterans are abundant and widespread in arthropod food webs and have potentially broad ecological effects, because the presence of honeydew-producing hemipterans dramatically alters the abundance and predatory behaviour of ants on plants. Future studies should focus on the ecological factors that influence the consequences of ant–hemipteran interactions to provide greater insight into the role of positive species interactions in food web dynamics and greater predictability of the direct and indirect effects of herbivores and natural enemies on host plants. Such predictability could substantially benefit biological control in agricultural systems with ants and honeydew-producing hemipterans. Finally, we encourage a more concerted effort to study the consequences of ant–hemipteran interactions involving invasive ants on arthropod communities and host plants and to make comparisons with native ants. Invasive ants have the potential to wreak ecological havoc in invaded habitats; thus, understanding the consequences of their interactions with honeydew-producing hemipterans could help predict and even manage their effects.

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