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The Evolution and Ecology of Interactions Between Ants and Honeydew-Producing Hemipteran Insects

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Abstract

The interactions between ants and certain sap-feeding insects in the order Hemiptera are classic examples of food-for-protection mutualisms. In these associations, herbivorous hemipterans use a highly specialized, straw-like mouthpart to consume sap directly from plant phloem and xylem and, as a result, excrete a sugar-rich waste product called honeydew. Ant foragers in turn use specialized adaptations to collect and share honeydew with nestmates and, in exchange, protect hemipterans against predators. The two key innovations underlying this interaction—hemipteran sap feeding and ant harvesting of honeydew—have driven the evolutionary success and ecological dominance of ants. These interactions also carry unique costs and benefits for each partner and are highly context dependent. Understanding the factors mediating this mutualism is critical, as these interactions have broader ecological consequences for the natural and agricultural ecosystems in which they are embedded.

1. INTRODUCTION

The associations between ants (Hymenoptera: Formicidae) and herbivorous sap-feeding insects in the order Hemiptera are canonical examples of mutualisms. In these interactions, shown in **Figure 1**, hemipterans reward ants with food in exchange for protection against predators and parasitoids. Herbivorous hemipterans are unique among insects for their ability to access sap in plant phloem and xylem elements, a feeding mode made possible by their highly specialized, straw-like mouthpart. As a result of this diet, all herbivorous hemipterans excrete a liquid waste, commonly called honeydew, that is rich in plant-derived simple sugars, amino acids, proteins, and other compounds (e.g., plant-derived secondary metabolites) (Buckley 1987, Way 1963). Hemipteran taxa that are ant tended further fortify honeydew with complex sugars that are attractive to ants (Detrain et al. 2010) and retain honeydew on their abdomens in small droplets to facilitate its collection (Banks & Nixon 1958, Del-Claro & Oliveira 1993). For ants, honeydew is a reliable and abundant carbohydrate resource (Davidson et al. 2003) that has been shown to increase ant colony growth (Helms & Vinson 2008, Wilder et al. 2011a), and in exchange for honeydew, ants tend hemipterans, protecting them against predators and providing the sanitary service of waste removal (Nielsen et al. 2010). Hemipteran tending occurs within a subset of ants with anatomical and behavioral adaptations that allow them to collect and share liquid resources with nestmates (Oliver et al. 2008), and honeydew feeding has played an important role in facilitating the diversification and ecological dominance of these ants. For hemipterans, ant protection increases fitness, although the production of ant-attractive honeydew carries energetic costs. As a result, association with ants is rare, except in a few hemipteran families, and there is little evidence ants have facilitated hemipteran ecological or evolutionary dominance. These food-for-protection mutualisms are common within many ecosystems and involve networks of dozens or even hundreds of species of hemipterans and ants (Blüthgen & Fiedler 2004a). Because of the tremendous ecological dominance of ants in most terrestrial ecosystems, ant–hemipteran mutualisms are potential keystone interactions, with evolutionary and ecological effects on ants that have broad consequences for the ecosystems in which the interactions are embedded (Styrsky & Eubanks 2007).

Previous reviews addressing ant–hemipteran interactions have focused on the hemipteran perspective, with a strong emphasis on one particular family, the Aphididae, or aphids (Buckley 1987, Stadler & Dixon 2005, Styrsky & Eubanks 2007, Way 1963; but see Delabie 2001, Stadler & Dixon 2008, Wood 1993). At the same time, reviews on ants have focused on the evolution and ecology



Figure 1

Examples of ant–hemipteran associations, representing the three hemipteran suborders: (*a*) Juvenile leaf-footed bug (hemipteran suborder Heteroptera, family Coreidae) tended by the ant *Dinomyrmex gigas* (ant subfamily Formicinae), (*b*) Treehopper nymphs (hemipteran suborder Auchenorrhyncha, family Membracidae) tended by the ant *Paratrechina longicornis* (ant subfamily Formicinae), and (*c*) Aphids (hemipteran suborder Sternhorryncha, family Aphididae) tended by the ant *Crematogaster laeviuscula* (ant subfamily Myrmicinae). Photo in panel *a* adapted with permission; copyright Chien C. Lee, **https://photos.chienclee.com/**; photos in panels *b* and *c* adapted with permission; copyright Dr. Alex Wild, **https://www.alexanderwild.com/**.

of feeding upon liquid resources derived from plants (Davidson et al. 2003, Meurville & LeBoeuf 2021, Nelsen et al. 2018), with relatively less attention given to the role of hemipteran honeydew (but see Grover et al. 2007, Wilder et al. 2011b). Fully understanding ant–hemipteran interactions requires a more comprehensive comparison across ant and hemipteran taxa. Here, we begin by tracing the deep evolutionary history of key innovations in hemipterans and ants that have made their interactions possible. Next, we examine the ecology of the interactions, including the benefits and costs to each partner and sources of context dependency. We then broaden the scope, discussing the consequences of these interactions for the ecosystems in which they are embedded. Finally, we outline some of the outstanding questions and promising directions for future research.

2. EVOLUTION OF THE INTERACTION

2.1. Hemipteran Evolution

Although 25% of hemipterans are predatory (Wiens et al. 2015), all ant-tended hemipterans are herbivorous. Herbivory evolved early on within the Hemiptera (Grimaldi & Engel 2005) and is key to associating with ants, as the production of honeydew depends on access to plant sap. Accordingly, understanding the evolutionary origins of this interaction (depicted in **Figure 2**) begins with understanding the origins of herbivory via hemipterans' unique, highly specialized mouthparts and digestive systems, shown in **Figure 3**. In the Devonian Period (420–360 Ma), the insect clade that includes the order Hemiptera—the superorder Paraneoptera (which also includes thrips, booklice, and lice)—arose from an ancestral condition of chewing mouthparts used for detrital and surface microbe feeding (Grimaldi & Engel 2005). Early in Paraneoptera evolution, these chewing mouthparts became simple, straw-like puncturing tubes for specialization on liquid diets. The order Hemiptera—first arising 315–307 Ma—evolved a unique, even more highly specialized mouthpart in which features of the mandibles were modified into slender tubes, or stylets, positioned within a protective sheath (**Figure 3**) (Yoshizawa & Lienhard 2016). Herbivores in the other orders within the Paraneoptera use their entire straw-like mouthpart to puncture host surfaces and feed on the contents of ruptured cells. In contrast, hemipterans navigate their slender stylets to phloem (or more rarely xylem) vessels, encasing their delicate mouthparts within a protective feeding track of salivary secretions to directly access sap while largely bypassing plant physical defenses (**Figure 3**). This mouthpart has been proposed to be the key innovation that enabled Hemiptera to expand into new feeding niches and become hyperdiverse (Grimaldi & Engel 2005). Today, Hemiptera consists of approximately 100,000 described species and 145 families, making it among the most diverse insect orders (Gullan & Cranston 2014).

The digestive system of hemipterans also evolved to accommodate a liquid diet. Because of the large volume of plant sap that must be digested to obtain limiting nutrients such as nitrogen, most herbivorous hemipterans produce liquid, carbohydrate-rich excreta, commonly referred to as honeydew, although there are some rare examples where the unwanted constituents of ingested sap are returned to the plant (Gullan & Kosztarab 1997). The hemipteran gut is modified into a filter in which the foregut and hindgut are closely opposed, allowing excess sugar and water to bypass the absorptive portion of the midgut (**Figure 3**), thus concentrating more limiting nutrients (Stadler & Dixon 2005).

Although herbivory was ancestral for Hemiptera, the order subsequently diversified into three major suborders, each with differing degrees of herbivory and interactions with ants (Gullan & Cranston 2014). The suborder Heteroptera (true bugs, including stink bugs and plant bugs; approximately 40,000 described species) (**Figure 1*a***) has the weakest association with ants. This suborder initially evolved away from herbivory into predatory habits, with multiple subsequent reversions to herbivory or omnivory (i.e., feeding on both plants and other insects) (Eubanks et al.

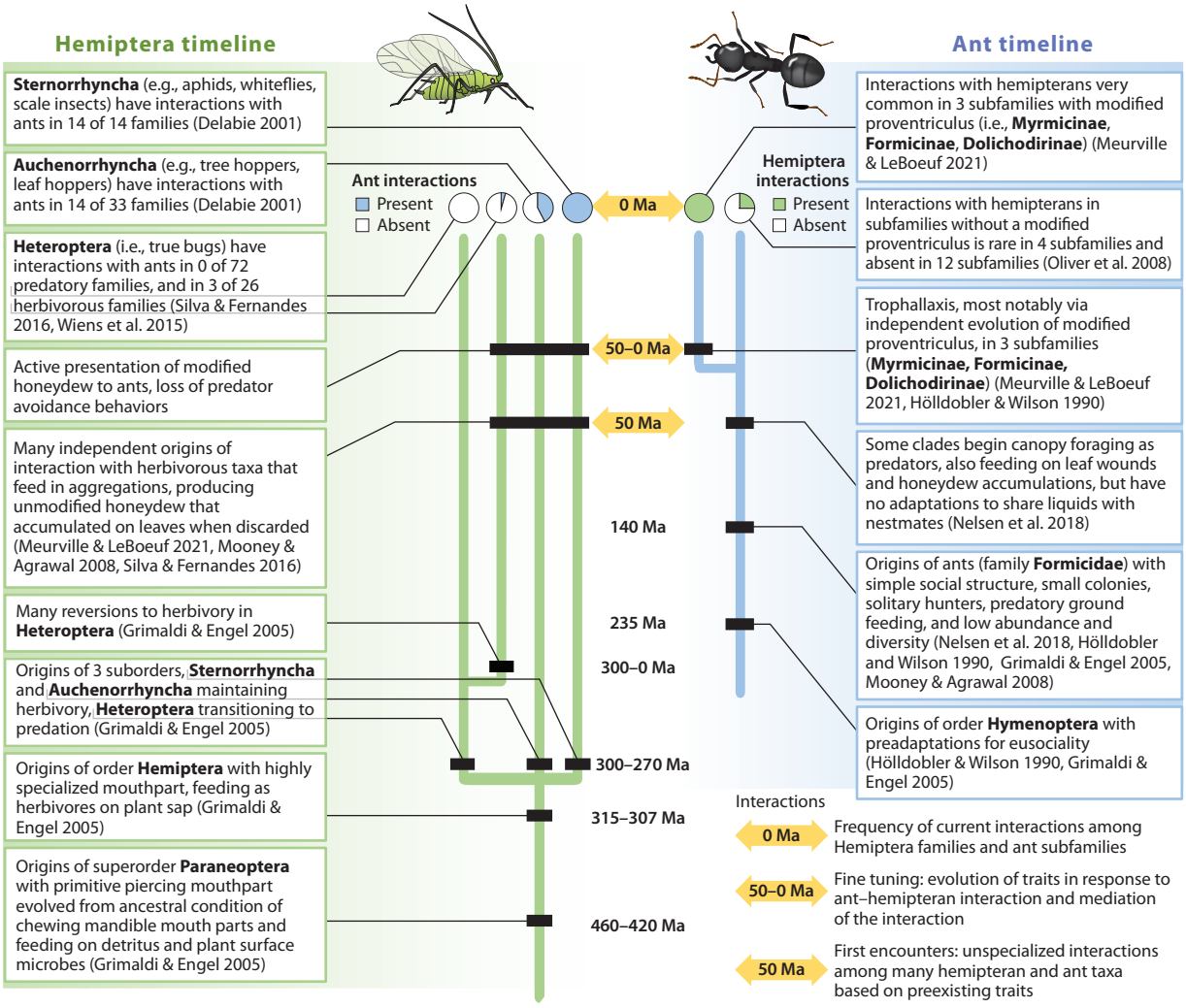

Figure 2

Evolutionary timeline of ant–hemipteran interactions. The left side (*vertical green bars*) indicates the approximate timing of origin of Hemiptera sub-orders (Sternorrhyncha, Auchenorrhyncha, Heteroptera) and traits relevant to interactions with ants, including specialized mouthparts, feeding mode (predation vs. herbivory), and the production and presentation of honeydew. The right side indicates the approximate timing of origin of the ant sub-families with the strongest interactions with Hemiptera (Myrmicinae, Formicinae, Dolichodirinae) and traits relevant to these interactions, including the modification of the proventriculus for trophallaxis. Timing of origin listed in center (millions of years before present) correspond to species traits (*horizontal black bars*) and interaction (*horizontal yellow arrows*). The top pie charts indicates the frequency of the contemporary interaction among hemipteran sub-orders and ant sub-families.

2003) (**Figure 2**) such that approximately one-third of extant Heteroptera are herbivorous (Wiens et al. 2015). Within extant heteropterans, ant tending is reported only for a handful of species in three of the 26 herbivorous families (**Figure 2**) (Silva & Fernandes 2016). In contrast, the suborders Auchenorrhyncha and Sternorrhyncha both maintained the ancestral condition of herbivory and have stronger associations with ants. The auchenorrhynchans (including cicadas, leafhoppers, planthoppers, treehoppers, and spittle bugs; approximately 44,000 described species) (**Figure 1*b***)

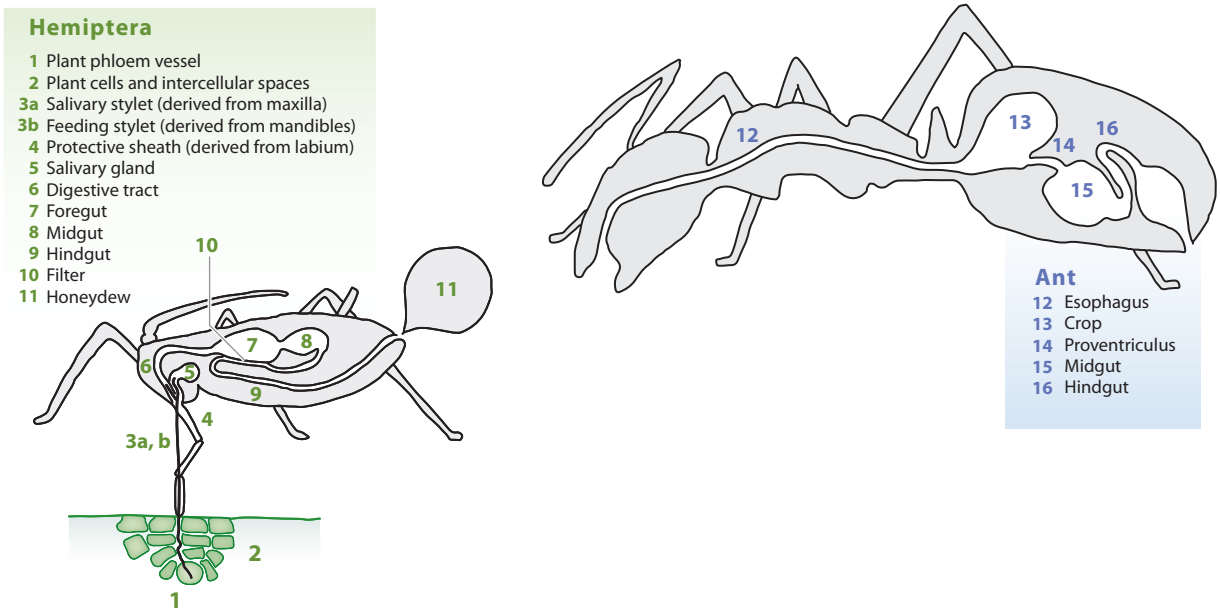

Figure 3

Diagram of key innovations underlying the ant–hemipteran interaction. The hemipteran diagram (*left*) shows the structure of the mouthpart relevant to sap-feeding and aspects of the digestive system relevant to honeydew production. The ant diagram (*right*) shows the structure of the digestive system relevant to trophallaxis.

associate with ants in 14 of 33 families, although only frequently in the treehoppers (Membracidae) and, to a lesser extent, leafhoppers (Cicadellidae) (Delabie 2001). The strongest association with ants is observed in the Sternorrhyncha (including aphids, jumping plant lice, scale insects, and whiteflies; approximately 16,000 described species) (**Figure 1*c***), with ant tending occurring in all 14 families, although only frequently in the aphids (Aphididae), soft scales (Coccidae), mealybugs (Pseudococcidae), and hard scales (Stictococcidae) (Delabie 2001). Collectively, of the 73 hemipteran families that are herbivorous, ant tending occurs in 31 families (42%) and is common only in 6 families (8%).

This infrequent but broad phylogenetic distribution of association with ants thus leads to the question of what traits within the herbivorous Hemiptera (listed in **Table 1**) are associated with ant tending. Most ant-tended species occur within hemipteran lineages that feed in aggregations and have sedentary lifestyles (Delabie 2001, Stadler & Dixon 2005, Wood 1993). In the Sternorrhyncha, these aggregations form due to rapid generation times, especially in taxa like aphids that reproduce asexually and have live births (Delabie 2001, Stadler & Dixon 2005). For treehoppers—one of the few families in the Auchenorrhyncha with strong ant associations—aggregations are due to sociality and maternal care (Cryan et al. 2004). The association between aggregative feeding and ant tending is likely due to density-dependent ant foraging, with larger aggregations recruiting more ants (Mailleux et al. 2003). Honeydew composition and presentation also have commonalities across ant-tended hemipteran taxa (**Table 1**). Ants prefer honeydew with higher concentrations of complex sugars, such as melezitose, sucrose, and raffinose (Detrain et al. 2010). Higher concentrations of the sugar melezitose have been observed in ant-tended taxa in the Sternorrhyncha, including aphids (Fischer & Shingleton 2001) and mealybugs (Zhou et al. 2015), as well as the Auchenorrhyncha, including treehoppers (Blüthgen & Fiedler 2004b). Presentation of honeydew

Table 1 Traits associated with ant–hemipteran interactions

Trait	Reference(s)
Hemipterans	
Herbivory with a piercing-sucking mouthpart for accessing plant sap	Grimaldi & Engel 2005
Honeydew production	Grimaldi & Engel 2005
Filter gut for processing diluted nutrients in sap	Delabie 2001
Large aggregations and sedentary lifestyle	Delabie 2001
Longer mouthparts and deeper feeding within plant tissues for faster feeding rate	Shingleton et al. 2005
Reduced investment in defense and predator avoidance, including maternal care	Henry et al. 2015, Stadler et al. 2003
Supplementation of honeydew with ant-attractive compounds	Blüthgen & Fiedler 2004a, Fischer & Shingleton 2001, Zhou et al. 2015
Reduced dispersal, including wing formation	Nelson & Mooney 2021, Xu et al. 2021
Feeding on woody plants and plants with extrafloral nectaries	Shingleton et al. 2005, Offenberg 2000
Ants	
Eusociality	Hölldobler & Wilson 1990
Foraging in plant canopies	Moreau et al. 2006, Nelsen et al. 2018
Traits promoting trophallaxis: modification of proventriculus, infrabuccal pocket, expandable gaster, dilation of esophagus, specialized liquid-storage castes	Meurville & LeBoeuf 2021
Large aggregations of foragers with small body and liquid load sizes as well as slow liquid uptake rates	Davidson et al. 2004, Oliver et al. 2008
Endosymbiotic gut microbes to facilitate feeding on liquid-sugar-based diets poor in nitrogen	Anderson et al. 2012, Davidson et al. 2003, Sanders et al. 2017, Russell et al. 2009
Positive correlation of mutualisms with hemipterans and ants but negative correlation with fungal mutualism.	Oliver et al. 2008
Superorganismicity, including the complete (versus facultative) loss of ability to reproduce in worker castes	Davidson et al. 2003, Meurville & LeBoeuf 2021
Ecological dominance	Davidson et al. 2003, Meurville & LeBoeuf 2021, Nelsen et al. 2018
Polygynous (multiple queen) colonies, invasiveness, disturbed habitats	Davidson et al. 2004, Oliver et al. 2008
Reduction in nomadism and polymorphism in foragers	Davidson et al. 2004, Oliver et al. 2008

also mediates interactions, as ant-tended hemipterans produce smaller droplets of honeydew that they hold on their abdomen for collection (Banks & Nixon 1958, Del-Claro & Oliveira 1993). Ant tending is also more weakly associated with several other characteristics. Ant tending is positively correlated with hemipterans feeding on woody plants (Stadler & Dixon 2005, Wood 1993) and plants with ant-attractive extrafloral nectaries (Offenberg 2000). Ant tending also occurs more frequently in habitats with greater ant activity, including at warmer temperatures associated with lower elevations and sunny meadows (see Section 5.4) (Mooney et al. 2016; Nelson et al. 2019a,b).

The hemipteran traits associated with ant tending might either represent preadaptations, i.e., existing traits that facilitated ant tending or, alternatively, may represent evolutionary convergence in response to the interaction. For most traits, answering this interesting question requires phylogenetic analysis of the distribution of these traits and ant tending across the Hemiptera. Nevertheless, we can speculate in a few instances. Aggregative feeding is likely a readaptation. Aggregative feeding is common throughout the Sternorrhyncha, suggesting this is an ancestral

trait of this suborder, whereas ant tending is rarer and appears to have evolved independently and secondarily many times. This dynamic could also explain the paucity of ant interactions in the Heteroptera, which typically feed individually or at low densities (Silva & Fernandes 2016). In contrast, the production of ant-attractive honeydew is likely a case of evolutionary convergence. While untended hemipteran species have been shown to produce melezitose at low concentrations (Fischer & Shingleton 2001), the production of honeydew with higher concentrations of these ant-attractive compounds carries fitness costs (see Section 3.1) (Nelson & Mooney 2021, Stadler & Dixon 1998) that hemipterans would presumably not bear in the absence of the corresponding rewards of ant attendance.

2.2. Ant Evolution

Ants (Hymenoptera: Formicidae) originated during the Cretaceous Period, approximately 140–160 Ma (**Figure 2**) (Hölldobler & Wilson 1990, Moreau et al. 2006) and today consist of more than 17,000 described species within 17 subfamilies (Parr & Bishop 2022). Before 50 Ma, ants were largely tropical and had low abundance and taxonomic diversity and small colony sizes. They had simple social traits with solitary foragers feeding as predators in the leaf litter (Wilson & Hölldobler 2005) and soil (Lucky et al. 2013). Coincident with angiosperm diversification 50 Ma, some ant lineages began foraging in plant canopies (**Table 1**) (Moreau et al. 2006, Nelsen et al. 2018). Hemipteran diversification into the major extant lineages thus predated the origin of ants (**Figure 2**), making initial interactions between ants and multiple hemipteran lineages determined by hemipteran preadaptations (see Section 2.1) (**Table 1**) (Bourgoin 1997, Meurville & LeBoeuf 2021, Nelsen et al. 2018). In initial encounters, hemipterans would have engaged in predator avoidance behaviors (e.g., fleeing by dropping from the plant), while ants would have collected discarded honeydew that accumulated on leaves beneath hemipterans and from leaf wounds, although not from extrafloral nectaries, which had yet to evolve (Nelsen et al. 2018, Staab et al. 2017). These interactions would have in turn selected for ants to reduce predation on hemipterans; reduced predation and indirect honeydew collection (i.e., honeydew fallen on leaves rather than on hemipterans themselves) has been observed for both heteropterans (Silva & Fernandes 2016) and untended aphid taxa (Mooney & Agrawal 2008), likely representing a first step in the evolution of more highly specialized food-for-protection mutualisms.

In these initial encounters, ants consumed liquid resources to fuel their otherwise predatory foraging bouts, but they lacked specialized adaptations for collecting and sharing liquid resources with nestmates (Meurville & LeBoeuf 2021). Ants collected and carried honeydew and other liquids externally in mandibles or on sponge-like tools (Davidson et al. 2004, Hölldobler & Wilson 1990). Access to liquid resources in the plant canopy then imposed selection on ants for trophallaxis, which is the collection and sharing of liquid resources with dependent, nonforaging nestmates, including developing larvae and queens (**Table 1**) (Meurville & LeBoeuf 2021, Nelsen et al. 2018). Today, two-fifths of extant ant subfamilies and genera contain species engaged in some degree of trophallaxis (Oliver et al. 2008). While all ants capable of trophallaxis appear to collect hemipteran honeydew, trophallactic ant species vary significantly in the resources devoted to tending, including forager number, the consistency of hemipteran attendance, and the aggression displayed against potential hemipteran predators (Novgorodova 2015).

The lineages with the greatest ability for liquid feeding consist of three subfamilies—Myrmicinae, Formicinae, and Dolichoderinae—that independently evolved trophallaxis through modifications to the proventriculus, the constriction between the ant crop and midgut (**Figure 3**, **Table 1**) (Meurville & LeBoeuf 2021, Oliver et al. 2008). These modified proventriculi segregate a communal food supply in the crop (sometimes called the social stomach) from the personal supply

in the midgut where digestion occurs (Davidson et al. 2004). Outside of these three subfamilies, the proventriculus can only briefly separate crop and midgut content, limiting liquid uptake rate, load size, and retention time (Eisner & Brown 1958). Additional anatomical modifications that facilitate trophallaxis include a cavity beneath the tongue that filters out and compacts solid material that would otherwise clog the narrow proventriculus channel, an expandable body and esophagus that allow for increased liquid food storage, and specialized ant castes that remain in the nest with the sole function of storing liquids for the colony (**Table 1**) (Meurville & LeBoeuf 2021). With the evolution of trophallaxis came a set of correlated traits presumed to be adaptive in mediating associations with hemipterans. For instance, large aggregations of foragers with small bodies and liquid load sizes as well as slow liquid uptake rates may allow ants to forage more efficiently from hemipterans that deliver honeydew slowly in small droplets. Additionally, hemipteran-tending ants are often polygynous (multiple queens in the same colony), invasive, able to thrive in disturbed habitats, and less likely to be nomadic or have polymorphic workers (**Table 1**) (Davidson et al. 2004, Oliver et al. 2008), although these characteristics do not serve clear purposes in the interaction.

Within ant genera or subfamilies, associating with hemipterans is correlated with participating in other mutualisms (**Table 1**). Among genera, there is a positive association between interacting with hemipterans and interacting with extrafloral-nectar-producing plants (Oliver et al. 2008), as both mutualisms rely on the consumption of liquid resources. In contrast, these trophallaxis-based mutualisms are negatively associated with ant–fungal farming mutualisms among genera, as they are not based on the consumption of liquid diets (Oliver et al. 2008). Interestingly, all three mutualisms are positively associated among subfamilies, suggesting that there are a set of common traits underlying these functionally disparate mutualisms.

Endosymbiotic microbes of ants may also play a role in facilitating the evolution of ant–hemipteran interactions. Evidence suggests that symbiotic gut bacteria of ants facilitated shifts from predatory lifestyles to feeding on honeydew and other liquid-sugar-based diets that are especially poor in nitrogen (Davidson et al. 2003). Liquid-feeding ant species harbor endosymbiont communities that are distinct from those of predatory species (Anderson et al. 2012, Sanders et al. 2017), and phylogenetic evidence suggests multiple independent evolutionary origins of ant–gut symbiont associations facilitated the convergent evolution of herbivory (i.e., the consumption of plant-derived liquids) in ants (Russell et al. 2009).

3. BENEFITS AND COSTS OF THE ASSOCIATION

3.1. Benefits and Costs to Hemipterans

Associating with ants provides a variety of benefits to hemipterans, listed in **Table 2**, which include increased fitness through accelerated development, as well as increased body size, fecundity, longevity, and survival (Flatt & Weisser 2000, Nelson & Mooney 2021). Among the most widely recognized benefits is the protection that ants provide against predators and parasitoids (Stadler & Dixon 2005), with hundreds of studies showing that for ant-tended hemipterans, survival and population growth are much higher in the presence of ants. Associating with ants is believed to also allow hemipterans to escape ant predation itself, as ants are major predators of arthropods in many terrestrial ecosystems (Camacho & Avilés 2021).

As a result of the protection provided by ants, hemipterans reduce their investment in defense and dispersal, both of which can be risky and carry energetic and fitness costs (Nelson & Mooney 2021). When hemipterans receive protection, they are less likely to need to quickly withdraw their mouthparts from the plant to escape predation and can instead feed more deeply and efficiently in the phloem (Shingleton et al. 2005). As a result, they can utilize additional host plants and

Table 2 Benefits, costs, and sources of context dependency associated with the interaction for hemipterans and ants

Effect	Description	Reference(s)
Hemipterans		
Ecological benefit	Protection against natural enemies	Hundreds of studies, reviewed in Stadler & Dixon 2005, Way 1963
	Escape from ant predation	Camacho & Avilés 2021
	Reduced investment in defense and dispersal	e.g., Henry et al. 2015, Stadler et al. 2003
	Expanded feeding niches	Shingleton et al. 2005, Stadler et al. 2003
	Sanitation	Nielsen et al. 2010
	Shelter	Reviewed in Delabie 2001
	Transportation	Collins & Leather 2002
	Reduced competition	Smith et al. 2008
	Reduced need for maternal care	Del-Claro & Oliveira 2000
Physiological benefit	Increased body size	Reviewed in Nelson & Mooney 2021
	Increased fecundity	Reviewed in Nelson & Mooney 2021
	Reduced development time[a]	Reviewed in Nelson & Mooney 2021
	Increased survivorship and growth	Rice & Eubanks 2013
Ecological cost	Threat of predation by ants	e.g., Oliver et al. 2012
	Increased apparency to specialized natural enemies	e.g., Völkl 1995
	Increased risk of dispersal	Morales 2002
	Reduced dispersal rates	Many studies, including Nelson & Mooney 2021, Xu et al. 2021
Physiological cost	Reduced feeding efficiency	Yao & Akimoto 2001
	Increased production of ant-attractant sugars in honeydew	Fischer & Shingleton 2001
	Reduced body size	Reviewed in Nelson & Mooney 2021
	Reduced fecundity	Reviewed in Nelson & Mooney 2021
	Slower development time	Reviewed in Nelson & Mooney 2021
Source of Context Dependency	Ant identity, traits, and perceived value of associating with hemipterans	e.g., Blüthgen & Fiedler 2004b, Mooney & Mandal 2010
	Natural enemy abundance, identity, and diversity	Many studies, including Nelson et al. 2019a, Snyder et al. 2006, Völkl 1997
	Host plant identity and quality	Many studies, including Abdala-Roberts et al. 2012, Mooney & Agrawal 2008, Pringle et al. 2014
	Microbial mediation of honeydew quality, hemipteran detectability, and ant diet	Hertaeg et al. 2021, Russell et al. 2009, Schillewaert et al. 2017
	Abiotic environment	Many studies, including Barton & Ives 2014; Mooney et al. 2016; Nelson et al. 2019a,b
Ants		
Ecological benefit	Access to honeydew as a carbohydrate resource	Davidson et al. 2003; reviewed in Stadler & Dixon 2005 and Way 1963
	Access to wax secretions as a lipid resource	Reviewed in Delabie 2001
	Access to hemipterans as prey	e.g., Offenberg 2001, Oliver et al. 2012, Wood 1993
	Range expansions (especially for invasive species)	e.g., Helms et al. 2011, Wilder et al. 2011b
	Increased ecological dominance	Plenty of indirect observational data, e.g., Blüthgen & Fiedler 2004a; first hypothesized by Davidson 1998

(*Continued*)

Table 2 (*Continued*)

Effect	Description	Reference(s)
Physiological benefit	Increased survival, growth, and activity	e.g., Brightwell & Silverman 2011, Helms et al. 2011
Ecological cost	Opportunity costs	Not previously quantified
	Energetic costs	Not previously quantified
	Mortality and other risks associated with foraging	Not previously quantified but indirect evidence for avoidance of risk, e.g., from Nonacs & Dill 1990
	Strong competition for access to honeydew	Many studies, including Blüthgen & Fiedler 2004a,b; Tanner 2008
	Potential for exploitation	Kudo et al. 2021, Salazar et al. 2015, Völkl et al. 1996
Physiological cost	None identified	n.a.
Sources of Context Dependency	None previously quantified from the ant perspective	n.a.

[a]For some factors, the mutualism has been shown to have both positive and negative effects (depending on context), and we therefore list them in both sections.
Abbreviation: n.a., not applicable.

feeding locations (e.g., woody plant parts) with deeper phloem elements (Shingleton et al. 2005). A comparison of 112 aphid species showed that ant tending is strongly associated with decreased mobility, decreased production of alates (winged aphids) for dispersal, and increased frequency of feeding on woody plant parts (Stadler et al. 2003). Recent work has demonstrated that two facultative microbial symbionts that defend aphids against natural enemies are also less likely to occur in ant-tended (versus untended) species, suggesting reduced investment in endosymbionts as another form of defense (Henry et al. 2015).

Ant tending additionally improves hemipteran sanitation and defense against pathogens (Nielsen et al. 2010). Honeydew accumulation presents a challenge for sessile aggregations of hemipterans, as it leads to fungal contamination, physical fouling, and predator attraction. Hemipterans that are not ant tended use a variety of methods to dispose of this waste, including flicking away honeydew droplets with leg or abdominal movements and producing hollow tubular ducts to conduct honeydew away (Cox & Pearce 1983). Ant collection of honeydew directly from feeding hemipterans provides an alternative solution to this key challenge (Buckley 1987) and dramatically increases hemipteran feeding rates (Banks & Nixon 1958, Del-Claro & Oliveira 1993), which in some cases results in increased growth and reproduction (Rice & Eubanks 2013) but can also carry costs (see later in this section).

Additional benefits of ant attendance include the construction of shelter (e.g., tents made of plant debris that protect against enemies or rain) (Delabie 2001), transportation to suitable feeding sites (Collins & Leather 2002), and reduced competition with other herbivores preyed upon by ants (Smith et al. 2008). Ants also take over maternal care from some treehoppers (Membracidae) and mealybugs (Pseudococcidae), improving their reproductive success by allowing females to leave their first brood to lay an additional clutch (Delabie 2001, Del-Claro & Oliveira 2000). In treehoppers, sociality and maternal care are positively associated with ant tending because adult-produced honeydew attracts ants that would otherwise not recruit to nymphs alone (Cryan et al. 2004). In fact, the primary benefit of maternal care can be ant attraction (Billick et al. 2001), and some treehopper lineages have evolved maternal care subsequent to ant attendance, presumably to strengthen it (Cryan et al. 2004). Nevertheless, some membracid lineages engaged in maternal

care prior to ant attendance, and it thus served as a preadaptation to associating with ants (see Section 2.1) (Cryan et al. 2004).

Associating with ants also carries multiple ecological costs (**Table 2**). Numerous studies have shown that the same ants that tend hemipterans prey upon them in some contexts (Offenberg 2001, Oliver et al. 2012, Sakata 1994). Some research suggests that ants simultaneously prey on and protect hemipterans in the same colony (Billick et al. 2007), and ants are more likely to attack hemipterans when their diets are more limited by protein relative to sugar, they have alternative sources of sugar, or hemipterans fail to provide them with honeydew (Offenberg 2001, Oliver et al. 2012, Sakata 1994). Beyond the threat of ant predation, ant attendance increases the apparency of hemipterans to specialized natural enemies (Völkl 1995). A dependency on ant attendance also increases the risk of dispersal, since the success of ant-tended hemipterans depends on not only finding a suitable host plant but also being near ants (Mooney & Agrawal 2008, Morales 2002). Perhaps due to these risks, many ant-tended hemipterans display reduced dispersal, although ants also suppress dispersal via the synthesis and application of hormone analogs (Nelson & Mooney 2021, Xu et al. 2021).

Associating with ants also imposes multiple direct physiological and fitness costs on hemipterans (**Table 2**). Ant attendance has been found to increase the production of ant-attractant sugars in honeydew that are costly to produce, such as the trisaccharide melezitose (by 156%) (Fischer & Shingleton 2001), which trades off with dispersal ability in aphids (Vantaux et al. 2015). Ant attendance also increases hemipteran feeding rates, and the stimulation of hemipterans with antennae induces them to produce smaller droplets of honeydew, to retain those droplets on their abdomen for collection, and to increase honeydew production fivefold (Banks & Nixon 1958, Del-Claro & Oliveira 1993). By allowing for increased feeding, ant attendance sometimes increases hemipteran colony growth (Rice & Eubanks 2013), but it can also reduce the efficiency of sugar digestion (Yao & Akimoto 2001). Likely as a result of reduced digestive efficiency, ant attendance in some cases reduces hemipteran body size and embryo number and size, while increasing age at fecundity (Stadler & Dixon 1998). However, a recent meta-analysis failed to find consistent evidence for such direct physiological costs of ant attendance on aphids, instead finding high variability (from negative to positive effects) across the nine studies evaluated, suggesting that such effects are highly context dependent (see Section 4) (Nelson & Mooney 2021).

While there is clear evidence that ants provide a variety of benefits and costs to individual hemipterans (Nelson & Mooney 2021), the net effects of ants on the fitness of hemipteran clonal genotypes remain unknown. Many hemipterans do not reproduce only sexually; individual genotypes also reproduce clonally, such that many individuals of the same genotype occur together in multiple clustered, physically distinct colonies (Moran 1992). As a result, the genotype, not the individual hemipteran, is the unit of selection, and the net genotype effects of associating with ants should depend on the degree to which ants alter the survival, growth, and dispersal of hemipteran colonies, as well as on the relative importance of each of these factors in determining genotype fitness. Existing evidence suggests that ant-associated reductions in hemipteran dispersal result in aphid species having lower genetic diversity and higher genetic differentiation among colonies, although the long-term consequences of such differences are not known (Ivens et al. 2012, Yao 2010).

There is no evidence that associating with ants has promoted the ecological dominance of hemipterans. The interaction is labile in Hemiptera (Shingleton & Stern 2003), but only a minority of the hemipteran families that are herbivorous (42%), and only a small subset of species within those families, are ant tended (see Section 2.1). For example, even in aphids (Aphididae), the family with the most frequent ant associations, only 40% of species are ant tended (Stadler & Dixon 2005). Tended and untended congener species coexist on the same host plants, suggesting

that mutualism with ants does not provide an inherent competitive advantage (e.g., Mooney & Tillberg 2005, Smith et al. 2008). Rather, it appears that predatory ants are fundamentally antagonists of hemipterans (see Section 2.2), and the association represents a specialized strategy to reduce predation by ants and other natural enemies. Nevertheless, by diversifying the possible strategies available to hemipterans for avoiding predation, ant attendance may promote the diversity of coexisting aphid species by providing alternative niches (Smith et al. 2008).

3.2. Benefits and Costs to Ants

From the ant perspective, the benefits and costs of associating with hemipterans (**Table 2**) have been largely unexplored, due to the difficulties of measuring ant colony fitness and demography in the field. In addition, because ants are highly mobile, it has been assumed they participate in the interaction by choice, based upon the benefits provided (Ness et al. 2010). The primary benefits that ants receive are presumably access to honeydew as a reliable and abundant carbohydrate resource (Davidson et al. 2003) and access to wax produced by some armored scales (Diaspididae), aphids (Aphididae), and mealybugs (Pseudococcidae) as a lipid resource (Delabie 2001). Honeydew has been shown to increase captive ant colony growth by 50–100% (Helms & Vinson 2008, Wilder et al. 2011a). Yet, honeydew alone is insufficient to sustain ant colonies, which additionally require protein-rich foods (e.g., insect prey) to feed their brood (Helms & Vinson 2008). To this end, ants also benefit from consuming tended hemipterans themselves, especially when they require more protein relative to carbohydrates (Oliver et al. 2012).

The primary costs associated with tending hemipterans are opportunity, energetic, and mortality costs. Ants invest time and energy into searching for honeydew-producing hemipterans, although the magnitude of such investments has not previously been quantified. There is reason to believe that ants employ multiple foraging strategies to minimize these costs. For instance, ants forage more in higher-quality resource patches (Veena & Ganeshaiah 1991), closer to the nest (Wimp & Whitham 2001), and in environments with lower mortality risk (Nonacs & Dill 1990). Ants also assess honeydew quantity and quality when deciding whether to lay pheromone trails to recruit nestmates (Detrain et al. 2010, Mailleux et al. 2003) and when allocating foragers to tending (Mailleux et al. 2003).

Additionally, associating with hemipterans makes ants vulnerable to exploitation or parasitism by their partners. Ants appear to be particularly vulnerable in highly specialized interactions. For example, some ants are known to shelter aphids in their nests in the winter, and these aphids in turn parasitize the ants, feeding upon ant larval hemolymph (Salazar et al. 2015). More recent evidence suggests that hemipterans also manipulate ants in less specialized associations, such as when the aphid *Macrosiphoniella yomogicola* produces dopamine in honeydew that increases ant aggression (Kudo et al. 2021). Additional work is needed to determine whether this increased aggression translates to increased defense against natural enemies, as well as whether behavior-altering drugs such as dopamine in honeydew are widespread across hemipterans.

At the colony and population level, ant abundance and ecological dominance have been found to be positively correlated with, and sometimes driven by, the abundance of tended hemipterans (Helms et al. 2011). Access to honeydew appears to be important for determining the distribution and abundance of ant colonies (Brightwell & Silverman 2011, Wilder et al. 2011b) and can, for instance, increase the persistence of ant colonies exposed to harsh abiotic conditions (e.g., a twofold increase in survival through the winter) (Brightwell & Silverman 2011). Thus, ants that consume honeydew tend to be among the most dominant species in ecological communities (Blüthgen et al. 2004, Davidson 1998), and honeydew is believed to facilitate ant invasions (see Section 5.4). Yet, much remains to be learned about the net effects of hemipteran associates on

ant colonies and populations. For instance, although we know that hemipterans improve ant colony survival and growth, it is unclear whether they also affect ant sexual reproduction or the foundation of new colonies.

In contrast to hemipterans, there is clear evidence that the mutualism has contributed to the ecological and evolutionary success of ants. Ants represent a single family of insects and 2% of all named terrestrial insects, but they are arguably the most ecologically dominant group of animals on Earth, estimated to comprise one-third of all insect individuals (Hölldobler & Wilson 1990, Wilson & Hölldobler 2005). With the exception of army ants, the most dominant ant species feed upon honeydew and other plant-derived carbohydrates (Davidson et al. 2003, Helms et al. 2011, Hölldobler & Wilson 1990, Meurville & LeBoeuf 2021, Nelsen et al. 2018, Oliver et al. 2008). In this regard, the importance of honeydew relative to other plant-based sugars is poorly understood. Nevertheless, competitively dominant ants often abandon other nectar sources in favor of honeydew (Blüthgen et al. 2000, Katayama et al. 2013), suggesting it plays a strong role in driving ant ecological dominance and evolutionary diversification.

4. CONTEXT DEPENDENCY

The benefits and costs of ant–hemipteran mutualisms (see Section 3) (**Table 2**) vary strongly across space and time. The net outcome of the interaction, including both the direction (mutualistic versus parasitic) and strength (weak to strong), is contingent on both biotic and abiotic context. Ant–hemipteran interactions are embedded within a larger multi-trophic food web, shown in **Figure 4**, that both affects and is affected by the mutualism. Because any of the species within this food web can respond to changes in abiotic conditions (e.g., those associated with global change, see Section 5.4) and not all species are affected equally, sources of context dependency (i.e., variation in the direction or strength of the interaction) are often interactive and complex. For instance, aphids have been found to be 17-fold more abundant in open meadows compared to shaded understories, due to not only increased ant attendance but also increased need for protection against natural enemies (Mooney et al. 2016). However, a quantitative synthesis is still needed to determine the generality of different sources of context dependency in ant–hemipteran mutualisms, as has been done previously for other mutualisms (Chamberlain & Holland 2009). In addition, context dependency has been quantified only from the perspective of hemipterans (i.e., as changes to colony growth) due to the difficulties of measuring ant colony fitness. Thus, we focus here and in **Table 2** on context dependency primarily from the perspective of hemipterans.

For hemipterans, the outcome of the association depends on ant identity and traits, with cooccurring ant species differing substantially in the benefits they provide (Novgorodova 2015). We hypothesize that the effectiveness of an ant as a mutualist should increase with its abundance in the environment, consistency of attendance across space and time, allocation of foragers to tending hemipterans, aggression toward natural enemies and competing ants, and invasive status. For instance, past work has shown that an aggressive, competitively dominant ant is a better mutualist for aphids compared to a more subordinate ant species (resulting in 11-fold larger aphid populations) (Mooney & Mandal 2010). However, the traits associated with high mutualist effectiveness are not necessarily linked (e.g., aggressive ants may not always allocate many foragers to tending hemipterans), and little is currently known about the relative importance of different trait combinations for determining interaction outcomes. Because the degree of ant attendance also depends on the relative benefits and costs to the ant (**Table 2**), the same ant species may not always be the most effective mutualist across contexts or for all hemipteran species (Blüthgen & Fiedler 2004b). Additional work is needed to compare the effectiveness of different mutualist ant partners, both individually and interactively, and to evaluate how hemipterans are affected by mutualist ant diversity.

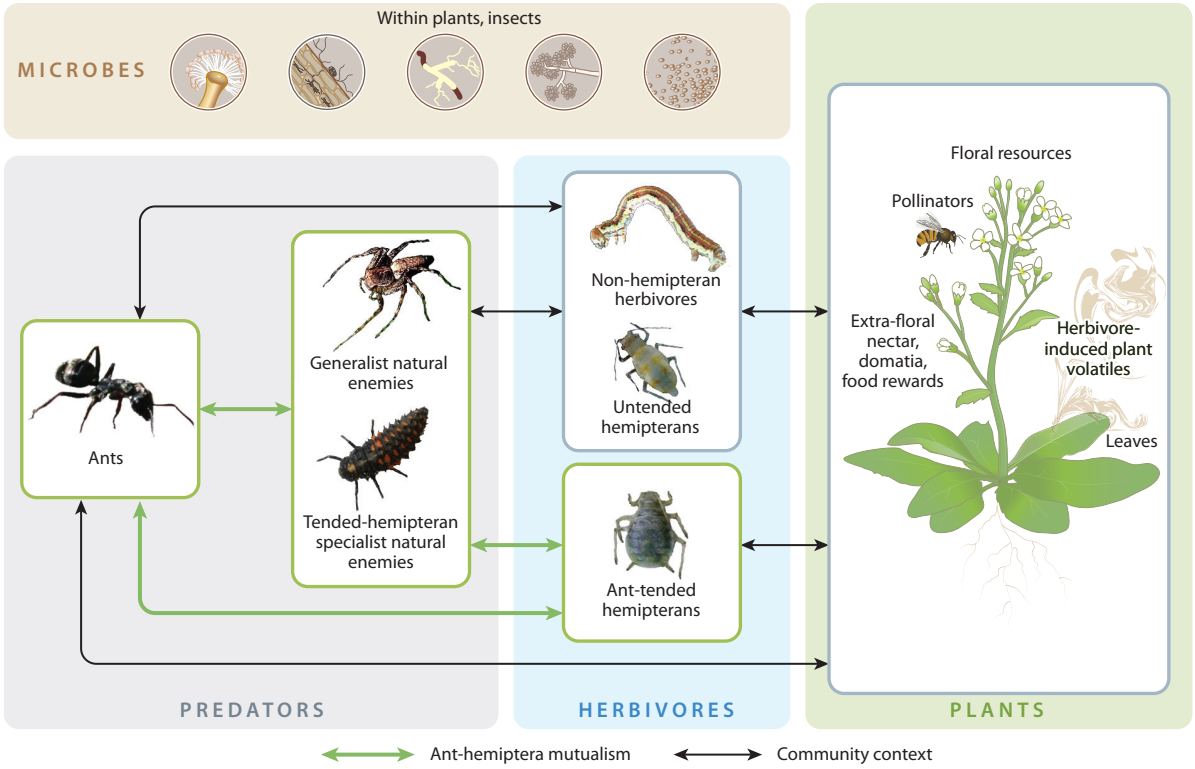

Figure 4

Diagram of an ant–hemipteran mutualism (*heavy green arrows and green boxes*) and the larger food web (*thin black arrows and gray boxes*) that both affects and is affected by the mutualism. Ants protect hemipterans against predatory arthropods in exchange for honeydew. At the same time, ants and other predatory arthropods also feeding upon other herbivorous insects. These higher trophic levels in turn influence, and are influenced by plant traits including herbivore defenses, volatile organic compounds, floral traits, and (in myrmecophilous plants) traits evolved to attract ants.

Because one of the primary benefits of ant attendance is protection against natural enemies, natural enemy abundance, identity, and diversity also strongly alter interaction outcomes. Where natural enemies are rare, the interaction may not be mutualistic because hemipterans are not in need of defense (Nelson et al. 2019b). In addition, natural enemy diversity may matter; predator diversity can increase the suppression of honeydew-producing hemipterans (Colfer & Rosenheim 2001, Snyder et al. 2006), and hemipterans should thus rely more heavily on ant protection in communities with higher natural enemy diversity.

Furthermore, host plant identity and quality influence the outcome of ant–hemipteran associations. Plant secondary metabolites and nutrients vary among and within plant species, affecting hemipterans not only directly but also indirectly through effects on honeydew composition and thus hemipteran ability to attract ants (Pringle et al. 2014). For instance, although ants increase the average abundance of the aphid *Aphis asclepiadis* on milkweed (*Asclepias syriaca*) by 59%, such effects depend strongly on milkweed genotype, and ants are even antagonists (i.e., they reduce aphid abundance) on more than one-third of plant genotypes (Mooney & Agrawal 2008) due to varying concentrations of plant toxins in aphid honeydew (Züst & Agrawal 2017). Moreover, host plant quality can depend upon other ecological interactions, such as previous damage by other herbivores. Such effects depend on the identity of the previous herbivore; whereas feeding damage

by another sap-feeding herbivore induces hemipteran resistance via activation of the salicylic acid defense pathway, damage by a leaf-chewing herbivore activates the jasmonic acid defense pathway, suppressing the salicylic acid pathway and thus increasing plant quality for hemipterans (Thaler et al. 2012). Herbivore-induced effects vary both among and within plant species; for example, the indirect effects of caterpillar feeding on ant–aphid interactions varies among the genotypes of a single plant species (Abdala-Roberts et al. 2012).

The resource environment in which ant–hemipteran interactions are embedded also influences the interaction outcome. Hemipterans compete for ant attendance (Cushman & Addicott 1989, Cushman & Whitham 1991), and provisioning ants with alternative resources can reduce ant tending (Petry et al. 2012) and increase the likelihood of ants preying on hemipterans (Offenberg 2001). These dynamics, as well as the nutritional demands of ants, vary both seasonally and spatially (Mooney & Tillberg 2005; Mooney et al. 2016; Nelson et al. 2019a,b).

Moreover, behavior of ants toward potentially mutualistic hemipterans is shaped by learning from previous interactions. Recognition of hemipteran partners is learned (Hayashi et al. 2015, Nelson et al. 2020), as seen, for example, when ants reduce attacks on previously tended hemipteran species (Hayashi et al. 2015). This learning is based upon hemipteran cuticular hydrocarbons (CHCs). For instance, ants mark hemipterans with their own CHCs (Endo & Itino 2012) and transmit information to nestmates (Hayashi et al. 2017), thus reducing attacks on hemipteran partners by naive foragers.

Microbes also modify ant–hemipteran mutualisms by affecting honeydew quality, hemipteran detectability, and ant diet. Many hemipterans host one or more facultative endosymbionts that provide nutritional or defensive benefits [that trade off with ant attendance as defense; see Section 3.1 (Henry et al. 2015)] but also reduce amino acid concentrations in honeydew (Schillewaert et al. 2017). Endosymbiont-driven changes in honeydew composition could potentially alter interactions with ants, but such effects have yet to be examined. Bacteria also produce volatiles in honeydew and modify hemipteran CHC profiles, increasing the detectability and species recognition of hemipterans by ants (but also by natural enemies) and thus strengthening the mutualism (Fischer et al. 2015, Hertaeg et al. 2021, Leroy et al. 2011). Evidence is beginning to suggest that microbes are transferred from hemipterans to ants when they consume honeydew or hemipterans themselves (Ivens et al. 2018, Renoz et al. 2019). It remains to be investigated whether the acquisition of microbes from hemipterans affects ant dietary preferences or fitness, though gut microbes have certainly played a key role in the convergent evolution of herbivory in ants (Russell et al. 2009).

5. BROADER ECOLOGICAL CONTEXTS

5.1. Community Ecology

Ants have strong effects on all components of the food webs in which they reside (**Figure 4**). Ants act as herbivores when they feed on plants directly by consuming floral or extrafloral nectar and indirectly by consuming hemipteran-produced honeydew (Davidson et al. 2003). Ants act as primary predators by consuming untended insect herbivores and, occasionally, the same hemipterans that they tend (Mooney & Tillberg 2005, Oliver et al. 2012). They also act as secondary predators by preying on both insect and even vertebrate predators of the hemipterans that they tend (Mooney & Mandal 2010). By attracting ants, ant-tended hemipterans mediate not only ant abundance and species composition but also ant behaviors, as honeydew increases ant activity and aggression (Davidson 1997, Grover et al. 2007). Through these effects, ant–hemipteran interactions dramatically alter the structure of entire arthropod communities (Wimp & Whitham 2001) and may thus be considered keystone interactions (**Figure 4**) (Styrsky & Eubanks 2007). In a study of

90 arthropod species on cottonwood (*Populus* spp.), total species richness and abundance were respectively 57% and 80% greater on trees with ant–aphid mutualists experimentally removed (Wimp & Whitham 2001). A meta-analysis of 49 studies found that ant–hemipteran mutualisms reduce the abundance of nontended herbivores, predators, and total arthropods by 56.6%, 113.9%, and 77.1%, respectively, although pollinators appear unaffected (Zhang et al. 2012). A similar meta-analysis of 30 studies found even stronger evidence for reductions in herbivory as a result of ants deterring nontended herbivore species (73% of cases) (Styrsky & Eubanks 2007).

Ant–hemipteran interactions also influence the evolutionary trajectories of other associated species, most notably in the case of predators that specialize in feeding upon ant-tended prey. Many hemipteran predators and parasitoids have morphological, chemical, and behavioral adaptations for evading detection by ants (Völkl 1997). In the most extreme examples, predators mimic hemipteran CHCs (Hayashi et al. 2015). Specialized predators that feed upon hemipterans while avoiding ant detection have access to hemipteran prey that are unavailable to other, unspecialized predators, and feeding among ants can even provide protection to those predators against their own enemies. In this way, ant–hemipteran interactions increase arthropod diversity by creating novel ecological niches.

5.2. Ant–Hemipteran Networks

Networks of ant–hemipteran interactions are characterized by many species of ant-tended hemipterans interacting with many species of hemipteran-tending ants. Neither ants nor hemipterans typically specialize in interactions with a single partner species, although exceptions exist, including *Acropyga* ants that interact obligately with particular mealybug (Pseudococcidae) mutualists and even carry them during mating flights when establishing new colonies (Smith et al. 2007). Rather, most ant–hemipteran associations consist of diverse networks of dozens or even hundreds of interacting ant and hemipteran species (Blüthgen & Fiedler 2004a). While the structure and function of these networks have received little investigation compared to other mutualism networks [e.g., pollination (Doré et al. 2021)], evidence demonstrates that ant–hemipteran networks have relatively low specificity (i.e., species do not interact with only a subset of potential partners) and low modularity (i.e., little division into distinct subcommunities) compared to plant–pollinator networks. However, they have higher specificity and modularity than networks between ants and extrafloral nectar-producing plants (Ivens et al. 2016).

A variety of traits of ants (e.g., competitive dominance) and hemipterans (e.g., honeydew quality) influence ant–hemipteran network structure (Blüthgen & Fiedler 2004a; Blüthgen et al. 2000, 2004). For instance, ants compete strongly for honeydew as a highly constant and sugar-rich resource. Because the most dominant ants competitively exclude subordinate species, not all ant species with the ability to consume liquid diets are observed actually participating in the mutualism (Blüthgen & Fiedler 2004a, Blüthgen et al. 2004). Compared to leafhoppers, planthoppers, and treehoppers, some scale insects and mealybugs are more reliably tended and aggressively defended by ants (Delabie 2001). It is possible that differences in hemipteran honeydew quality, aggregation size, or other mutualism-associated traits drive this pattern, but further investigation is needed into variation in network structure across hemipteran groups.

Ant–hemipteran networks are also modified by other species in the surrounding food web (**Figure 4**), including host plants and natural enemies. Host plant diversity, for example, has been found to increase the generality index of ant–hemipteran networks (Staab et al. 2015). Continuing to examine the factors that affect the structure and function of ant–hemipteran networks will contribute to our understanding of not only mutualistic but also multi-trophic networks (Ando et al. 2017, Pringle & Moreau 2017), presenting a promising area for future study.

5.3. Agriculture and Biological Control

Humans have long been fascinated by ant–hemipteran mutualisms, and as early as 300 A.D. in China, farmers manipulated ant assemblages to control agricultural pests (Buckley 1987). Many hemipterans and ants play important roles in agriculture, both individually and in association. Hemipterans are among the most damaging crop pests, with upward of 100 species causing significant economic losses (many of these species, such as the aphid *Aphis gossypii*, are ant tended) (van Emden & Harrington 2007). In addition to diverting plant nutrients away from growth and reproduction, hemipterans vector more than 80% of all known insect-transmitted plant viruses (Harris & Maramorosch 2014). While insecticides can reduce hemipteran damage, many hemipterans have evolved insecticide resistance (e.g., Bass et al. 2014), necessitating the use of additional management strategies. Biological control by releasing hemipteran natural enemies (e.g., parasitoid wasps) is common (Boivin et al. 2012), but ant defense limits the effectiveness of this approach.

Ants cause a variety of direct benefits (e.g., filtering water, enriching nutrients, controlling pests) and costs to agriculture (e.g., destroying farming equipment, stinging workers) (Evans et al. 2011, Jetter et al. 2002), but they also have indirect effects through their hemipteran associates (Styrsky & Eubanks 2007). While ants increase plant damage by increasing mutualist hemipteran abundance, they typically cause a net decrease in herbivory by reducing the abundance of other, more harmful herbivores (73% of cases reviewed) (Styrsky & Eubanks 2007). As a result, growers can use hemipteran-tending ants as biocontrol agents of nonhemipteran herbivores in some systems (e.g., cocoa) (Styrsky & Eubanks 2007).

In cases where ant attendance inflicts a net increase in herbivore damage, several approaches can limit such costs. Insecticides can reduce the abundance of hemipteran-tending ants, allowing natural enemies to be introduced as biocontrol with lower risk of ant attack. However, ant species are differentially susceptible to insecticides; in one study, a hemipteran-tending ant species increased in abundance due to pesticides suppressing other competing, nontending ant species (Kenne et al. 2003). Other approaches involve deploying sugar baits as decoys to distract ants from tending hemipterans (Pérez-Rodríguez et al. 2021). Overall, because monoculture and habitat simplification have been shown to reduce the effectiveness of biological control and increase the negative effects of ants, preserving biodiversity and habitat connectivity is essential for minimizing costs (Stutz & Entling 2011, Tena et al. 2013).

5.4. Global Change

Multiple abiotic factors implicated in climate change, including increased temperature, aridity, and atmospheric carbon dioxide concentrations, are emerging as strong drivers of context dependency for ant–hemipteran mutualisms (**Table 2**) (Kremer et al. 2018; Mooney et al. 2016; Nelson et al. 2019a,b). For instance, although warming sometimes disrupts ant–hemipteran mutualisms or causes shifts to antagonism (Barton & Ives 2014, Mooney et al. 2019), warming can also strengthen these mutualisms, at least up to a point (Nelson et al. 2019a,b). Several recent studies found that along natural climatic gradients in temperature and aridity, ants provided no benefits to aphids in the coolest, wettest sites but increased aphid population growth up to 4.5-fold in the warmest, driest sites (Mooney et al. 2016; Nelson et al. 2019a,b). While aphid performance was not directly affected by temperature, natural enemies had up to 2.5-fold stronger negative effects in warmer sites, but such effects were counteracted by even stronger positive effects of warming on ant activity, sugar consumption, and attendance of aphids (Mooney et al. 2016; Nelson et al. 2019a,b). Although much remains to be learned about the effects of climate change on ant–hemipteran mutualisms, these findings suggest that species at higher trophic levels (e.g., ants and natural

enemies) are particularly sensitive to changes in climate, with cascading effects on ant–hemipteran interaction strength and hemipteran abundance (Mooney et al. 2016; Nelson et al. 2019a,b).

Species invasions also mediate the outcome of these mutualisms. Invasive ants are often highly effective mutualist partners due to their high abundance and aggression, polydomy (occupancy of multiple nests by the same colony), and strong dependence on carbohydrates to fuel their activity (Lach 2003). At the same time, hemipterans are believed to be a primary driver of ant invasions (Holway et al. 2002). Fire ants (*Solenopsis invicta*), for example, rely more on honeydew in their invasive (versus native) range, where they dominate 36.5-fold more honeydew-producing hemipteran colonies and occupy a lower trophic position (Wilder et al. 2011b). Honeydew has been estimated to supply up to 48% of the diet of fire ants in invasive sites, and it plays a role in determining ant abundance (47.9% of variance explained) (Helms et al. 2011). Moreover, species invasions can reduce native ant and hemipteran species richness and interaction diversity (LeVan et al. 2018), causing invasional meltdowns, in which negative effects cascade across ecological communities (O'Dowd et al. 2003). Thus, in order to better predict and prevent such events, it is important to understand both the causes and consequences of the effects of global change on ant–hemipteran associations.

FUTURE ISSUES

1. How have ants affected the evolution and ecological dominance of hemipterans? Is the mutualism associated with adaptive radiations or, alternatively, evolutionary dead ends? Does associating with ants provide an ecological advantage to hemipterans compared to other strategies for avoiding predators, including ants?
2. Do plant species manipulate ant–hemipteran interactions, and might this be to the plant's benefit? Might hemipterans act as a sort of extrafloral nectary, attracting ants that prey against other, potentially more damaging herbivores?
3. What is the importance of honeydew compared to other plant-based sugars (e.g., extrafloral nectar) for driving ant performance, ecological dominance, and the evolution of trophallaxis? How does honeydew availability and composition influence patterns of ant abundance and diversity?
4. How does ant competitive dominance relate to the mutualistic services provided to hemipterans? Do the same ant morphological and behavioral traits underlie both functions such that ant competition serves to benefit hemipterans? And do ecological factors that alter ant competitive hierarchies indirectly have consequences for Hemiptera?
5. Although both tended and untended hemipterans are root feeders, relatively little is known about these subterranean interactions. How do they differ from above-ground interactions, and what do such differences reveal about the nature of these associations?
6. How do microbes mediate ant–hemipteran mutualisms, and what role do ant and hemipteran diets play in this regard? These questions can be addressed with experimental manipulations of microbiomes and comparative phylogenetic studies.

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