Evolutionary ecology of the interactions between trophobiotic ants and parasitoids of phloem-feeding hemipterans

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ABSTRACT

Ants and phloem-feeding hemipterans have established one of the most widespread and best-known mutualisms on Earth. In this mutualism, known as trophobiosis, ants feed on honeydew excreted by phloem-feeding hemipterans and, in exchange, protect hemipterans from their antagonists. Parasitoid wasps are among the main groups of antagonists of phloem-feeding hemipterans. Like trophobiosis, the interaction between trophobiotic ants and parasitoids of phloem-feeding hemipterans has evolved over millions of years and is widely distributed both geographically and phylogenetically. Ants protect phloem-feeding hemipterans from their parasitoids in many different ways, with outcomes for parasitoids that vary from altered reproduction or development to death. Consequently, parasitoids have evolved a series of behavioural, chemical, and morphological adaptations that reduce or limit the impact of trophobiotic ants. Our review shows that research on these interactions is asymmetric and strongly biased towards certain taxa and ecosystems, mostly aphids that feed on temperate crops. It will be necessary to broaden the range of taxa and ecosystems studied to evaluate how these interactions have shaped the evolution of phloem-feeding hemipterans, their parasitoids, and trophobiotic ants. While, in general, the presence of trophobiotic ants reduces the top-down regulation of phloem-feeding hemipterans by parasitoids, recent findings suggest that the mechanisms that explain this reduction are more complex than expected. By reviewing these interactions, the limitations of past research, and the advantages of current techniques, we provide perspectives to understand: (*i*) the mechanisms that ants use to protect hemipterans from parasitoids; (*ii*) the strategies evolved by parasitoids to counteract these ants; and (*iii*) the multiple factors that modulate the effects of trophobiotic ants on parasitoids of hemipterans. We suggest that a better understanding of these interactions will improve the management of phloem-feeding hemipterans, which constitute one of the most damaging groups of pests to global agriculture.

Key words: Formicidae, mutualism, multitrophic interaction, parasitism, Hemiptera, honeydew, Hymenoptera, hyperparasitism, parasite, pests.

CONTENTS

I. INTRODUCTION

Hemipterans constitute one of the most diverse, ubiquitous, and abundant groups of herbivorous insects worldwide (Vea & Grimaldi, 2016; Szwedo, 2016). Among this diverse group of insects, hemipterans that feed on plant phloem cause severe damage to agriculture and forestry (Gullan & Martin, 2009; Emdem & Harrington, 2017; Kondo &

Watson, 2022). These include major global pests, such as aphids, whiteflies, scale insects, and mealybugs. These hemipterans must excrete excess sugar from their phloem diet, which is sugar-rich but protein-limited (Douglas, 2009; Urbaneja-Bernat *et al.*, 2024). This sugar-rich excretion is called honeydew. A diverse plethora of organisms feed or develop on honeydew (Way, 1963; Wackers, Van Rijn & Heimpel, 2008; Dhami *et al.*, 2013; Tena *et al.*, 2016), and it therefore partially drives both the interactions of hemipterans with other organisms and variation in life histories of phloem-feeding hemipterans through their interactions with antagonists and mutualists (Styrsky & Eubanks, 2007; Tena *et al.*, 2016; Pringle, 2021; Fernández de Bobadilla *et al.*, 2024).

Phloem-feeding hemipterans are attacked by different natural enemies including microorganisms, generalist and oligophagous predators, and oligophagous parasitoids (Hirose, 2006; Daane *et al.*, 2012; Diehl *et al.*, 2013). Among these, parasitoid wasps belonging to the order Hymenoptera are likely the most diverse and widespread group of antagonists of phloem-feeding hemipterans (Labandeira & Li, 2021; Cruaud *et al.*, 2024). These wasps lay eggs inside or on hemipterans and immatures live as parasites that eventually kill their hosts. Parasitoid wasps are effective top-down regulators of phloem-feeding hemipterans and, thereby reduce herbivore pressure (Godfray & Müller, 1998; Hirose, 2006; Mills, 2009; Boivin, Hance & Brodeur, 2012; Kapranas & Tena, 2015). However, defensive mechanisms of hemipterans, including chemical, physiological, morphological, and behavioural, can limit top-down suppression caused by their parasitoids (Blumberg & Van Driesche, 2001; Villagra, Ramírez & Niemeyer, 2002; Desneux *et al.*, 2009; Le Ralec *et al.*, 2010; Vorburger, 2014; Tena *et al.*, 2018*a*). Among these defensive mechanisms, the mutualistic relationships that many phloem-feeding hemipteran species establish with ants is an important constraint for parasitoids (Hölldobler & Wilson, 1990; Völkl, 1997; Delabie, 2001).

Ants are among the most abundant arthropods in terrestrial environments and a prime example of interspecific dominance (Ward, 2014; Parker & Kronauer, 2021). Several groups of ants have specific adaptations to feed on honeydew excreted by phloem-feeding hemipterans. These adaptations include the ability to collect, transport, and share liquid food with nestmates (Ward, 2014; Nelson & Mooney, 2022). In exchange, these honeydew-feeding ant species attend phloem-feeding hemipterans and defend them from their natural enemies, including their parasitoids (Fig. 1) (Way, 1963; Hölldobler & Wilson, 1990; Delabie, 2001). This aggressive behaviour of ants defending hemipterans is accompanied by specific adaptations of many hemipteran species that facilitate ant attendance, resulting in one of the most widespread and best-known mutualisms on Earth (Ness, Mooney & Lach, 2010; Nelson & Mooney, 2022). This 'food-for-protection' mutualism, known as trophobiosis, is widely spread phylogenetically and geographically, and can modulate the arthropod community structure of many ecosystems, including the abundance and diversity of hemipteran parasitoids (Styrsky & Eubanks, 2007; Zhang, Zhang & Ma, 2012; Clark *et al.*, 2019). Despite this widespread mutualism, parasitoids have also evolved a wide range of adaptations that allow them to exploit their hemipteran hosts even when trophobiotic ants protect them (Völkl, 1992, 1997; Kaneko, 2002; Daane *et al.*, 2007; Sime & Daane, 2014).

The interactions between trophobiotic ants and parasitoids of phloem-feeding hemipterans, along with the biotic and abiotic factors that modulate these interactions, may contribute to explaining the evolutionary success of phloem-feeding hemipterans in many ecosystems. Ant–hemipteran interactions have been extensively studied and reviewed (e.g. Styrsky & Eubanks, 2007; Nelson & Mooney, 2022). However, few works have synthesized the interactions between trophobiotic ants and the parasitoids of hemipterans, despite the high impact of parasitoids on hemipterans and the large number of case studies. Prior reviews on these interactions are restricted to a single family of hemipterans: the aphids (Stary, 1966; Völkl, 1997). Moreover, recent research with novel techniques and a higher diversity of ants, parasitoids, and hemipterans has revealed that the mechanisms that explain the effects of trophobiotic ants in the regulation of phloem-feeding insects *via* their parasitoids are more complex than previously thought.

Herein, we first synthesize the evolutionary history of the interactions between trophobiotic ants and parasitoids of phloem-feeding hemipterans. We then explain how ants protect phloem-feeding hemipterans from parasitoids; and how some parasitoid species have adapted to exploit ant-attended hemipterans. The outcome of these interactions and the main factors that modulate them are also discussed. We use these findings to propose future research directions on these interactions, and to discuss different approaches to enhance the control of phloem-feeding hemipteran pests.

II. EVOLUTIONARY HISTORY OF THE INTERACTIONS BETWEEN TROPHOBIOTIC ANTS AND PARASITOIDS OF PHLOEM-FEEDING HEMIPTERANS

(1) Origin of hemipteran–parasitoid interactions

Hemipterans appeared 330–310 million years ago (Ma) from an herbivorous ancestor belonging to the order Paraneoptera, which already had specialized mouthparts for feeding on liquid diets (Nel *et al*., 2013; Yoshizawa & Lienhard, 2016). Hemipterans then evolved more specialized mouthparts, known as stylets, that allowed them to reach phloem vessels of plants (Szwedo, 2016). During this evolutionary process, the order Hemiptera diversified into three suborders. The suborders Sternorrhyncha and

Auchenorrhyncha remained specialized in feeding on phloem, while the suborder Heteroptera evolved predatory habits (Nelson & Mooney, 2022). Most extant clades of phloem-feeding hemipterans, including those that are major agricultural pests, are found in the suborder Sternorrhyncha, which appeared around 300 Ma (Drohojowska *et al.*, 2020). The infraorder Aphidomorpha originated in the mid-Permian (around 280 Ma), Aleyrodomorpha in the Middle Jurassic (around 160 Ma), and Coccidomorpha in the early Cretaceous (around 140 Ma) (Drohojowska *et al.*, 2020). Sternorrhyncha radiated rapidly during the Cretaceous, coinciding with the origin of angiosperms (Vea & Grimaldi, 2016; Hardy, 2018). Some abundant and diverse extant Sternorrhyncha families such as Pseudococcidae originated before the Mid-Cretaceous (150 Ma), while others, such as Coccidae and Aphididae, appeared in the Late Cretaceous (100–66 Ma).

The spreading and diversification of phloem-feeding hemipterans was followed by an increase in abundance and diversity of higher trophic levels. Different clades of generalist predators and parasitoids gradually evolved into specialists (Labandeira & Li, 2021). Among these, hymenopteran parasitoid wasps reached notable diversity and abundance (Cruaud *et al.*, 2024), with a radiation that began around 266–195 Ma (Peters *et al.*, 2017). The oldest records of parasitoids of phloem-feeding hemipterans can be dated to the Triassic (206 Ma) for representatives of the superfamilies Ichneumonoidea and Cynipoidea (Blaimer *et al.*, 2023; Labandeira & Li, 2021). In the Early Cretaceous (145–100 Ma), there was an extensive radiation within the Hymenoptera, which resulted in the origin of several clades of parasitoids exploiting phloem-feeding hemipterans, including the superfamilies Ceraphronoidea (family Megaspilidae) and Chalcidoidea (families Aphelinidae, Calesidae, Idioporidae, Trichogrammatidae, and Eulophidae) (Cruaud *et al.*, 2024; Blaimer *et al.*, 2023; Labandeira & Li, 2021; Peters *et al.*, 2017). Many groups of parasitoids of phloem-feeding hemipterans originated in the Late Cretaceous (100–66 Ma), including the family Encyrtidae (Chalcidoidea) and the superfamilies Apoidea (family Crabronidae) and Neostrepsiptera (family Halictophagidae). Parasitoid clades attacking phloem-feeding hemipterans, including most Chalcidoidea families, underwent notable diversification in Palaeocene (66–56 Ma) and Eocene (56–33.9 Ma) (Cruaud *et al.*, 2024).

(2) The involvement of ants in hemipteran–parasitoid interactions

Ants originated approximately 160 Ma, primarily exploiting resources from the ground (Moreau *et al.*, 2006; Vizueta *et al.*, 2025). Ants began foraging in plant canopies during the Early Cretaceous (about 120 Ma), and different arboreal-foraging traits emerged following angiosperm diversification in the Late Cretaceous (100–66 Ma) (Nelsen, Ree & Moreau, 2018; Nelson & Mooney, 2022). This process involved a shift from exclusively predatory behaviour to incorporating plant-based food sources into their diet. Several extant canopy-foraging ant species, even some that feed on honeydew, still prey on hemipterans to meet their protein requirements (Sakata, 1994; Offenberg, 2001). While foraging in plant canopies, ants also began to consume sugary liquid resources, including plant nectar and honeydew excreted by phloem-feeding hemipterans. As a result, several clades of ants developed trophallaxis, which is the collection and sharing of liquid resources with nestmates that do not forage, including larvae and queens. Trophallaxis allowed ant colonies to become ecologically dominant (Nelsen *et al.,*2018; Meurville & LeBoeuf, 2021). Ant–hemipteran trophobiotic associations occurred as early as the Eocene (56 Ma) (Nelsen *et al.*, 2018). Over the last 50 Ma, different traits evolved in ants in response to ant–hemipteran interactions, such as the symbiotic gut bacteria that facilitated further shifts from predatory to honeydew-feeding habits (Davidson *et al*., 2003; Nelson & Mooney 2022).

While honeydew-feeding ants took advantage of a high-energy food resource, phloem-feeding hemipterans also benefitted from the exploitation of honeydew by ants. First, the ants reduced predation on the attended honeydew-producing hemipterans. In addition, ants evolved behaviours that favoured honeydew-producing hemipterans, including transportation of hemipterans (Ho & Khoo, 1997), cleaning and sanitizing (Queiroz & Oliveira, 2001; Nielsen, Agrawal & Hajek, 2010), and protection from natural enemies (Delabie, 2001; Styrsky & Eubanks, 2007). These 'food-for-protection' interactions, called trophobiosis, extended across multiple clades of ants and phloem-feeding hemipterans to become one of the most widespread mutualisms (Pringle, 2021; Nelson & Mooney, 2022). This represents an important defensive advantage for hemipterans attended by ants, which were likely attacked by abundant and diverse parasitoid wasps when ant–hemipteran trophobiotic associations emerged (Blaimer *et al*., 2023; Cruaud *et al*., 2024).

Ant attendance, however, also has direct and indirect costs for phloem-feeding hemipterans (Stadler & Dixon, 1998; Yao, Shibao & Akimoto, 2000; Katayama & Suzuki, 2002). This trade-off may explain why many lineages of phloem-feeding hemipterans are not tended by ants, and why most ant–hemipteran mutualisms are facultative (Stadler & Dixon, 1999, 2005). The presence of parasitoids can be critical for the benefits to outweigh the costs for hemipterans in these interactions. For example, an increased concentration of melezitose in the excreted honeydew carries a fitness cost for hemipterans, but this compound attracts ants that can provide services including reduced mortality from parasitoids (Itioka & Inoue, 1996; Fischer & Shingleton, 2001;Zhou *et al*., 2015*c*). Indeed, the rapid expansion and diversification of ant–

hemipteran trophobiotic interactions may have been an important mechanism that promoted adaptive radiation in the parasitoids of hemipterans in the Eocene. Radiation of parasitoids of phloem-feeding hemipterans over the last 100 Ma has been linked to radiations of both angiosperms and hemipterans (Cruaud *et al*., 2024; Jouault *et al*., 2025). It is likely, however, that ant attendance also became an important mechanism promoting the radiation of some groups of hemipterans around 50 Ma due to the negative impacts of tending ants on parasitoids of phloem-feeding hemipterans in many different ecosystems.

III. HOW DO TROPHOBIOTIC ANTS PROTECT PHLOEM-FEEDING HEMIPTERANS FROM THEIR PARASITOIDS?

Ants protect their mutualistic phloem-feeding hemipterans in several ways. These protective mechanisms have been widely studied both in the field and under laboratory conditions (see online Supporting Information, Table S1), and have variable consequences for the parasitoids, ranging from reduced longevity or fertility to mortality (Fig. 2).

(1) Direct mechanisms

(*a*) *Ants attack adult parasitoids*

To attack adult parasitoids, ants first need to recognize the parasitoids of phloem-feeding hemipterans using either olfactory, mechanical, or visual cues. Among these cues, chemical–olfactory signals, such as cuticular hydrocarbons (CHCs) of parasitoids, are likely the most important (Liepert & Dettner, 1993; Hertaeg *et al*., 2023). Ants can also detect volatile alarm cues released by hemipterans when these are attacked by parasitoids (Verheggen *et al*., 2012). In addition, previous experience can help trophobiotic ants recognize parasitoids as antagonists, as it is assumed for some predators of hemipterans (Novgorodova, 2015).

Once attending ants recognize the searching parasitoid approaching the colony, they rapidly approach it and usually tap it with their antennae (Takada & Hashimoto, 1985; Völkl & Mackauer, 1993; Kaneko, 2002; Feng *et al*., 2015). Afterwards, the ants typically open their mandibles to seize the parasitoid (Kaneko, 2002; Hübner & Völkl, 1996; Fanani *et al*., 2020). Most parasitoids tend to flee, but ants can follow (Völkl & Kroupa, 1997), or capture them with their mandibles (Völkl *et al*., 1996; Völkl & Mackauer, 1993; Dejean, Ngriegeu & Borgoin, 1996). Additionally, neighbouring ant workers can join the pursuit to attack the parasitoid (Völkl *et al*., 1996; Dejean *et al*., 1996; Barzman & Daane, 2001). During capture, ants may bite the parasitoid on different body parts (Hübner & Völkl, 1996; Völkl *et al*., 1996; Völkl, 1992; Stechmann, Völkl & Starý, 1996; Tanga *et al*., 2015; Takada & Hashimoto, 1985; Barzman & Daane, 2001). Ants sometimes transport the seized parasitoid to their nest (Dejean *et al*., 1996). While most studies have observed that ants pursue and bite parasitoids, none has reported that ants spray formic acid or other compounds against parasitoids.

Attending ants will attack the adult parasitoid at all stages of its approach: while recognizing the hemipteran colony using its antennae; laying its egg/s (Heimpel, Rosenheim & Mangel, 1997; Kaneko, 2003*b*; Daane *et al*., 2007; Beltrá, Soto & Tena, 2015; Tanga *et al*., 2015; Feng *et al*., 2015; Fanani *et al*., 2020); or while feeding on hemipteran haemolymph (host feeding) or honeydew (Chan & Godfray, 1993) (Fig. 2). If the parasitoid succeeds in parasitizing its host, ants can also attack its offspring when they emerge. Ants might also attack adult parasitoids when they are resting, searching, mating or feeding on other resources (e.g. nectar or pollen) on outside the hemipteran colony (Vollhardt *et al*., 2010; Nyabuga *et al*., 2012; Tanga *et al*., 2015; Tena, Bouvet & Abram, 2022).

The consequences of these ant attacks are highly variable for adult parasitoids (Fig. 2). While captured parasitoids can be severely injured or killed, most parasitoids jump or fly away to avoid ant attacks (Hübner & Völkl, 1996; Völkl *et al.*, 1996, 1992; Stechmann *et al.,* 1996; Powell & Silverman, 2010; Feng *et al*., 2015; Tanga *et al*., 2015; Tena, Stouthamer & Hoddle, 2017). Even if parasitoids escape, ant attacks can have a cost for the surviving parasitoid, such as reduction of its current or future reproductive capacity, or longevity (e.g. Völkl, 1992, 1994; Zhou *et al*., 2014; Barzman & Daane, 2001; Martínez-Ferrer, Grafton-Cardwell & Shorey, 2003; Beltrá, Soto & Tena, 2015; Tena *et al*., 2017; Fanani *et al*., 2020). Additionally, ant attacks can affect the sex ratio of the parasitoid offspring when, because of an attack, female parasitoids are unable to fertilize their eggs (Tanga *et al*., 2015). Finally, ant attacks can reduce parasitoid resting time (Vinson & Scarborough, 1991; Völkl & Novak, 1997), with the resulting increase in energy consumption potentially reducing parasitoid longevity and fecundity.

(*b*) *Ants attack immature parasitoids*

Parasitoids of phloem-feeding hemipterans are mainly endoparasitoids (Labandeira & Li, 2021; Cruaud *et al*., 2024). This means that their larvae and pupae develop inside the parasitized hemipteran until they emerge as adults. Interestingly, some ant species can detect and bite parasitized hemipterans, likely killing the immature parasitoids (Fig. 2) (Takada, 1983; Vinson & Scarborough, 1991; Tanga *et al*., 2015; Plata *et al*., 2025), although the signals ants use to recognize parasitized hemipterans remain to be clarified.

(2) Indirect mechanisms

The presence of ants tending to hemipterans can deter a searching parasitoid (Fig. 2). Adult parasitoids can detect ants using visual, mechanical, and chemical cues (Dicke & Grostal, 2001; Xu *et al*., 2020; Mouratidis *et al*., 2021). Chemical cues, such as CHCs of ants, can deter a searching parasitoid even when ants are not attending the hemipteran colonies (Xu *et al*., 2020; Mouratidis *et al*., 2021), which can be considered as an example of 'ecology of fear' (Zanette & Clinchy, 2019). This deterrence may explain the increased time invested by the adult parasitoid to locate a suitable hemipteran host when ants are present (e.g. Vinson & Scarborough, 1991; Tanga *et al*., 2015; Fanani *et al*., 2020), with a potential cost in terms of energy, longevity and fecundity. Additionally, ant cues might affect other parasitoid behaviours such as feeding, mating, or resting in the ant foraging areas.

IV. COUNTERSTRATEGIES OF PARASITOIDS

Parasitoids of phloem-feeding hemipterans have evolved behavioural, chemical, and morphological traits that can reduce or limit the impact of trophobiotic ants (Table 1). While many of these adaptations include generalist responses to avoid attacks from ants or other organisms, others, such as chemical mimicry, are highly specific. In a few cases, these adaptations of parasitoids even allow them to benefit from the presence of ants.

(1) Behavioural strategies

Adult parasitoids run, jump, or fly away to escape from antagonists, including ants (e.g. Novak, 1994; Barzman & Daane, 2001; Herbert & Horn, 2008) (Table 1). In addition to these generalist behaviours, some parasitoid species show better adaptations to trophobiotic ants and move quickly or parasitize faster to avoid their attacks. These species may increase their success in the presence of trophobiotic ants because of reduced competition or intraguild predation (Barzman & Daane, 2001; Daane *et al*., 2007; Powell & Silverman, 2010; Zhou *et al*., 2014; Kistner *et al*., 2017; Xu *et al*., 2020; Mouratidis *et al*., 2021). For example, the mealybug parasitoid *Pseudaphycus flavidulus* is able to parasitize in the presence of tending ants, while the parasitoid *Leptomastix epona*, which moves more slowly while handling its host, can be attacked and killed by ants before it is able to oviposit (Daane *et al*., 2007). *Coccidoxenoides perminutus*, another mealybug parasitoid, has rapid and non-discriminatory oviposition behaviour which enables it to be less affected by tending ants than slower-ovipositing mealybug parasitoids such as *Anagyrus pseudococci* (Sime & Daane, 2014). *Metaphycus hageni*, a soft scale parasitoid with a long handling time and slow oviposition, is unable to parasitize its host when it is ant-attended. Other *Metaphycus* species with shorter oviposition time are more successful (Barzman & Daane, 2001). Parasitoid species that perform other activities, such as mating or feeding, faster might have a higher likelihood of success in the presence of aggressive ants, although these traits have not been evaluated.

Some species of hemipteran parasitoids perform cryptic movements (i.e. inconspicuous movement by walking slowly) or show ant-like locomotory behaviour (e.g. ant-like antennation). These behaviours may reduce ant detection and/or aggression, but may also function to deceive other potential antagonists or to reduce defensive behaviours of hemipterans (Hübner & Völkl, 1996; Rasekh *et al*., 2010). Another parasitoid strategy to defeat ants is to forage in areas where ants move less effectively, where it is harder for them to capture parasitoids (Völkl & Kroupa, 1997).

Some parasitoid species detect ant cues and use this to reduce their exposure to trophobiotic ants (e.g. Zhou *et al*., 2014; Sime & Daane, 2014; Beltrá *et al*., 2015). Ant-avoidance might also explain why some parasitoid species forage and mate outside their natal patch (Mackauer & Völkl, 2002; Nyabuga *et al*., 2012). Future research could also investigate whether parasitoids of hemipterans search for hosts when ants are less active. For example, during hot Mediterranean summers, the trophobiotic ant species *Lasius grandis* reduces hemipteran attendance at noon, and parasitoids might use this window to attack their hemipteran hosts (Pekas *et al*., 2011).

Finally, the ability of parasitoids to learn may also modulate the effects of trophobiotic ants (Giunti *et al*., 2015). Some parasitoid species can learn from encounters with trophobiotic ants and modify their behaviour accordingly. For example, naïve females of the aphid parasitoids *Pauesia picta* and *Pauesia pinicollis* flee when encountering an ant. However, after non-aggressive ant encounters, experienced female parasitoids change their behaviour by approaching ants from the side and at an increased distance. These experienced females have a higher oviposition rate than naïve females or females searching for an unattended host (Völkl 2001).

(2) Chemical strategies

In general, ants have high sensitivity to chemical cues, and many organisms use chemical signals to deceive them (Akino, 2008). Some parasitoids of phloem-feeding hemipterans use chemical mimicry (e.g. a CHC profile similar to that of their hemipteran hosts) to avoid detection by tending ants or to reduce ant aggressiveness (Hübner & Völkl, 1996; Völkl, 1997) (Table 1). Host chemical mimicry has been studied in aphid parasitoids of the genus *Lysiphlebus*, which are often not attacked by trophobiotic ants of the genera *Lasius* and *Myrmica* (Völkl, 1992, 1994; Völkl &

Mackauer, 1993; Liepert & Dettner, 1993, 1996; Hertaeg *et al*., 2023). Alternatively, other parasitoid species possess a CHC profile similar to that of ant larvae. This has been observed in two species of parasitoids of root aphids belonging to genus *Paralipsis* (Takada & Hashimoto, 1985; Völkl *et al*., 1996; Akino & Yamaoka, 1998). *Paralipsis* parasitoids wrongly identified as ant larvae are carried by ant workers to their colony and fed through trophallaxis. By rubbing the ants, parasitoids acquire the specific odour of the ant colony. Outside the colony, this odour allows them to parasitize their aphid hosts without being attacked by workers from the ant colony they have lived with. It has been observed that parasitoids with chemical mimicry strategies that allow them to avoid being attacked by ants prefer to forage in ant-attended patches (Völkl, 1994; Akino & Yamaoka, 1998).

Another strategy of parasitoids is to release ant deterrents (Völkl, Hübner & Detner, 1994; Hübner, 2000). Females of the aphid hyperparasitoid *Alloxysta brevis* release a mandibular secretion containing actinidin and other compounds in response to an ant attack. This secretion functions both in self-defence if the female is seized by an ant worker, by acting a repellent, and prevents ant attacks during subsequent encounters (Völkl *et al*., 1994). Hübner *et al*. (2002) found these mandibular gland secretions to be present in many alloxystine parasitoids belonging the genera *Alloxysta* and *Phaenoglyphis*, including species of parasitoids whose hemipteran hosts are not attended by ants. They found that the released compounds were also deterrent to other parasitoid antagonists such as spiders (Hübner & Dettner, 2000), implying that this defensive mechanism is not ant specific. Although the release of defensive chemicals is common among other natural enemies of hemipterans, such as predatory coccinellids (Majerus *et al*., 2007; Plata *et al*., 2024*c*), for hemipteran parasitoids it has only been demonstrated in alloxystine wasps. Ant-deterrent chemicals have been identified in parasitoids of flies, such as the figitid *Leptopilina heterotoma* (Stökl *et al*., 2012). This strategy may be widespread but remains to be investigated for most parasitoids.

(3) Morphological adaptations

The morphology of parasitoids can also play a key role against ants. For example, features of parasitoids such as body hardness and shape can also vary among species. One study showed that the body of the parasitoid *Aphidius ervi* can survive greater pressures than that of smaller parasitoids such as *Lysiphlebus cardui* and *Aphidius rhopalosiphi* (Hübner & Dettner, 2000). This increased hardness translated into lower mortality when the parasitoids were attacked by a spider, although it was not evaluated against ants. On the other hand, the small size of some parasitoids, such as *Coccidoxenoides*, has been postulated as a morphological adaptation to reduce detection by ants (Sime & Daane, 2014). Other morphological traits, such as the tubiform and telescoped abdomen found in female parasitoids of the genus *Protaphidius*, have also been associated with ants. *Protaphidius* parasitoids are specialized to *Stomaphis* aphids that live in bark crevices and are always attended by ants. It has been suggested that this telescoped abdomen may serve not only to reach the aphids in deep crevices of the bark, but also to oviposit from behind the attending ants (Takada, 1983). Furthermore, myrmecomorphy, a morphological resemblance to ants, is known from several parasitoids of phloem-feeding hemipterans (Table 1). For example, *Encyrtus* and *Holcencyrtus* resemble ants by either an absence of wings or camouflaging them (McIver & Stonedahl, 1993; Kelly *et al*., 2022). Although these visual signals might not deceive ants because they typically use chemosensation (Jackson & Ratnieks, 2006), an ant-like appearance may benefit parasitoids against other antagonists, such as intraguild predators (Malcicka *et al*., 2015).

V. FACTORS MODULATING INTERACTIONS BETWEEN TROPHOBIOTIC ANTS AND PARASITOIDS OF PHLOEM-FEEDING HEMIPTERANS

The outcome of interactions between trophobiotic ants and parasitoids of phloem-feeding hemipterans will depend on traits of hemipterans, ants, and parasitoids, which may vary both inter- and intraspecifically (Table S2; see Table S3 for definitions of each measure). Furthermore, various external biotic and abiotic factors can modulate ant–hemipteran–parasitoid interactions (Fig. 3).

(1) Hemipteran host

The effects of trophobiotic ants on parasitoids of phloem-feeding hemipterans have been studied in 45 hemipteran species, belonging to 30 genera and ten families (Fig. 4). Most of studies focus on a few aphid species, mainly *Aphis fabae*, that dominate in temperate ecosystems; the number of studies on hemipteran families that dominate in tropical ecosystems is much lower (Vilcinskas, 2016; Kondo & Watson, 2022). This lack of knowledge is particularly important because hemipteran-tending ants dominate plant canopies in the tropics (Davidson & Patrell-Kim, 1996; Blüthgen *et al.*, 2000).

The general pattern is that ants have negative effects on parasitoidss of hemipterans, but these effects depend on the species of hemipteran that ants attend (Table S2). This is likely because the number of tending ants per hemipteran (i.e. relative ant attendance) and their aggressivity depends on the quantity and quality of the honeydew excreted (Völkl *et al.*, 1999; Woodring *et al.*, 2004; Völkl & Novak, 1997; Pekas *et al.*, 2011; Tena, Hoddle & Hoddle, 2013*a*; Plata *et al.*, 2024*b*, 2025), and both quantity and quality vary inter- and intraspecifically among hemipterans (Detrain *et al.*, 2010; Vantaux *et al*., 2011; Katayama *et al*., 2013; Hogervorst, Wäckers & Romeis, 2017; Tena, Llácer & Urbaneja 2013*b*, Tena *et al*., 2018*b*; Urbaneja-Bernat *et al*., 2024). In addition to honeydew nutritional value, hemipteran specific semiochemicals such as pheromones, CHCs, and volatiles produced by honeydew bacteria, mediate location, recognition, selection and learning by mutualistic ants (Xu & Chen, 2021). For instance, some hemipterans produce CHCs that resemble those of tending ants, which may inhibit ant aggression and induce ant attendance (Endo & Itino, 2013). Thus, ant attendance is highly variable among hemipteran species, from hemipterans that are obligate ant-mutualists, such as the aphid tribe Fordini, to those that are not attended by ants, such as the aphid *Brachycaudus mimeuri* (Depa *et al*., 2020).

Importantly, the ant-attention received by a hemipteran and the aggressiveness of ants protecting it are also modulated by the presence and abundance of neighbouring honeydew-producing hemipterans both at the intra- and interspecific levels. On some plants, different hemipteran species can share ants from the same nest and compete for their attendance at low ant densities (Cushman & Addicott, 1989; Cushman & Whitham, 1991; Woodring *et al*., 2004; Pekas *et al*., 2011; Tena, 2013*b*). For example, in the Mediterranean region, mealybugs infesting citrus trees are highly attended by dominant trophobiotic ants that do not attend aphids or whiteflies when mealybugs are present (Pekas *et al*., 2011; Tena *et al*., 2013*a*). Hemipterans also compete for ant-attention intraspecifically, and individuals that excrete a lower quality or amount of honeydew may not be attended and may even be predated by ants (Cushman & Addicott, 1989; Sakata, 1994; Vantaux *et al*., 2011; Matsuura *et al*., 2025). Interestingly, hemipteran traits facilitating ant attendance can also indirectly affect parasitoids in various ways. For example, an improvement in the quality of honeydew, or the development of structures that retain rather than expel honeydew, would benefit both tending ants and also parasitoids that feed on honeydew (Tena *et al.*, 2016).

Another important factor modulating the effect of ants on parasitoids is the size of the hemipteran colony attended by ants. Several studies suggest that the effects of ants on parasitoids is enhanced as hemipteran colony size increases (Völkl, 1994; Itioka & Inoue,). This is likely because larger colonies of hemipterans are more attractive to ants and, therefore, have a higher probability of ant attendance and a higher number of tending ants (absolute ant attendance) (Plata *et al.*, 2024*b*, 2025). By contrast, the ant:hemipteran ratio (relative ant attendance) is higher in smaller attended colonies. Therefore, although the likelihood of being attended by ants increases with hemipteran colony size, individuals in smaller attended colonies may be better protected (Breton & Addicott, 1992; Harmon & Andow, 2007).

Finally, microbial endosymbionts of hemipterans, which can vary extensively among species but also intraspecifically, can influence many ecologically relevant traits of their hosts (Olivier *et al.*, 2010). Some of these endosymbionts can provide protection for hemipterans against their parasitoids. Interestingly, the presence of tending ants may reduce the abundance of these defensive endosymbionts of hemipterans (Mandrioli *et al.*, 2016). These endosymbionts also can indirectly modulate the impact of trophobiotic ants on the parasitoids of hemipterans. First, they can modulate the attraction of ants because they can affect the composition of honeydew and thus its volatiles (Schillewaert *et al.*, 2017). Second, endosymbionts can affect the CHC profile of hemipterans that is used by ants for trophobiont recognition (Hertaeg *et al.*, 2021). This may have important implications for the establishment of mutualisms between ants and hemipterans. Strikingly, the CHCs of hemipteran hosts may also affect the CHC profiles of parasitoids and the aggressiveness of ants towards them (Hertaeg *et al*., 2023).

(2) Trophobiotic ant

The effects of trophobiotic ants on parasitoids of hemipterans have been evaluated in 40 ant species belonging to 18 different genera, with *Lasius* being the most studied genus in terms of both the number of species the number of studies (Fig. 4; Table S2). Some trophobiotic ant species are more aggressive than others when they attend to hemipterans (Buckley & Gullan, 1991; Stechmann *et al*., 1996; Hübner & Völkl, 1996; Hübner, 2000; Kaneko, 2007), and aggressiveness may determine their impact on parasitoids of hemipterans (Buckley & Gullan 1991). For example, *Lasius niger* is more aggressive than *Pristomyrmex pungens* against the aphid parasitoid *Lysiphphlebus japonicus* (Kaneko, 2003*b*). Similarly, the parasitoid *Anagyrus lopezi* is more affected by the ant *Oecophylla smaragdina* than by *Anoplolepis gracilipes* or *Dolichoderus thoracicus*, which are less aggressive, when the parasitoid attacks the cassava mealybug *Phenacoccus manihoti* (Fanani *et al*., 2020). Both the number of tending ants and their aggressiveness in defending hemipterans from parasitoids can also be strongly influenced by seasonality. This is because the nutritional demands of ants change throughout the year, leading to significant dietary shifts across seasons (Mooney & Tillberg, 2005).

The behavioural responses of ants toward hemipterans and their parasitoids also depends on the ability of ants to recognize hemipterans as trophobiont partners and their parasitoids as antagonists. This cognitive ability may vary considerably among ants and can be both innate and based on previous experience. For example, some ant species can innately recognize long-chain CHCs produced by certain hemipterans (Endo & Itino, 2013; Salazar *et al*., 2015). Ants also leave their own CHCs on the attended hemipterans, resulting in reduced aggression from ant nestmates towards these ‘marked’ hemipterans (Sakata, 1994; Endo & Itino, 2012; Foronda *et al*., 2025). Furthermore, ants are exceptionally skilled at associating scents with food rewards (e.g. Huber & Knaden, 2018; Czaczkes & Kumar, 2020). Different ant species, including *Linepithema humile*, *Pristomyrmex punctatus*, *Tetramorium tsushimae*, and *Lasius niger*, can learn to associate the CHCs of hemipterans with a honeydew reward (Choe & Rust, 2006; Hojo *et al*., 2014; Hayashi, Nakamuta & Nomura, 2015; Hertaeg *et al*., 2021). Trophobiotic ant species with higher learning capacity therefore might establish new trophobiotic relationships with non-coevolved hemipterans more easily (Plata *et al*., 2024*b*, 2025). Similarly, the aggressiveness of ants towards the natural enemies of hemipterans can be innate (Novgorodova, 2015; Dorosheva, Yakovlev & Reznikova, 2011), but experience may also play a role in the recognition of antagonists by some ant species (Hollis *et al*., 2017). The variability of innate *versus* learned responses towards the parasitoids of hemipterans among different ant species remains to be evaluated.

Other ant traits might modulate their impact on the parasitoids of hemipterans. For example, traits that facilitate resource monopolization by ants, such as increased colony size, polydomy (i.e. the ability to establish nests in various locations), or polygyny (i.e. several queens in the nest, which is associated with lower intraspecific aggression), have been linked to higher ant-attendance levels of hemipterans (Blüthgen & Fiedler 2004; Oliver, Leather & Cook, 2008; Nelson & Mooney, 2022).

(3) Parasitoid

The effects of ants on parasitoids of hemipterans have been specifically evaluated in 86 different parasitoid species (Table S2). Most studied parasitoid species are primary parasitoids, while the impact of ants on a few hyperparasitoids has been studied particularly for some aphid hosts such as *Aphis fabae* (Fig. 4; Table S2). A variety of chemical, morphological and behavioural traits of parasitoids modulate their interactions with trophobiotic ants and some of these traits are species specific (see Section IV). As illustrative examples, Barzman & Daane (2001) found that different species of parasitoids of the same genus respond differently when they attack the soft scale *Saissetia oleae* that it is tended by the Argentine ant *Linepithema humile*. Unlike *Metaphycus anneckei*, *Metaphycus hageni* is unable to parasitize *S. oleae* when it was attended by ants. The authors suggested that this is likely because *M. anneckei* needs less handling and oviposition time and, therefore, can escape before the ants attack. Likewise, Liepert & Dettner (1993) found that the ant *Lasius niger* is aggressive towards the aphid parasitoid *Trioxys angelicae*, but the parasitoid *Lysiphlebus cardui*, which possesses aphid-like CHCs, is not treated aggressively. Furthermore, genotypic variation can explain intraspecific variability of parasitoids facing trophobiotic ants. Using different lines of the parasitoid *Lysiphlebus fabarum*, Hertaeg *et al*. (2023) showed that the genotype affected parasitoid CHC profiles and aggression by the ant *L. niger*.

Ants can also negatively affect parasitoid antagonists, including parasitoid predators (Kaneko, 2003*a*, 2007), competing parasitoids, and hyperparasitoids (Völkl, 1992; Hübner & Völkl, 1996). Therefore, some parasitoid species may benefit indirectly from an enemy-free space created by tending ants. For example, the parasitoid *Lysiphlebus cardui* benefits indirectly when its host *Aphis fabae* is attended by *Lasius niger* ants because these ants reduce the density of hyperparasitoids (Völkl, 1992). The same occurs with the parasitoid *Prionomitus mitratus*, which benefits from the ants *Lasius niger* and *Formica pratensis* attending its host, the psyllid *Cacopsylla crataegi,* due to a decrease in hyperparasitism (Novak, 1994). Kaneko (2003*a*) observed that the parasitoid *Lysiphlebus japonicus* suffered less hyperparasitism and predation when its aphid host *Toxoptera citricidus* was attended by the ant *Pristomyrmex pungens*.

(4) Host plant

The host plant where the hemipteran settles and feeds can also modulate the interactions between trophobiotic ants and parasitoids of phloem-feeding hemipterans. For example, Völkl (1997) found that the parasitoid *Trioxys angelicae* has a higher oviposition success in colonies of the aphid *Aphis fabae* that are attended by ants when these colonies are on goosefoot (*Chenopodium* spp.) rather than on creeping thistle (*Cirsium arvense*) or spindle bush (*Euonymus europaeus*). Similarly, Zhou, Kuang & Gao (2015*b*) found that the parasitoid *Anagyrus babawalei* parasitizes more mealybugs of the species *Phenacoccus solenopsis* attended by *Tapinoma melanocephalum* when the mealybug is settled on tomato (*Solanum lycopersicun*), rather than on cotton (*Gossypium hirsutum*) plants.

How host plants modulate these interactions is poorly known, but there are several possibilities. First, plant-derived food sources rich in sugars, such as nectar, extrafloral nectar, or guttation, might compete with hemipterans for the attention of ants (Engel *et al*., 2001; Blüthgen, Stork & Fiedler, 2004; Blüthgen & Fiedler, 2004; Del-Claro *et al*., 2016; Heil, 2015; Urbaneja-Bernat *et al*., 2023), and can also supply food to the interacting parasitoids (Jamont, Crépellière & Jaloux, 2013). Therefore, plant species with different types of resources might affect the interaction between ants and parasitoids in different ways. Similarly, host plants have specific phloem composition that affects the composition of honeydew excreted by the same hemipteran species (Fischer & Shingleton, 2001; Fischer, Völkl & Hoffmann, 2005; Pringle *et al*., 2014;

Tena *et al*., 2018*b*; Urbaneja-Bernat *et al*., 2024). As explained in Section V.1, honeydew composition affects both the number and aggressivity of ants attending hemipterans (Völkl *et al*., 1999; Woodring *et al*., 2004). Furthermore, the foraging behaviour of parasitoids is affected by plant volatiles (Pickett & Khan, 2016; Turlings & Erb, 2018). Interestingly, the presence of trophobiotic ants attending hemipterans can induce changes in the volatile compounds emitted by plants, which can mediate parasitoid attraction (Paris, Llusia & Peñuelas, 2010; Huang *et al*., 2017). Other factors, such as plant architecture, may be also important because some plant structures can serve as refugia for parasitoids against ants (Mackauer & Völkl, 1993).

Even within the same plant, the effect of ants on parasitoids of phloem-feeding hemipterans might vary depending on the plant organ where the interaction occurs. For example, the parasitoid *Pauesia silvestris* suffers lower mortality due to aggression of the ant *Formica polyctena* when it searches for the aphid *Cinara pineae* on pine needles than for *Cinara pini* on pine bark (Völkl & Kroupra, 1997). Although there are two variables here (aphid species and plant organ), Völkl & Kroupa (1997) suggested that the parasitoid could avoid ant attacks in the pine needles because ants move less easily on this substrate.

(5) Other factors

The interactions between trophobiotic ants and parasitoids of hemipterans occur in plants that are part of complex ecosystems modulated by multiple external factors. For example, surrounding habitats can affect the entire arthropod community of a host plant (Landis, Wratten & Gurr, 2000; Smith & Schmitz, 2016). While the mutualistic interaction between ants and hemipterans can be independent of the landscape context in some ecosystems (Stutz & Entling, 2011), recent studies have revealed that landscape composition may have a strong effect on ant–hemipteran–parasitoid interactions in others. For example, in urban green spaces in the UK, the abundance of the aphid *Aphis fabae* feeding on *Vicia faba* plants was not affected by landscape composition, but attendance by the ant *Lasius niger* decreased with habitat diversity, which may result in a reduced impact of ants on parasitoids (Rocha & Fellowes, 2020). Kulikowski (2020) found that parasitism of the soft scale *Alecanochiton marquesi* was negatively affected by the presence of the trophobiotic ant *Wasmannia auropunctata*, but only at sites with high surrounding landscape forest cover. Interestingly, this suggests that habitat-management strategies on a landscape scale could be used to reduce the impact of ants on the parasitoids of hemipterans. These habitat-management strategies could also be applied on a local scale. For example, Blubaugh *et al.* (2024) found that cover crops can elicit a shift in the foraging behaviour of the ant *Solenopsis invicta* in cotton, from foraging on leaves of cotton plants to foraging on the ground, thus reducing ant attendance of aphids feeding on cotton plants. Other habitat-management strategies include providing artificial sugar sources to distract ants from attending hemipterans, reduce ant aggressivity, and facilitate parasitoid attacks on hemipterans (Wäckers *et al.*, 2017; Chinarelli *et al.*, 2021; Pérez-Rodríguez *et al.*, 2021; Fernández de Bobadilla *et al.*, 2024; Schifani, Giannetti & Grasso, 2024).

In agroecosystems, conventional agronomic practices can also modulate the impact of trophobiotic ants on parasitoids of phloem-feeding hemipterans. For example, tillage can have wide effects on arthropod community structure in the host plant (Sharley, Hoffmann & Thomson, 2008; Patterson, Sanderson & Eyre, 2019). Irrigation or fertilization both influence the growth and nutritional status of host plants, which in turn affects the amount and composition of honeydew excreted by hemipterans (Baqui & Kershaw, 1993; Blua & Toscano, 1994). Critically, the use of insecticides may affect hemipterans, parasitoids, ants, and the organisms interacting with them in different ways (Waage, Hassell & Godfray, 1985; Teder & Knapp, 2019; Calvo-Agudo *et al*., 2022).

Climatic conditions can also affect ant–hemipteran mutualisms by altering hemipteran growth and behaviour, honeydew composition, or semiochemistry (Blanchard *et al*., 2019). These conditions can also impact the behaviour of trophobiotic ants within ant–hemipteran interactions (Barton & Ives, 2014; Mooney *et al*., 2019). For example, Barton & Ives (2014) found that warmer temperatures reduced the aggressivity of winter ants when attending aphids. By contrast, warming can also strengthen ant–hemipteran mutualisms (Zhou *et al*., 2017; Nelson *et al*., 2019). Zhou *et al*. (2017) found that the performance of the ant *Tapinoma melanocephalum* attending the mealybug *Phenacoccus solenopsis*, including tending level, aggression, activity, and honeydew consumption, was enhanced by temperature warming, which might result in enhanced protection of hemipterans against parasitoids.

Finally, ant–hemipteran–parasitoid dynamics can be altered by the spread of invasive species. In fact, hemipterans and ants are themselves amongst the most invasive arthropod species (Bertelsmeier *et al*., 2015; Liebhold *et al*., 2024). These invasions often result in novel interactions between ants and non-coevolved hemipterans. Ants can rapidly adapt to attend hemipterans with which they have not coevolved. Thus, invasive hemipterans may compete with resident hemipterans for the attention of ants, while invasive ants may compete with resident ants to exploit hemipterans (Tena *et al*., 2013*a*; Wang *et al*., 2021; Plata *et al*., 2024*a*, 2025). Such emerging interactions between non-coevolved ants and hemipterans also represent a challenge for the parasitoids of hemipterans. For example, the parasitoid *Tamarixia radiata*, native to Asia, was imported to California to control the psyllid *Diaphorina citri* in citrus, but the presence of the Argentine ant *Linepithema humile* decreased the establishment and efficacy of the parasitoid in urban areas (Milosavljević *et al*., 2021). It is possible that parasitoids may be able to reduce the impact of these non-coevolved ants, as has been specifically evaluated for some predators of hemipterans (Plata *et al*., 2024*c*). However, these remain to be assessed.

VI. CONCLUSIONS

(1) The interactions between parasitoids of phloem-feeding hemipterans and trophobiotic ants have evolved over millions of years and are widely distributed both geographically and phylogenetically. However, research on these interactions is asymmetric, with a bias towards certain taxa and ecosystems. Most studies have focused on temperate climates, crop plants, a few aphid species such as *Aphis fabae* and their parasitoids, and the ant species *Lasius niger*. Broadening the range of taxa and ecosystem types will shed light on how these interactions have shaped the evolution of phloem-feeding hemipterans, their parasitoids, and trophobiotic ants. We especially encourage studies of these interactions in natural and semi-natural habitats from tropical and subtropical ecosystems that are dominated by other phloem-feeding hemipterans, such as mealybugs, psyllids, or soft scales. This knowledge gap is particularly significant considering the dominance of canopy-foraging ants in the tropics.

(2) In general, the presence of trophobiotic ants reduces parasitism of phloem-feeding hemipterans. However, recent findings suggest that the underlying mechanisms are more complex than expected and still not well understood. For example, while extensive research has evaluated the direct attacks of trophobiotic ants on adult parasitoids, very few have assessed their impact on immature parasitoids that may also be recognized and attacked by ants. Similarly, the role of the ‘ecology of fear’ in these

interactions has been poorly recognized, and may reveal new mechanisms that imply different costs for parasitoids.

(3) Parasitoids have evolved a series of behavioural, chemical, and morphological traits that can reduce the impact of trophobiotic ants. The diversity and specificity of these traits suggest that ant attendance may represent an important ecological constraint that led to adaptive radiation in parasitoids of phloem-feeding hemipterans. Multi-trait phylogenetic analyses should explore whether these traits have arisen as a result of selection by trophobiotic ants. In addition, it would be interesting for future studies to evaluate the plasticity of the varied behavioural strategies of parasitoids. Such behavioural plasticity could be critical for the success of parasitoids in future changing environments.

(4) Cognitive abilities of both ants and parasitoids may determine the outcome of their interactions. Some parasitoid species learn from ant encounters and adjust their behaviours, and there is ample evidence that the associative learning ability of ants plays a key role in recognizing hemipterans as trophobionts. However, little is known about the innate and learned responses of ants towards the parasitoids of hemipterans. The interactions between ants, mutualistic hemipterans, and their parasitoids, represent an excellent model to study the cognitive ecology of multi-trophic interactions.

(5) Microbial endosymbionts of hemipterans can modulate the impact of trophobiotic ants on hemipteran parasitoids. These endosymbionts can affect the composition of honeydew, and the CHC profiles of hemipterans, thereby modulating the chemical communication between ants and hemipterans. Hemipteran endosymbionts may also affect some traits of their parasitoids, including their CHC profiles, which can determine the aggressivity of ants towards them. Recent advances in molecular techniques that

facilitate the study of microecology could provide important insights into the role of endosymbionts in these interactions.

(6) The spread of invasive species means bringing together phloem-feeding hemipterans, trophobiotic ants and parasitoids that do not share an evolutionary history. Ants can adapt rapidly to attend non-coevolved hemipterans, thus the parasitoids of these hemipterans will also encounter these ants. However, the mechanisms that allow parasitoids of hemipterans to adapt to these non-coevolved ants need to be investigated. We propose that classical biological control programs, where parasitoids are introduced to control invasive hemipterans, represent useful model systems to study if and how parasitoids adapt to new trophobiotic ant species.

(7) Knowledge regarding the interactions between trophobiotic ants and parasitoids of phloem-feeding hemipterans could be used to improve Integrated Pest Management programs for these hemipterans. For example, recent studies have demonstrated that different habitat-management strategies can distract ants from attending hemipterans and reduce their aggressivity toward parasitoids. We suggest that the identification of parasitoid traits that reduce the impact of trophobiotic ants should be used to select parasitoid species in augmentative and classical biological control strategies. These traits could also be considered in genetic breeding programs for parasitoids of phloem-feeding hemipteran pests.

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IX. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Studies investigating the interactions between tending ants and parasitoids of honeydew-producing hemipterans.

Table S2. Effects of trophobiotic ants on parasitoids of phloem-feeding hemipterans.

Table S3. Parameters used in Table S2 to evaluate the effects of ants on parasitoids of honeydew-feeding hemipterans.

Fig. 1. Trophobiotic ants can recognize and attack immature and adult parasitoids of phloem-feeding hemipterans. (A) A *Lasius* ant approaches an *Aphidius* parasitoid wasp attempting to parasitize the aphid *Aphis spiraecola*. (B) A *Lasius* ant recognizes a mummy of *Aphis gossypii* with an immature parasitoid developing inside.

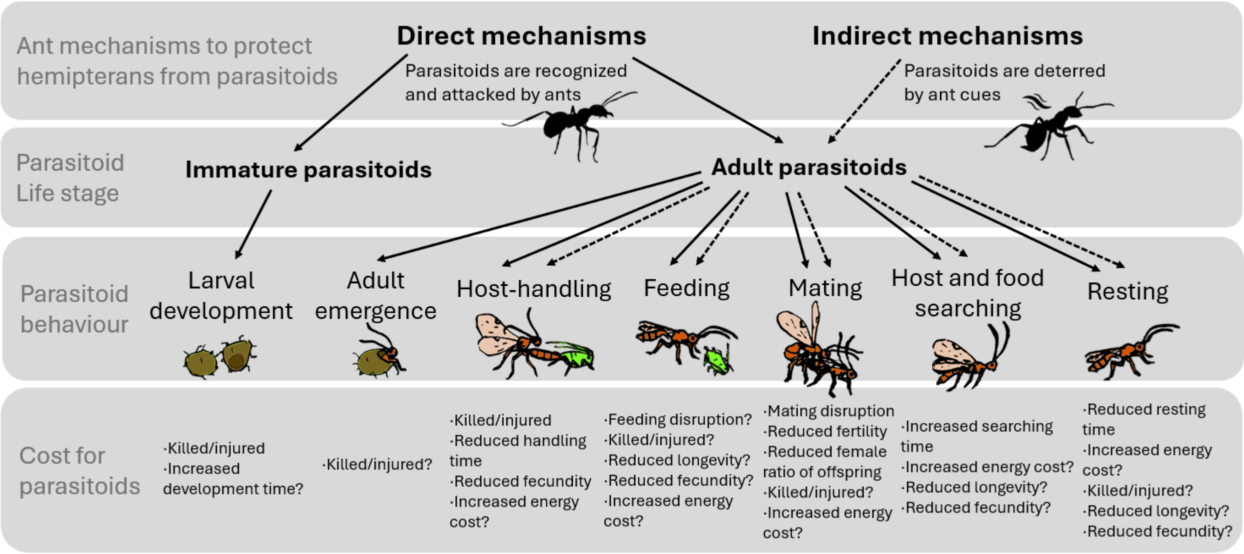
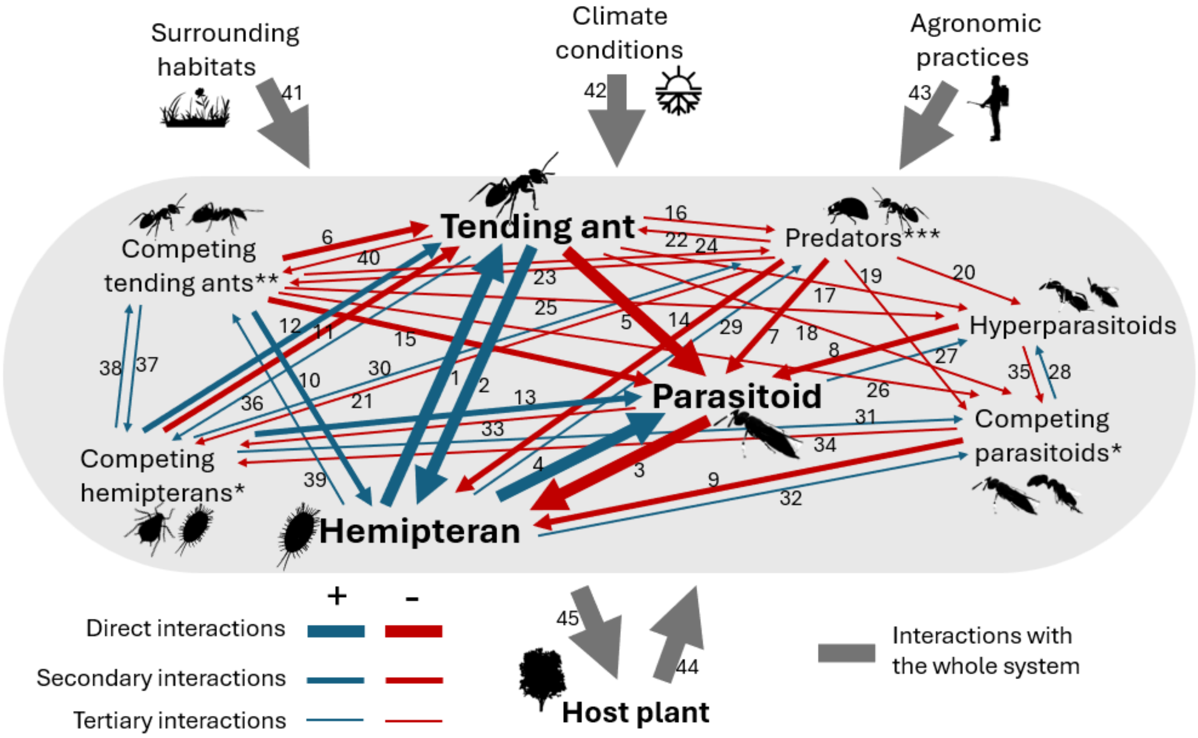


Fig. 2. Direct and indirect mechanisms by which trophobiotic ants protect phloem-feeding hemipterans from their parasitoids, and the negative outcomes of these interactions for parasitoids. Solid arrows represent direct mechanisms, and dashed arrows represent indirect mechanisms. Potential outcomes for parasitoids that have not been specifically evaluated are represented with a question mark (?).



Direct interactions
1: Tending ant feeds on hemipteran honeydew
2: Hemipteran can obtain several ant services not mediated by natural enemies
3: Hemipteran is attacked and killed by the parasitoid
4: Bottom-up effects of hemipterans on the parasitoid (increased host availability)
5: Parasitoid is attacked by tending ants

Secondary interactions
6: Tending ant can be attacked by other ants competing for resources or space
7: Parasitoid can be attacked and killed by predators
8: Parasitoid can be attacked and killed by hyperparasitoids
9: Hemipteran can be attacked and killed by other parasitoids
10: Hemipteran can obtain several direct services from competing tending ants
11: Ant attendance can be reduced because tending ants can be attracted to honeydew excreted by competing hemipterans
12: Tending ant can feed on the honeydew of other hemipteran species
13: Bottom-up effects of other hemipterans on the parasitoid (increased host availability)
14: Hemipteran is attacked and killed by predators
15: Parasitoid is attacked by other tending ants

Tertiary interactions
16,17,18: Tending ants attack predators, hyperparasitoids and competing parasitoids to protect hemipterans
19,20,21,22,23: Predators can attack competing parasitoids, hyperparasitoids and competing hemipterans. Some predators can also attack tending ants.
24,25,26: Competing ants can attack predators, hyperparasitoids and competing parasitoids
27,28: Bottom-up effects of the parasitoid and competing parasitoids on hyperparasitoids (increased host availability)
29,30,31,32: Bottom-up effects of hemipterans on predators and competing parasitoids (increased prey and host availability)
33,34: Competing hemipterans are attacked and killed by the parasitoid and competing parasitoids
35: Competing parasitoids are attacked and killed by hyperparasitoids
36,37: Competing hemipterans can obtain direct services from tending ants and competing tending ants
38,39: Competing tending ants feed on honeydew excreted by hemipteran and competing hemipterans
40: Competing tending ants can be attacked by tending ants

Interactions with the hole system
41,42,43,44: The whole system is affected by surrounding habitats, climate conditions, agronomic practices, and host plant.
45: Host plant is affected by the whole system

Fig. 3. Direct and indirect interactions mediating the effects of trophobiotic ants on parasitoids of phloem-feeding hemipterans. *Competing parasitoids and competing hemipterans can belong to the same species (intraspecific competition), or to different species (interspecific competition). **Competing tending ants can belong to the same species from a different colony (intraspecific competition) or different species (interspecific competition). ***Tending ants might also act as predators.

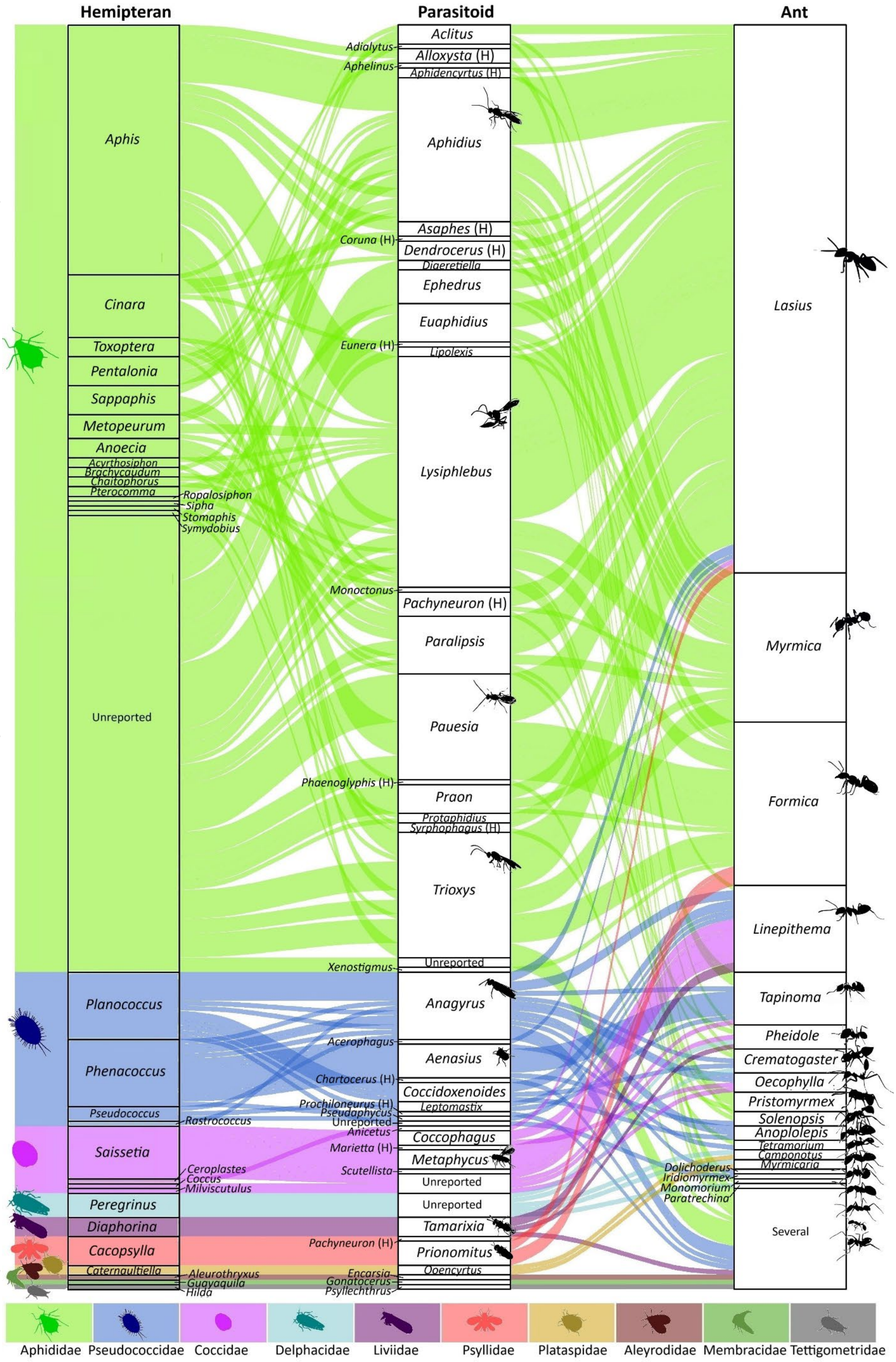

Hemipteran
Parasitoid
Ant
Aphis
Cinara
Toxoptera
Pentalonia
Sappaphis
Metopeurum
Anoecia
Acyrthosiphon
Brachycaudum
Chaitophorus
Pterocomma
Ropalosiphon
Sipha
Stomaphis
Symydobius
Unreported
Planococcus
Phenacoccus
Pseudococcus
Rastrococcus
Saissetia
Ceroplastes
Coccus
Milviscutulus
Peregrinus
Diaphorina
Cacopsylla
Caternaultiella
Aleurothryxus
Guayaquila
Hilda
Aclitus
Adialytus
Alloxysta (H)
Aphelinus
Aphidencyrtus (H)
Aphidius
Asaphes (H)
Coruna (H)
Dendrocerus (H)
Diaeretiella
Ephedrus
Euaphidius
Eunera (H)
Lipolexis
Lysiphlebus
Monoctonus
Pachyneuron (H)
Paralipsis
Pauesia
Phaenoglyphis (H)
Praon
Protaphidius
Syrphophagus (H)
Trioxys
Unreported
Xenostigmus
Anagyrus
Acerophagus
Aenasius
Chartocerus (H)
Coccidoxenoides
Prochiloneurus (H)
Leptomastix
Pseudaphycus
Unreported
Anicetus
Coccophagus
Marietta (H)
Metaphycus
Scutellista
Unreported
Unreported
Tamarixia
Pachyneuron (H)
Prionomitus
Ooencyrtus
Encarsia
Gonatocerus
Psyllechthrus
Lasius
Myrmica
Formica
Linepithema
Tapinoma
Pheidole
Crematogaster
Oecophylla
Pristomyrmex
Solenopsis
Anoplolepis
Tetramorium
Camponotus
Myrmicaria
Dolichoderus
Iridiomyrmex
Monomorium
Paratrechina
Several
Aphididae
Pseudococcidae
Coccidae
Delphacidae
Liviidae
Psyllidae
Plataspidae
Aleyrodidae
Membracidae
Tettigometridae

Fig. 4. Proportion of studies evaluating different ant–parasitoid–hemipteran interactions, grouped by genus. Different colours represent interactions of each family of hemipterans (see key at bottom of figure). See Table S2 for summary of results and search terms used to identify the relevant literature. Full details of the 66 selected studies are provided in Table S1). The height allocated to each genus is proportional to the number of studies multiplied by the number of species in each genus for each tri-trophic interaction. (H) = parasitoid genera that are hyperparasitoids.

Table 1. Strategies of parasitoids of phloem-feeding hemipterans that may limit/reduce the impact of trophobiotic ants. Examples of species with each strategy are included.

Strategy	e.g. Parasitoid species	References
Behavioural strategies		
Running	*Pauesia silvestris*, *Lysiphlebus japonicus*	Völkl & Kroupa (1997); Kaneko (2002)
Jumping	*Prionomitus mitratus*, *Aphidius aphidivorus*, *P. aphidis*, *Asaphes vulgaris*, *Metaphycus* spp., *Lysiphlebus testaceipes*, *Anagyrus pseudococci*	Novak (1994); Hübner & Völkl (1996); Barzman & Daane (2001); Vinson & Scarborough (1991); Tanga *et al.* (2015)
Sensitivity of flight behaviour	*Pachyneuron aphidis*, *Pauesia silvestris*, *Asaphes vulgaris*, *Tryoxis angelicae*, *Anagyrus pseudococci*, *Aphidius colemani*, *Alloxysta brevis*	Völkl & Kroupa (1997); Völkl & Mackauer (1993); Tanga *et al.* (2015); Herbert & Horn (2008), Hübner (2000)
Rapid movements and reduced host handling time	*Coccidoxenoides perminutus*, *Pseudaphycus flavidulus*, *Metaphycus aenneckei*	Daane *et al.* (2007); Sime & Daane (2014); Barzman & Daane (2001)
Rapid oviposition	*Coccidoxenoides perminutus*, *Syrphophagus* sp., *Lysiphlebus testaceipes*, *Metaphycus aenneckei*, *Aphidus colemani*	Sime & Daane (2014); Kaneko (2002); Völkl & Mackauer (1993); Barzman & Daane (2001); Powell & Silverman (2010)
Non-discriminatory oviposition	*Coccidoxenoides perminutus*	Sime & Daane (2014)
Cryptic movements	*Pachyneuron aphidis*, *Lysiphlebus cardui*	Hübner & Völkl (1996); Völkl & Mackauer (1993)
Ant-like movements	*Lysiphlebus fabarum*, *Paralipsis enervis*	Rasekh *et al.* (2010), Völkl *et al.* (1996)
Learning capacity from encounters with aggressive ants	*Pauesia picta*, *Pauesia. pinicollis*	Völkl (2001)
Foraging in sites avoided by ants	*Pauesia silvestris*	Völkl & Kroupa (1997)
Reduced foraging time in host patches with ants or ant cues	*Lysiphlebus testaceipes*, *Tryoxis angelicae*, *Aenasius bambawalei*, *Anagyrus vladimiri*, *Tamarixia radiata*, *Acerophagous* sp., *Anagyrus lopezi*	Völkl & Mackauer (1993); Tanga *et al.* (2015); Fanani et al. (2020); Xu *et al.* (2020); Mouratidis *et al.* (2021); Kistner *et al.* (2017); Zhou *et al.* (2014)
Reduced oviposition attempts in host patches with ants or ant cues	*Anagyrus lopezi*, *Anagyrus pseudococci*, *Acerophagous*, *Aenasius babawalei*	Fanani *et al.* (2020); Tanga *et al.* (2015); Beltrá *et al.* (2015); Xu *et al.* (2020); Sime & Daane (2014)
Mating outside the natal patch	*Pauesia pini*	Mackauer & Völkl (2002); Nyabuga *et al.* (2012)
Chemical strategies		

Chemical mimicry of hemipteran hosts	*Lysiphlebus cardui*, *Lysiphlebus fabarum*, *Lysiphlebus hirticornis*, *Lysiphlebus japonicus*, *Adialytus arvicola*, *Paralipsis enervis*	Völkl (1992); (1994); Völkl & Mackauer (1993), Völkl *et al*. (1996); Liepert & Dettner (1993); Hertaeg *et al*. (2023); Mackauer & Völkl (2002); Kaneko (2002)
Chemical mimicry of ants	*Paralipsis eikoae*, *Paralipsis enervis*	Stary (1966); Akino & Yamoka (1998); Völkl *et al*. (1996)
Secretion of ant-deterrent substances	*Alloxysta* spp., *Phaenoglyphis* spp.	Völkl *et al*. (1994); Hübner (2000); Hübner *et al*. (2002)
Recognition and avoidance of ant chemicals	*Aenasius babawalei*, *Anagyrus vladimiri*	Xu *et al*. (2020); Mouratidis *et al*. (2021)
Morphological strategies		
Increased size and body hardness	*Aphidius ervi*	Hübner & Dettner (2000)
Reduced size	*Coccidoxenoides perminutus*	Sime & Daane (2014)
Telescoped abdomen	*Protaphidius nawaii*	Takada (1983)
Myrmecomorphy	*Encyrtus* spp., *Holcencyrtus* spp.	McIver & Stonedahl (1993); Kelly *et al*. (2022)