

Mutualisms between ants (Hymenoptera: Formicidae) and honeydew-producing insects: Are they important in ant invasions?

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Abstract

Recent studies suggest that the extraordinary success of invasive ants may be facilitated by facultative mutualisms with honeydew-producing insects. I evaluate this possibility in a review of the literature, focusing on five invasive ants that exhibit exceptionally large populations and whose impacts are considered to be most severe: *Anoplolepis gracilipes* (FR. SMITH, 1857), *Linepithema humile* (MAYR, 1868), *Pheidole megacephala* (FABRICIUS, 1793), *Solenopsis invicta* BUREN, 1972, and *Wasmannia auropunctata* (ROGER, 1863). For each, I consider whether they are strongly associated with honeydew-producing insects in their introduced range, whether honeydew or its constituent nutritional components can promote large population sizes, whether honeydew is utilized to a greater extent in the introduced than native range, and whether the ants promote larger populations of honeydew-producing insects, thereby further increasing honeydew availability. While each of these questions could not all be answered for all species, the evidence is consistent overall with the importance of honeydew-producing insects to invasive ants. Nevertheless, definitive studies remain to be conducted. Important questions to address include whether invasive ants are strongly associated with honeydew-producing insects throughout the broad geographic ranges they often occupy, and if the degree of association varies among locations, whether those locations also exhibit concordant differences in the size and impacts of invasive ant populations. In addition, it remains unclear whether associating with honeydew-producing insects may only be important in facilitating large populations of invasive ants, or whether those associations may also be important in determining if an introduced species actually becomes invasive. Finally, much of the work to date has focused on the characteristics of invasive ants, and little is known about the honeydew-producing insects that may promote them. What is known suggests that those most important to invasive ants may often be introduced or invasive themselves, and if so they may also exhibit important traits that facilitate their abundance at introduced locations.

Key words: Ants, carbohydrates, Hemiptera, honeydew, invasive species, review.

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Introduction

Mutually beneficial associations among species are frequent in nature, and they often have important consequences for ecological communities (BRONSTEIN 1994). Such mutualisms are exceptionally common between ants and honeydew-producing insects, with many ants engaging in them, including most species in the Myrmicinae, Dolichoderinae, and Formicinae (WHEELER 1910, WAY 1963, HÖLDOBLER & WILSON 1990). For the ants, honeydew can be a reliable and renewable source of food, while ant attendance can provide honeydew-producing insects with protection from their predators, parasites, and disease (WAY 1963, HÖLDOBLER & WILSON 1990, GULLAN 1997). However, the degree of associations between ants and honeydew-producing insects vary greatly, ranging from coincidental collection of honeydew by ants that provide little if any protection, to facultative mutualisms of a non-specific nature, to obligate co-evolved mutualisms and co-dependence among species (EISNER & BROWN 1958, WAY 1963, BUCKLEY 1987, EASTWOOD & FRASER 1999, DAVIDSON & al. 2004).

Research on associations between ants and honeydew-producing insects has progressed in two general directions, with one focusing on natural systems with the aim of understanding the ecological importance of mutualisms among native species (e.g., BUCKLEY 1987, DELABIE 2001). The other approach has focused on quantifying and mitigating the negative impacts of associations between introduced ants and honeydew-producing insects in agricultural and urban environments (e.g., GULLAN 1997, TOLLERUP & al. 2004). More recently, a third focus has emerged where the study of introduced ants and honeydew-producing insects is addressed within the ecological framework of invasion biology (ELTON 1958, SANDERS & SUAREZ 2011).

The role of honeydew-producing insects in ant nutrition

Honeydew is secreted by a variety of plant-feeding insects and it is often rich in carbohydrates, one of the primary macronutrients necessary for the growth and maintenance of ant colonies. The other macronutrient of primary importance is protein. In the ants, proteins supply the amino acids

necessary for growth, while carbohydrates are important sources of metabolic energy (e.g., ABBOTT 1978, STRADLING 1978, CASSILL & TSCHINKEL 1999). Proteins and carbohydrates are not utilized equally by all colony members, however, and how they are processed and utilized differs according to developmental stage. Adult workers consume and digest carbohydrates, relying upon them to fuel their activities, and they appear largely unable to digest proteins; even moderately high protein diets cause substantial worker mortality (COOK & al. 2010, DUSSUTOUR & SIMPSON 2012). Larvae, however, are dependent upon proteins to supply the amino acids necessary for their development, and most if not all protein digestion within colonies is accomplished by the developing brood (e.g., DUSSUTOUR & SIMPSON 2009, 2012). Moreover, the proteins acquired by ant colonies are often bulky solids such as insect prey, and adults are prevented from consuming them by the infra-buccal pocket located anterior to the crop (EISNER & HAPP 1962). Thus, while larvae can process and digest a variety of foods, including solid animal tissues, the survival and maintenance of workers is dependent upon carbohydrates in solution. In nature, such carbohydrates are often plant-based and occur as sugars in nectar and honeydew produced by insects feeding on plant phloem (e.g., AUCLAIR 1963, DELABIE 2001). While these sources of carbohydrates have long been known to be of great importance for many ant species, recent studies have also suggested that they play an important role in ant invasions.

Invasive ants and facultative mutualisms with honeydew-producing insects

Approximately 150 ant species, or about one-percent of those described, have been introduced outside their native range (MCGLYNN 1999, RABITSCH 2011). As many as 21 of these are considered invasive; however, the impacts of a relatively small number of species are exceptionally great (HOLWAY & al. 2002, SANDERS & SUAREZ 2011, GISD 2012). In general, the most important negative consequences of invasive ants occur because their populations can become extraordinarily large, much larger than within their native range (PORTER & al. 1997, SUAREZ & al. 1999, ABBOTT 2005, GRODEN & al. 2005). A variety of characteristics can facilitate such large populations, including release from natural enemies, a relaxed competitive environment, being adapted to disturbed environments, and colony social structures that reduce intraspecific competition and facilitate dispersal (MACOM & PORTER 1996, ROSS & al. 1996, PORTER & al. 1997, TSUTSUI & al. 2000, HOLWAY & al. 2002, ABBOTT 2005, NAKAMARU & al. 2007, CREMER & al. 2008, KING & TSCHINKEL 2008, TANAKA & al. 2011). Fundamentally, however, if other factors regulating population size such as predation pressure are equal, larger populations must be based on greater food resources. This can occur because more food is available in the introduced range or because the invasive species is better able to monopolize what is available.

Many studies have anecdotally noted that large populations of invasive ants are associated with large populations of honeydew-producing Hemiptera: most often aphids (Aphididae), soft scales (Coccidae), and mealybugs (Pseudococcidae) (e.g., HELMS & VINSON 2002, HOLWAY & al. 2002). Recently, studies have begun to rigorously document these associations and test how they may be important to

invasive ants and the Hemiptera with which they are associated. In reviewing these studies, I will focus on the five species of invasive ants often considered to have the most important negative impacts, *Anoplolepis gracilipes* (FR. SMITH, 1857), *Linepithema humile* (MAYR, 1868), *Pheidole megacephala* (FABRICIUS, 1793), *Solenopsis invicta* BUREN, 1972, and *Wasmannia auropunctata* (ROGER, 1863) (e.g., GISD 2012). Of these, *S. invicta*, *L. humile*, and *A. gracilipes* are best studied and considered in separate sections, while the information on *P. megacephala* and *W. auropunctata* are summarized together. For each, I will consider four general questions. First, are the ants strongly associated with honeydew-producing insects in their introduced range? Second, does honeydew or its primary ingredients, carbohydrate sugars, result in larger population sizes than would otherwise occur? Third, is honeydew utilized to a greater extent in the introduced range than in the native range? Fourth, is there a positive feedback loop where the ant promotes larger populations of honeydew-producing insects, further increasing the ants' access to honeydew? I then consider what the studies of the different species may tell us about the overall importance of honeydew-producing insects to invasive ants, and speculate on some of the important remaining questions.

***Solenopsis invicta*:** The red imported fire ant, *Solenopsis invicta*, is native to South America and has been introduced to the Caribbean Islands, North America, Taiwan, Australia, New Zealand, and China, where it has important negative consequences for ecological, urban, and agricultural systems (VINSON 1997, HOLWAY & al. 2002, TSCHINKEL 2006, ASCUNCE & al. 2011). Most early studies of *S. invicta* in its introduced range suggested that it is primarily a predator and scavenger of other arthropods (e.g., VINSON & GREENBERG 1986, WOJCIK & al. 2001, TSCHINKEL 2006). However, a study in the southeastern United States found that a majority of the food returned to nests were liquids with a chemical profile consistent with either honeydew or plant phloem (TENNANT & PORTER 1991). Further research found that *S. invicta* extensively tend both native and introduced honeydew-producing Hemiptera across the southeastern United States, and estimated from the density of hemipterans being tended that honeydew could provide an average colony with roughly one-half of its daily energy requirements (HELMS & VINSON 2002). Other studies found that a single widespread and abundant invasive mealybug, *Antonina graminis* (MASKELL, 1897), accounted for approximately 70% of all Hemiptera tended, and the size of *S. invicta* populations at field sites in Texas were found to be positively and significantly correlated with the abundance of the mealybug and indirectly by the mealybug's host plants (HELMS & VINSON 2002, HELMS & al. 2011). Furthermore, *S. invicta* has been found to construct shelters that house aphids and mealybugs, and studies show that they protect honeydew-producing Hemiptera from their natural enemies (HELMS & VINSON 2002, 2003, KAPLAN & EUBANKS 2002, COPPLER & al. 2007).

Although honeydew could supply *Solenopsis invicta* colonies with a significant portion of their energy budget, additional studies suggest that the importance of honeydew may not stem from its caloric content per se, but because it contains an important nutrient not readily available in other food sources. For example, when *S. invicta* colonies were provided with access to honeydew-producing mealybugs

in addition to unlimited insect prey, they grew significantly and substantially (~ 50%) larger over a 60 day period than did colonies fed unlimited insect prey in the absence of mealybug honeydew (HELMS & VINSON 2008). Thus, even though insect prey provided colonies with more calories than they could consume, the addition of honeydew still substantially increased growth. Similarly, WILDER & al. (2011a) found a significant increase in *S. invicta* colony size (~ 20%) over a seven week period when colonies were provided with access to honeydew-producing aphids in addition to ad libitum insect prey over when colonies were provided with ad libitum insect prey in the absence of aphids. A controlled field experiment over a seven week period also found a near doubling of *S. invicta* captured in pitfall traps within field plots that had plants colonized by aphids over plots where there were plants where the aphids were removed (WILDER & al. 2011a). Thus, the evidence available shows that honeydew must supply a resource important for *S. invicta* colony growth that is limited or unavailable in insect prey.

While honeydew is a complex mixture of substances, its primary ingredients are sugars such as sucrose, glucose, and fructose (e.g., AUCLAIR 1963), suggesting that these are the nutritional components important in increased colony growth. This has been substantiated by studies that supplement the diet of *Solenopsis invicta* with sugars in the absence of other substances available in honeydew. In an early study, PORTER (1989) found that the addition of unlimited sucrose to a diet of unlimited insect prey resulted in significantly increased colony growth over a diet of only unlimited insect prey; over a six-week period, total biomass of colonies fed sucrose in addition to insect prey diet was nearly three-times that of colonies that were fed only insect prey. Similarly, WILDER & al. (2011b) found that supplementing a diet of ad libitum insect prey with sucrose, glucose, and fructose resulted in an almost doubling of the dry mass of workers in colonies, and more than double the dry mass of brood, over that which occurred in colonies fed ad libitum insect prey alone. Moreover, worker mortality in their carbohydrate deprived treatment was approximately twice that in the carbohydrate supplement treatment, and they hypothesized that carbohydrate consumption has two important effects on colony growth: first, that it provides energy for workers to forage, and second, that it increases the rate of larval development because it decreases the degree that they must process food for distribution to worker maintenance (WILDER & al. 2011b; also see COOK & al. 2010).

The evidence is consistent with the potential that honeydew-producing Hemiptera promote larger populations of *Solenopsis invicta* in its introduced range; however, an important remaining question is why honeydew would promote exceptionally large populations at introduced locations while not in its native range. There appear to be two possible and not mutually exclusive hypotheses. The first is that the abundance of honeydew-producing insects and similar sources of carbohydrates are greater at introduced locations than within the native range, while the second is that *S. invicta* has greater access to those that occur at introduced locations. In studies that compare the nutritional ecology of *S. invicta* in its native range in Argentina versus its introduced range in the United States, WILDER & al. (2011a) found from stable isotope analysis that *S. invicta*

in the southeastern United States occupy a lower trophic position than those in Argentina, consistent with honeydew and / or plant exudates being a more important component of the diet in the introduced range. Moreover, *S. invicta* is largely excluded from sources of honeydew and plant exudates by competitor ant species in Argentina, while they are able to largely monopolize them in the United States. WILDER & al. (2011a) conclude that large populations of *S. invicta* in the southeastern United States are facilitated by access to honeydew and other similar sources of carbohydrates, and that those sources are more available in the introduced range due to differences in the competitive environment. Whether carbohydrate resources are more abundant in the introduced than native range of *S. invicta* has not been directly studied; however, consistent with the possibility, HELMS & VINSON (2002) found that *S. invicta* in the southeastern United States were more often associated with an exceptionally abundant invasive mealybug of Asian origin than with less abundant native honeydew-producing insects (Fig. 1).

***Linepithema humile*:** The Argentine ant, *Linepithema humile*, is native to South America and occurs as an invasive species in Africa, Asia, Australia, the Middle East, Europe, North America, and on many oceanic islands (SUAREZ & al. 2001, WETTERER & al. 2009). At most introduced locations, it is an important ecological, urban, and agricultural pest. It has long been known to tend honeydew-producing Hemiptera extensively in its introduced range, and correlative historical data suggest that associations with those Hemiptera could have been important in early invasions (NEWELL & BARBER 1913, WAY 1963, MARKIN 1970, HUMAN & al. 1998, ADDISON & SAMWAYS 2000, AGUIAR & WETTERER 2006). Moreover, experiments suggest that carbohydrate availability may be important in whether *L. humile* is able to invade new habitats in their introduced range (ROWLES & SILVERMAN 2009), and other studies suggest that the carbohydrate constituents of honeydew and / or plant exudates could be important in facilitating large populations. GROVER & al. (2007) fed *L. humile* colonies different combinations insect prey (zero, low and high) and sucrose (zero, low, and high) over a 12-week period, and while they found that the interactions between different levels of carbohydrates and proteins were complex, they also found that brood mass increased significantly with increasing sucrose level, consistent with studies of *Solenopsis invicta* outlined in the previous section. They also found that sucrose resulted in increased worker activity and aggression while insect prey did not, suggesting that carbohydrates may be important in successful competitive interactions and resource acquisition (GROVER & al. 2007; also see KAY & al. 2010). In another experiment, KAY & al. (2010) also fed *L. humile* colonies diets that differed in their sucrose to insect prey content. Over 12 weeks, they found that the ratio of carbohydrates to proteins had a large and significant effect on final colony size (worker numbers), with an approximate doubling of worker number in the highest carbohydrate to protein ratio over the lowest, with intermediate worker numbers at intermediate ratios.

The previous studies show that honeydew has the potential to result in larger *Linepithema humile* populations in their introduced range if it is in greater supply or else they are able to monopolize it to a greater degree. A stable iso-



Fig. 1: Trophic interactions between an invasive ant, mealybug, and grass in the southeastern United States. A: Native to South America, the invasive ant *Solenopsis invicta* solicits and collects honeydew produced by a mealybug native to Asia, *Antonina graminis*, while the mealybug feeds on a preferred host grass native to Africa, *Cynodon dactylon* (L.) PERS., 1805. For more information on this system see HELMS & VINSON (2002) and HELMS & al. (2011). B: In the absence of ant tending, *A. graminis* produces wax tubes that transports honeydew droplets away from the body. Photographs are by the author.

tope analysis by TILLBERG & al. (2007) suggests that this could be the case. Their analysis found that honeydew and / or plant exudates appear to form a greater proportion of their diet at sites in the United States (California) than at sites in their native range in Argentina (TILLBERG & al. 2007). However, a stable isotope analysis along an active invasion front in California found that the diet and population size of *L. humile* shifted over time. Population size was greatest just behind the invasion front and decreased in habitat invaded in previous years. Seemingly inconsistent with the importance of carbohydrates in promoting *L. humile* invasions, the stable isotope signature of ants along the invasion front indicated that their diet consisted of relatively more animal tissues, while those in previously invaded areas consisted of relative more honeydew and / or plant exudates. The amino acids in animal tissues are important in colony growth (e.g., HELMS & VINSON 2008), and TILLBERG & al. (2007) proposed that this trend occurs because animal-based foods are depleted during initial invasion which necessitates an overreliance on carbohydrates. However, it is unclear whether these results are inconsistent with a general importance of plant-based carbohydrates to *L. humile* during invasion. For example, TILLBERG & al. (2007) point out that the diet shift they observed could have been influenced by differences in the availability of food resources over time resulting from annual variation in the environment; abnormally wet years occurred early in the study, while abnormally dry years followed. Whether dietary shifts are a common feature of *L. humile*, or other ant invasions, and what they tell us about the importance of plant-versus animal-based foods during the invasion process clearly deserves further study. Most important, we need studies that assess whether carbohydrates are in fact a key resource important in determining the population size of invasive ants by determining the availability of carbohydrates and proteins in the environment relative to the ability of invasive ant colonies to utilize them.

Whether carbohydrate resources are more abundant in the introduced than native range of *Linepithema humile* has apparently not been studied. However, because *L. humile*

commonly displaces many native ant species during invasion (HUMAN & GORDON 1996, HOLWAY 1999), a shift to increasing use of honeydew and / or plant exudates during invasion may indicate that they are better able to monopolize whatever carbohydrate resources are available in the introduced range. Moreover, substantial observational as well as experimental evidence show that *L. humile* provide protection for honeydew-producing Hemiptera and promote large hemipteran populations, providing positive feedback in increasing carbohydrate resources with increasing utilization (e.g., NEWELL & BARBER 1913, WAY 1963, POWELL & al. 2009, BRIGHTWELL & SILVERMAN 2010).

***Anoplolepis gracilipes*:** The native range of the yellow crazy ant, *Anoplolepis gracilipes*, is uncertain, although it is hypothesized to be either Africa or Asia. It occurs as an invasive species in Australia, Central America, and many oceanic islands, where populations can become extremely large and result in important negative impacts on ecological and agricultural systems (MCGLYNN 1999, LESTER & TAVITE 2004, ABBOTT 2005, WETTERER 2005, GREEN & al. 2011). *Anoplolepis gracilipes* makes extensive use of honeydew and plant exudates in its introduced range, and it is hypothesized that mutualisms with introduced honeydew-producing Hemiptera are important in facilitating their negative effects (HAINES & HAINES 1978, O'DOWD & al. 2003, LESTER & TAVITE 2004, KRUSHELNYCKY & al. 2005, GREEN & al. 2011, SAVAGE & al. 2011). Probably the best studied location is Christmas Island in the Indian Ocean, where *A. gracilipes* arrived sometime around 1930, persisted at low densities for decades, and then began to form supercolonies, resulting in extremely large populations. These colonies are altering the Island's flora and fauna by tending large populations of honeydew-producing scale insects, preying upon native land crabs, and facilitating the invasion of introduced land snails (O'DOWD & al. 2003, ABBOTT 2005, GREEN & al. 2011).

While there are many reports of abundant *Anoplolepis gracilipes* associated with large populations of honeydew-producing Hemiptera (e.g., BAKER 1972, HAINES & HAINES 1978, O'DOWD & al. 2003, LESTER & TAVITE 2004, AB-

BOTT 2005, TANAKA & al. 2011), apparently no experiments have been conducted to test for the effect of honeydew or similar carbohydrate resources on colony growth. Nevertheless, one experiment does suggest that carbohydrates are likely to be particularly important to *A. gracilipes*. When SAVAGE & al. (2011) experimentally increased carbohydrate (sucrose) availability on plants, they found that the density of foraging ants nearly quadrupled, while those tending honeydew-producing insects decreased by approximately one-half. This result suggests that carbohydrates are important to *A. gracilipes* because of their preference for unadulterated sugar over the mixture of sugars, amino acids, and other substances that occur in honeydew (SAVAGE & al. 2011).

Because the native range of *Anoplolepis gracilipes* is unclear, it is obviously unknown whether honeydew and plant exudates are used more extensively in the introduced range, or whether they are more readily available. However, it is known that *A. gracilipes* can facilitate large populations of honeydew-producing insects. When they were excluded from swaths of forest on Christmas Island, populations of scale insects collapsed in the removal areas, consistent with the promotion of honeydew-producing Hemiptera (ABBOTT & GREEN 2007).

***Wasmannia auropunctata* and *Pheidole megacephala*:** *Wasmannia auropunctata* is native to Central and South America, while *Pheidole megacephala* is native to Africa. Both ants are invasive species on islands of the Pacific and Atlantic Oceans. *Wasmannia auropunctata* is also invasive in North America and Africa, while *P. megacephala* is also invasive in Asia, Australia, New Zealand, and Europe (MCGLYNN 1999, WETTERER & PORTER 2003, WETTERER 2007, 2012). Both ants have important negative consequences for agricultural and ecological systems in their introduced ranges (e.g., WETTERER & PORTER 2003, WETTERER 2007). Moreover, both *W. auropunctata* and *P. megacephala* are reported to tend honeydew-producing Hemiptera extensively and promote increased hemipteran populations (*P. megacephala*: BACH 1991, GONZÁLEZ-HERNÁNDEZ & al. 1999, WETTERER 2007, HOFFMANN & KAY 2009, GAIGHER & al. 2011, TANAKA & al. 2011; *W. auropunctata*: LUBIN 1984, WETTERER & PORTER 2003, LE BRETON & al. 2005, DUNHAM & MIKHEYEV 2009). However, the importance of honeydew or carbohydrates to colony growth has apparently not been tested experimentally for either species, and there are apparently no comparisons of trophic ecology in their native versus introduced ranges.

Conclusions

This review shows that all of the invasive ant species whose impacts are considered particularly important form extensive associations with honeydew-producing insects in their introduced ranges. If the studies of *Linepithema humile* and *Solenopsis invicta* are broadly applicable, these associations can promote large populations of invasive ants because the carbohydrates readily available in honeydew allow for increased colony growth. Furthermore, all of the reviewed species are known to provide protection for the honeydew-producing insects they tend, which could result in positive feedback loops where larger populations of invasive ants result in larger populations of honeydew-producing insects, which then promote even larger populations of invasive ants.

If associations with honeydew-producing insects are important in facilitating larger populations of invasive ants, then honeydew should form a larger proportion of the diet in introduced populations and a smaller proportion in populations within the native range. The information for *Solenopsis invicta* and *Linepithema humile* are consistent with this prediction, while the possibility has not been tested for the remaining species. Moreover, in order for honeydew to form a larger proportion of the diet in the introduced range, there must be larger populations of honeydew-producing insects, or else the invasive species must have greater access to what is available. For *S. invicta*, it appears that they have greater access because they are competitively dominant over other ants in the introduced range (PORTER & SAVIGNANO 1990, WILDER & al. 2011a, WILDER & al. in press). While untested, this could also be the case for the remaining species reviewed, as studies show that all can be competitively dominant over other ant species at introduced locations (CLARK & al. 1982, HOLWAY 1999, VANDERWOUDE & al. 2000, DRESCHER & al. 2011). In addition, the evidence is consistent with invasive ants promoting larger populations of honeydew-producing insects in their introduced ranges.

In considering the potential role of honeydew in promoting large populations of invasive ants, it is important to recognize that the carbohydrates within honeydew cannot by themselves result in population growth; the bulk of essential amino acids necessary to produce new offspring must be acquired elsewhere. For example, laboratory colonies of *Solenopsis invicta* can grow substantially when only insect prey is available, while no brood is produced and colony size declines when only sugar or honeydew are available (PORTER 1989, HELMS & VINSON 2008). Only when those carbohydrate sources are available in addition to insect prey do colonies exhibit exceptional growth (PORTER 1989, HELMS & VINSON 2008). Because carbohydrates are important for worker survival and in fueling their activity, they can result in a larger standing worker force and increased worker activity, and in nature this should result in greater colony success in acquiring additional food resources. Carbohydrates may also increase the rate of larval development if it decreases the degree that larvae must process food for distribution to worker maintenance (COOK & al. 2010, WILDER & al. 2011b). Thus, the evidence suggests that carbohydrates could be a key limiting resource affecting population size of invasive ants (WILDER & al. 2011a, b).

It is also important to note that the availability of food, whether it is honeydew, other carbohydrate sources, or animal tissue, is unlikely to be the only factor responsible for whether an introduced species will achieve the exceptionally large population sizes exhibited by many invasive ants. Many native and introduced ant species are likely to utilize honeydew extensively; however, they do not become important invaders, even though carbohydrates may still be important for colony growth (HÖLLDOBLER & WILSON 1990, WILDER & al. in press). In addition to having access to greater food resources in the introduced range, it seems that invasive species must also exhibit life history characteristics that allow for exceptional population growth when the resources are available to do so.

One of the least well-understood aspects of the facultative mutualisms formed between honeydew-producing insects and invasive ants is whether particular species of

Tab. 1: Native and non-native or invasive honeydew-producing Hemiptera associated with five major species of invasive ants in their introduced ranges. The term "non-native / invasive" is used for introduced Hemiptera because the terminology describing species' impacts often varies in the literature; e.g., a species can be variously described as introduced, a pest, invasive, or naturalized. This table is expanded and updated from table 3 in HELMS & VINSON (2002). ^a NEWELL & BARBER (1913) report that *Linepithema humile* tended 48 species of scale insects in a single park in New Orleans, Louisiana, but provide only a limited list of species identities. They are excluded from this table, but are discussed in the Conclusions section. ^b While considered to be an introduced species here, *Aphis gossypii* is of unknown geographic origin and widely distributed in tropical and temperate regions throughout the world where it is often considered an important agricultural pest. ^c HELMS & VINSON (2002) also report that *Solenopsis invicta* tends Hemiptera in the Aclerididae, Aphididae, and Coccidae; whether these were native or introduced species is unknown.

Honeydew-producing Hemiptera tended	References
by <i>Anoplolepis gracilipes</i>	
<p>Non-Native/Invasive: <i>Ceroplastes ceriferus</i> FABRICIUS, 1798, <i>Ceroplastes destructor</i> NEWSTEAD, 1917, <i>Ceroplastes rubens</i> MASKELL, 1893, <i>Coccus celatus</i> DE LOTTO, 1960, <i>Coccus hesperidum</i> (LINNAEUS, 1758), <i>Coccus viridis</i> (GREEN, 1889), <i>Milviscutulus mangiferae</i> (GREEN, 1889), <i>Paratachardina lobata</i> (CHAMBERLIN, 1923), <i>Saissetia coffeae</i> (WALKER, 1852), <i>Saissetia oleae</i> (OLIVIER, 1791), <i>Tachardina aurantiaca</i> (COCKERELL, 1903)</p> <p>Native: None</p>	<p>HAINES & HAINES (1978), KRUSHELNYCKY & al. (2005), ABBOTT & GREEN (2007), GREEN & al. (2011)</p>
by <i>Linepithema humile</i>	
<p>Non-Native/Invasive: <i>Chromaphis juglandicola</i> (KALTENBACH, 1843), <i>Coccus hesperidum</i>, <i>Coccus viridis</i>, <i>Dysmicoccus brevipes</i> (COCKERELL, 1893), <i>Dysmicoccus neobrevipes</i> BEARDSLEY, 1959, <i>Icerya purchasi</i> MASKELL 1878, <i>Planococcus citri</i> (RISSO, 1913), <i>Planococcus ficus</i> (SIGNORET, 1875), <i>Pseudococcus longispinus</i> (TARGIONI TOZZETTI, 1867), <i>Pseudococcus viburni</i> (SIGNORET, 1875), <i>Sacchariococcus sacchari</i> (COCKERELL, 1895), <i>Saissetia oleae</i>, <i>Toxoptera aurantii</i> (BOYER DE FONSCOLOMBE, 1841)</p> <p>Native: <i>Beaufortiana</i> DISTANT, 1916 sp., <i>Chaitophorus populicola</i> THOMAS, 1877, <i>Pseudococcus maritimus</i> (EHRHORN, 1900), <i>Toumeyella virginiana</i> WILLIAMS & KOSZTARAB, 1972</p>	<p>MARKIN (1970), FRAZER & VAN DEN BOSCH (1973), ROHRBACH & al. (1988), REIMER & al. (1990), GONZÁLEZ-HERNÁNDEZ & al. (1999), ADDISON & SAMWAYS (2000), DAANE & al. (2007), POWELL & al. (2009), BRIGHTWELL & SILVERMAN (2010), YOO & HOLWAY (2011), KRUSHELNYCKY & al. (2005), LACH (2007); Also see NEWELL & BARBER (1913) ^a</p>
by <i>Pheidole megacephala</i>	
<p>Non-Native/Invasive: <i>Coccus viridis</i>, <i>Coccus hesperidum</i>, <i>Dysmicoccus brevipes</i>, <i>Dysmicoccus neobrevipes</i>, <i>Phenacoccus manihoti</i> MATILE-FERRERO, 1977, <i>Planococcus citri</i>, <i>Pseudococcus longispinus</i>, <i>Pulvinaria urticae</i> COCKERELL, 1893, <i>Sacchariococcus sacchari</i></p> <p>Native: None</p>	<p>STEYN (1955), ROHRBACH & al. (1988), REIMER & al. (1990, 1993), BACH (1991), CUDJOE et al. (1993), CAMPBELL (1994), GONZÁLEZ-HERNÁNDEZ & al. (1999), HOFFMANN & KAY (2009), GAIGHER & al. (2011)</p>
by <i>Solenopsis invicta</i>	
<p>Non-Native/Invasive: <i>Antonina graminis</i> (MASKELL, 1897), <i>Aphis gossypii</i> GLOVER, 1877^b, <i>Toxoptera citricida</i> (KIRKALDY, 1907)</p> <p>Native: <i>Antoninoides boutelouae</i> PARROTT, 1900, <i>Antoninoides nortoni</i> (PARROTT & COCKERELL, 1899), <i>Antoninoides parrotti</i> (COCKERELL, 1903), <i>Chorizococcus</i> MCKENZIE, 1960 sp., <i>Phenacoccus</i> COCKERELL, 1893 sp., <i>Trionymus</i> BERG, 1899 sp.</p>	<p>MICHAUD & BROWNING (1999), HELMS & VINSON (2002)^c, DIAZ & al. (2004)</p>
by <i>Wasmannia auropunctata</i>	
<p>Non-Native/Invasive: <i>Aphis gossypii</i>, <i>Coccus viridis</i>, <i>Icerya purchasi</i>, <i>Planococcus citri</i>, <i>Saissetia hemisphaerica</i> TARGIONI-TOZZETTI, 1867, <i>Toxoptera aurantiae</i> (BOYER DE FONSCOLOMBE, 1841), <i>Tarophagus</i> OUDEMANS, 1924 sp.</p> <p>Native: Margarodidae MORRISON, 1927 (genus and species not identified)</p>	<p>SPENCER (1941), FOWLER & al. (1990), LUBIN (1984), DELABIE & al. (1994), FASI (2009), LE BRETON & al. (2005)</p>

honeydew-producers are exceptionally important, and if so, whether those species share some common key characteristics. One possible shared characteristic is that the insects tended by invasive ants may often be introduced species themselves (HELMS & VINSON 2002). Moreover, mutua-

lisms between introduced species could have general importance in facilitating biological invasions, a process known as "invasional meltdown" (SIMBERLOFF & VON HOLLE 1999). There is now strong evidence that invasional meltdown occurs between *Anoplolepis gracilipes* and intro-

duced honeydew-producing Hemiptera on Christmas Island (O'DOWD & al. 2003, GREEN & al. 2011). It is also known that *Solenopsis invicta* is strongly associated with an invasive mealybug of Asian origin in the southeastern United States (HELMS & VINSON 2002, HELMS & al. 2011). However, whether invasive ants are often facilitated by association with introduced honeydew-producing insects across their introduced ranges remains unclear. Nevertheless, there are indications that such facilitation could be common. For example, a review of the literature on the honeydew-producing Hemiptera associated with invasive ants shows that the Hemiptera that have been identified are very often non-native species (Tab. 1). One factor that may contribute to this result is that associations between invasive ants and honeydew-producing insects have often been studied in agricultural and island ecosystems, where a large proportion of the Hemiptera are introduced species whose identities are relatively well-known. Consistent with the possible under-reporting of the numbers of native Hemiptera species tended by invasive ants is the observation by NEWELL & BARBER (1913) that within a single city park in Louisiana, USA, *Linepithema humile* tended 48 species of scale insects over an 18 month period. Presumably a majority of those species were native. They also noted, however, that *L. humile* tended most species sparingly, and focused on six species. Five of these six are introduced species that often exhibit large populations and are considered to be important widespread pests, and the single native species appeared important to *L. humile* only a seasonal basis (NEWELL & BARBER 1913, MILLER & al. 2005). Thus, the high proportion of introduced Hemiptera associated with invasive ants (Tab. 1) may also be attributed to the numerical dominance of species being tended, and those relatively small numbers of introduced species could have major impacts.

The probability that invasive ants may encounter introduced honeydew-producing Hemiptera within their introduced ranges is high because so many species have become established outside their native range. For example, of the aphids, 18% (262 species) in the United States and Canada, and 7% (102 species) in Europe are non-native (FOOTITT & al. 2006, COEUR D'ACIER & al. 2010). Similarly, 21% (99 species) of the soft scales and mealybugs in the continental United States, and 40% (60 species) of those in Europe are non-native (MILLER & al. 2005, PELLIZZARI & GERMAIN 2010). Moreover, similar to invasive ants, it is likely that introduced honeydew-producing Hemiptera may lack natural enemies in their introduced range, and could have life history characteristics that allow for high reproductive potential. Such Hemiptera may also exhibit traits that result in exceptional attendance by ants, while the ants may exhibit traits that make them particularly effective at tending (e.g., PARIS & ESPADALER 2009, POWELL & al. 2009, TANAKA & al. 2011, MCPHEE & al. 2012). In these cases, both parties could potentially achieve larger populations than otherwise possible, resulting in environmental impacts greater than either would cause alone.

Whether or not non-native honeydew-producing insects are of particular importance in facilitating ant invasions is a question that clearly deserves further research. Such research must emphasize identifying and determining the relative abundances of native and introduced honeydew-producing insects associated with invasive ants. From there,

laboratory experiments would be able to determine the per capita and cumulative effects of the different honeydew-producing species on ant colony growth. Further experiments in the field or laboratory could then determine the relative effect of invasive ants on abundance of the different honeydew-producing insects. One challenging aspect of such studies is likely to be species identifications of honeydew-producing insects, and collaborations with expert taxonomists would be a great advantage.

Some future directions

Although the research reviewed is generally consistent with the importance of honeydew-producing insects to invasive ants, definitive answers await further study. At present, we have limited relevant information for the great majority of invasive ants, and we know very little about the importance of honeydew-producing insects to any invasive ant throughout the broad geographic ranges in which they often occur. If globally important, extensive associations with honeydew-producing insects should be ubiquitous within and across introduced geographic ranges, or if the degree of association varies geographically, then the population sizes and impacts of the invasive species should vary concordantly. These are important tests that remain to be conducted.

In understanding the potential role of honeydew-producing insects in promoting ant invasions, there are actually two related questions; one is whether honeydew-producing insects are important in promoting the abundance of species already invasive, and much of the research addressed in this review only clearly addresses that question. The second is whether associations with honeydew-producing insects are important in determining whether an introduced species has the capability to become invasive. While there may be a variety of ways to address this question, one approach is to study the importance of associations with honeydew-producing insects in invasive ants versus co-occurring introduced species that do not become invasive. The important question there is whether invasive species are more proficient on a per capita basis at utilizing honeydew-producing insects to increase their population growth than are other introduced ants, and whether they are better per capita at promoting those insects in order to ensure or increase honeydew availability. A complementary approach is to determine whether invasive species are superior in these regards to the native ant species they replace or suppress during the invasion process. Both types of studies should provide valuable information on whether the probability of becoming invasive is linked to adaptations for exploiting and promoting honeydew-producing insects.

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