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# Honeydew management to promote biological control[☆]

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Honeydew is the excretion of plant-feeding hemipterans and it is one of the most abundant source of carbohydrates for parasitoids and predators in agroecosystems. Being so abundant, honeydew mediates direct and indirect interactions that affect biological control. We describe these interactions and identify honeydew-management strategies to reduce pest pressure. First, the presence of nondamaging honeydew producers in cover crops and hedges increases the efficacy of parasitoids and predators. Second, breaking the mutualism between ants and honeydew-producing pests with alternative sugar sources promotes biological control of these pests. Third, we propose to explore honeydew volatiles to attract biological control agents and repel pests, as well as to induce plant defenses. Finally, we urge reducing the use of systemic pesticides that contaminate honeydew and negatively affect biological control agents that feed on it. Overall, we propose that honeydew management is integrated in pest management programs to contribute to sustainable agriculture.

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## Introduction

Honeydew is the excretion product of many plant-feeding hemipterans and some lepidopterans. Historically, honeydew has been viewed only as a problem in agriculture because it is the growth medium of sooty molds that reduce the photosynthetic capacity of the plant and cause aesthetic damage to the fruits. However, this excretion product is also one of the most abundant and accessible source of carbohydrates for parasitoids and predators in many agroecosystems and, thus, it mediates many interactions that affect biological control [1,2]. This perspective paper highlights how honeydew-mediated interactions can be managed to enhance biological control of arthropod pests in agriculture. For that, we i) describe the main groups of honeydew producers and honeydew feeders; ii) explain the interactions mediated directly or indirectly by honeydew; and iii) propose strategies to promote pest suppression by managing honeydew in agroecosystems.

### Honeydew producers

The biggest group of honeydew producers are hemipterans of the suborder Sternorrhyncha (Figure 1). This group is one of the most diverse insect orders and comprises ca. 18 700 species, including many difficult-to-manage pests such as aphids, whiteflies, psyllids, mealybugs, and soft scales [3]. In general, honeydew excreted by these hemipterans is rich in carbohydrates because they feed on phloem sap [4]. On the

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other hand, hemipterans belonging to the suborder Auchenorrhyncha are xylem sap feeders and excrete honeydew with low-carbohydrate concentration. This latter group includes important pest species such as froghoppers, leafhoppers, and treehoppers. Finally, larvae from the lepidopteran families Lycaenidae and Riodinidae excrete honeydew that is low in carbohydrates, but may contain substantial quantities of amino acids [4]. In this review, we will focus on hemipterans of the suborder Sternorrhyncha because they are very abundant and excrete carbohydrate-rich honeydew.

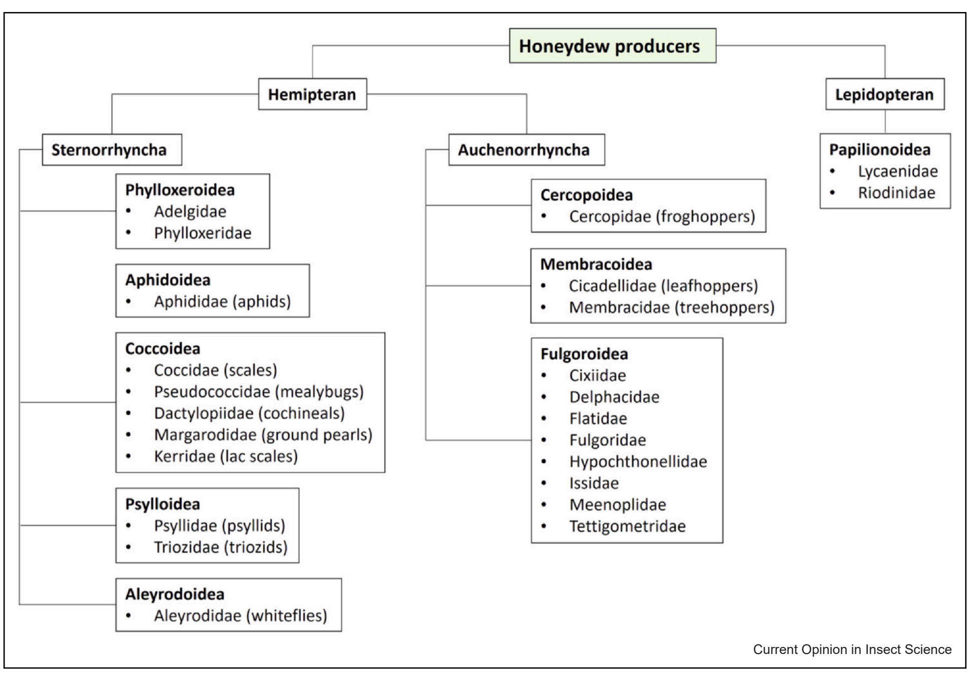
## Honeydew as a food source for arthropods in agroecosystems

Honeydew composition, and thus its nutritional value as food source for biological control agents, is highly variable. It depends on host-plant species, plant physiology, honeydew-producing species and its developmental stage and age, duration and rate of infestation, mutualism between honeydew producers and ants, presence of bacterial symbionts, and presence of plant secondary metabolites [5–7]. In general, more than 80% of honeydew dry matter contains sugars [5]. Some of those sugars are synthesized by the plant, such as fructose, glucose, sucrose, or maltose, whereas others are synthesized by the honeydew producer, such as trehalose, erlose, melezitose, raffinose, stachyose, mannitol, or sorbitol [1,6,8]. In addition to carbohydrates, honeydew can contain amino acids, micronutrients, sterols, plant secondary metabolites, and microorganisms [7,9]. While some of these reduce the nutritional value of honeydew (e.g. plant secondary metabolites), others increase it (e.g. antioxidant proteins) [9,10].

## Main groups of honeydew feeders: arthropods and microorganisms

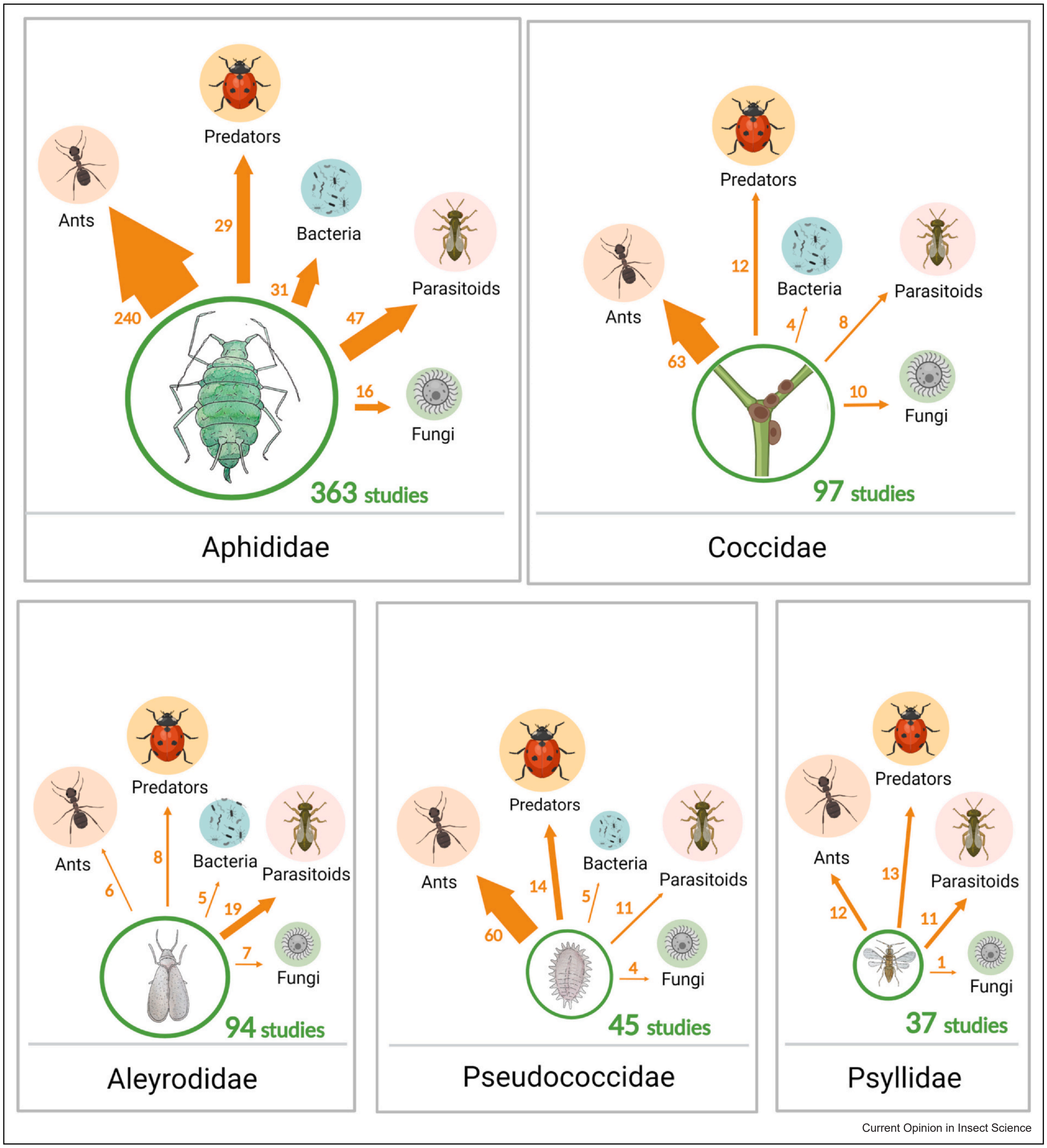
Even though the nutritional value of honeydew is highly variable, arthropods with different lifestyles feed on honeydew and rely on it as a carbohydrate source [1,2,11] (Figure 2). Among these arthropods, many beneficials need honeydew for survival and reproduction. Parasitoids, predators, and pollinators from different orders such as Hymenoptera (e.g. parasitic wasps, honey bees, solitary bees, and bumble bees), Diptera (e.g. tachinid flies, hoverflies), Coleoptera (coccinellids), Neuroptera (e.g. lacewings and coniopterygids), Lepidoptera (e.g. butterflies), Araneae (e.g. predatory spiders), and Mesostigmata (predatory mites) are some of the beneficial arthropods that use honeydew as a food source. However, honeydew is not only consumed by beneficial arthropods, but also by some pests and hyperparasitoids in the adult stage [8]. Moreover, some ant species have established mutualistic relationships with honeydew producers, feeding on honeydew and protecting the hemipterans from their natural enemies [12]. Besides

**Figure 1**




Honeydew-producing insects across the class Insecta. Sternorrhyncha feed on phloem sap and excrete honeydew to reduce the osmotic pressure results of a rich-sugar diet. Auchenorrhyncha feed on xylem sap. In the case of the Lepidoptera, larvae of some species in the Lycaenidae and Riodinidae families secrete honeydew through a specialized dorsal nectary gland, known as Newcomer's gland, to provide sugars to mutualistic species.

**Figure 2**




Interactions between honeydew producers and honeydew feeders. In the five panels, the five main families of honeydew producers are represented in the bottom, connected with arrows with the main groups of honeydew feeders. We selected the main groups of honeydew feeders based on their relevance for biological control. We included for each family, the number of publications that investigated honeydew produced by members of that family, and this number determines the size of the green circle around each honeydew producer. In addition, next to the arrows connecting the honeydew producers and the honeydew feeders, we include the number of studies that reported the honeydew-mediated interaction. The width of the arrows represents the number of studies that reports each interaction. For the literature search, we used Web of Science with the searching criteria specified in the supplemental materials.

arthropods, many fungi and bacteria grow on honeydew [7,13]. From these microorganisms, sooty mold fungi are the best-known in agriculture because they cause aesthetic damage on fruits and vegetables and reduce the photosynthetic capacity of the plant. Many other microorganisms also grow on honeydew, changing its volatile profile, its nutritional value, and, likely, the ecological interactions mediated by honeydew [7].

### Honeydew mediates interactions in biological control

The high accessibility of honeydew and the numerous organisms that excrete it, feed on it, or use it as a source of infochemicals make honeydew a key driver of interactions between arthropods within and across different trophic levels [14]. As many honeydew producers are considered pests and many honeydew feeders are biological control agents, honeydew-mediated interactions influence the outcome of biological control programs. A well-known example of a *direct, positive interaction* mediated by honeydew is the mutualism between ants and honeydew producers, where the ants gain food and provide protection to the honeydew producer. In contrast, honeydew mediates *direct, negative interactions* between honeydew-producing pests and their biological control agents. After feeding on honeydew of their host/prey, parasitoids and predators increase parasitism or predation rates. Finally, honeydew can also reduce the host/prey searching time of biological control agents as they may use it as infochemical [1,2,15].

In addition to direct interactions, honeydew mediates *indirect interactions* between arthropods. In these interactions, the impact of one species on another is mediated by the consumption of honeydew by a third species. These interactions are more complex than direct interactions and less frequently studied. For example, honeydew increases the fitness and performance of biological control agents of herbivore pests that do not excrete honeydew, such as beetles or armored scales [16,17]. Volatiles released by microorganisms growing on honeydew can also affect indirect interactions between insects in contrasting ways. While microorganism-produced volatiles can improve the ant-tending service to honeydew producers and thus indirectly benefit ants and honeydew producers, these volatiles can also attract biological control agents of honeydew producers [7,18]. Remarkably, because honeydew is known to be consumed by organisms from the second to the fourth trophic level, multitrophic interactions may occur when multiple insects feed on honeydew [8,19].

## How to manage honeydew-mediated interactions to improve biological control

As honeydew mediates interactions between biological control agents and pests, understanding how these interactions affect pest management is crucial. Here, we propose several ways in which honeydew-mediated interactions can be exploited to improve pest management in agriculture while reducing the application of pesticides (Figure 3).

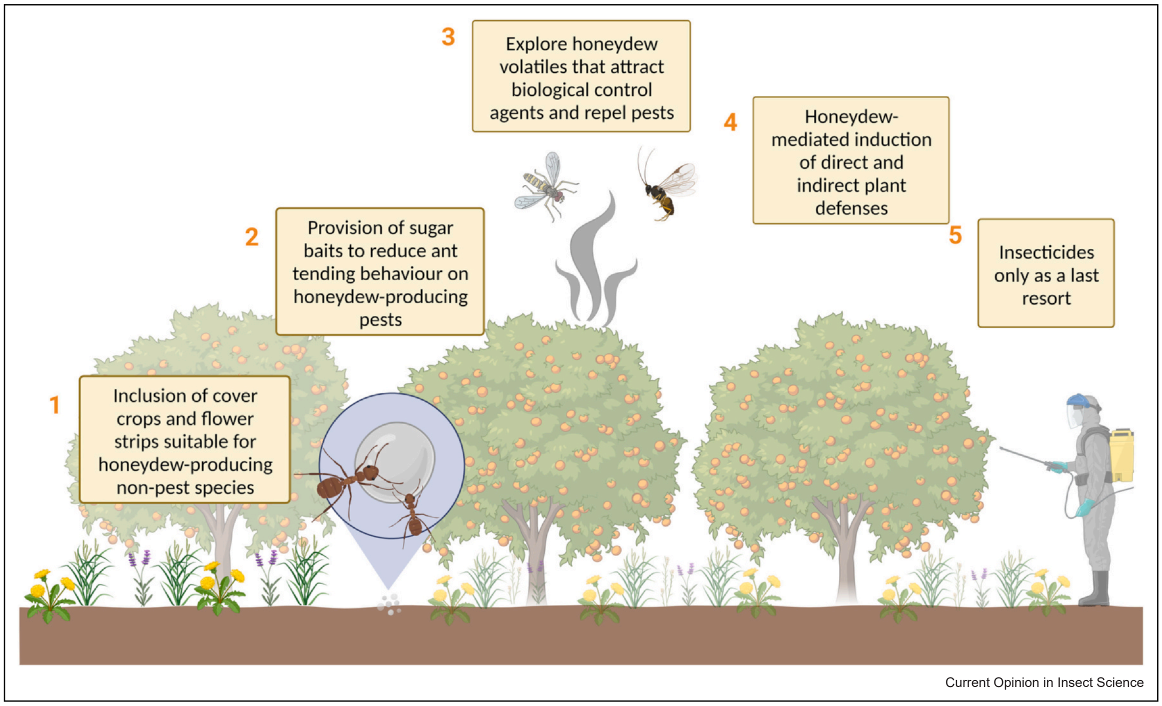
### Promote the presence of nondamaging honeydew-producing species to increase the attraction and fitness of parasitoids and predators

The inclusion of flower strips is a common sustainable agricultural practice to meet the carbohydrate requirements of biological control agents [20–24] (Figure 3.1). Many efforts are being made to design a proper flower combination to ensure season-long nectar provision for biological control [20]. Nonetheless, as weather conditions are becoming less predictable and more extreme, there is often low or no nectar availability [25]. In addition to flower strips, we propose designing cover plants suitable for honeydew-producing nonpest species. Plants infested with honeydew-producing nonpest species can provide extra carbohydrate sources for biological control agents that are independent of the flowering time [26]. Remarkably, many of these honeydew producers are preyed upon or parasitized by generalist arthropod species, opening opportunities for boosting conservation biological control [27]. Although it is more controversial and more difficult to implement, natural infestation with some honeydew-producing species may benefit biological control of key pest species. Some crops, especially evergreen fruit trees, can tolerate low infestation levels of nondamaging honeydew-producing species. These hemipterans can excrete high-quality honeydew for biological control agents that can boost their density and control key pest species [6,28]. These conservation biological control strategies have not yet been investigated to our knowledge. Finally, it is worth mentioning that some honeydew drops may end up on the soil surface and may alter the communities of soil microorganisms and biological control agents.

### Break ant protection of honeydew-producing species

Many invasive and difficult-to-manage hemipterans have established mutualistic interactions with ants [29,30]. Breaking this mutualism can improve biological control of honeydew-producing pests. This can be done by providing ants with sugar baits to reduce their tending behavior on honeydew-producing pests [31] (Figure 3.2). Many exciting advances have been reached in several crops such as pumpkin [32], apple [33], grapevine [34], and citrus [35]. However, long-term studies investigating the effects of this strategy on pest pressure and economic studies are still needed because it can be a labor-intensive practice. Additionally, whether the presence of flowering plants and/or honeydew producers in cover crops and hedges can be also used to break this mutualism remains to be investigated.

**Figure 3**




How to manage honeydew-mediated interactions to improve biological control.

### Using honeydew volatiles to attract biological control agents and to repel pests

Honeydew volatiles may provide information to other herbivores that a plant is already colonized, reducing herbivore pressure. However, it may also attract biological control agents [36–43]. Identifying which part of the volatile blend attracts biological control agents and repels pests is the first step to develop artificial infochemical blends to promote pest suppression in our crops (Figure 3.3). Here, it is important to highlight that honeydew is a microorganism-rich resource and biological control agents can use microorganism-produced volatiles to locate their hosts [7], as also occurs with nectar [44]. Production of microorganism-related volatiles or of the microorganisms that produce the volatiles may facilitate the identification and incorporation of honeydew-microbial volatiles in pest management programs [45]. We expect many exciting discoveries in the field of honeydew-microorganism-mediated interactions to promote pest management as the recent study by Liu et al. [46].

### Honeydew-mediated induction of direct and indirect plant defenses

Some studies have reported that honeydew induces direct and indirect plant defense responses [47–49]. For example, planthopper honeydew and bacteria present in the honeydew strongly elicit the accumulation of secondary metabolites in the leaves, and the release of volatile infochemicals that attract biological control agents [48]. Moreover, honeydew excreted by aphids and whiteflies induces salicylic acid and suppresses jasmonic acid [47,50]. Finally, potential elicitors of plant defense have been identified in honeydew [51,52]. Altogether, these studies show the potential of honeydew as a plant defense activator. Although many advances have been made in the field of plant defense priming during the last decade [53,54], the potential of honeydew to prime plant defense has not yet been investigated. Unravelling honeydew components that induce plant defense may help us with using them to vaccinate crop plants and make them more resistant to herbivore attack (Figure 3.4).

### Overcoming the risks of honeydew

In conclusion, honeydew may be used to promote pest management and biological control of pests. Nonetheless, there are some potential risks that should be considered when managing honeydew in agroecosystems. First, limiting sooty mold growth on the crop is crucial, as it may hamper the photosynthetic capacity of the plant and cause aesthetic damage to fruits. To reduce this risk, we should promote only hemipterans that do not reach pest status on the crop and promote the presence of sooty mold feeders (e.g. Tydeidae mites) [55]. Second, some pests (e.g. fruit flies, root flies) and hyperparasitoids feed on honeydew as adults [8,56]. In these cases, we would suggest evaluating the risks and benefits of providing honeydew. Third, a large amount of honeydew may hamper the movement of biological control agents [57]. To prevent that natural enemies are trapped in honeydew, the infestation levels of honeydew producers should not reach a certain threshold. Finally, recent studies show that systemic insecticides are transferred to honeydew excreted by hemipterans that feed on plants treated with these insecticides. This honeydew is then toxic to natural enemies of herbivores [58–60]. Therefore, we strongly suggest using insecticides only as a last option within a pest management program (Figure 3.5).

## Conclusions

Overall, with this perspective paper, we highlight that the mere presence of honeydew in agriculture should not be viewed only as a problem, but as an opportunity to improve pest management. For this aim, it is first necessary to understand the direct and indirect interactions mediated by this potential promoter of biological control. We hope that the suggestions in this paper motivate the execution of further studies in this research field to contribute to a more sustainable agriculture.

## Data Availability

No data were used for the research described in the article.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.cois.2023.101151.

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