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Chemical Ecology of Floral Resources in Conservation Biological Control

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Abstract

Conservation biological control aims to enhance populations of natural enemies of insect pests in crop habitats, typically by intentional provision of flowering plants as food resources. Ideally, these flowering plants should be inherently attractive to natural enemies to ensure that they are frequently visited. We review the chemical ecology of floral resources in a conservation biological control context, with a focus on insect parasitoids. We highlight the role of floral volatiles as semiochemicals that attract parasitoids to the food resources. The discovery that nectar-inhabiting microbes can be hidden players in mediating parasitoid responses to flowering plants has highlighted the complexity of the interactions between plants and parasitoids. Furthermore, because food webs in agroecosystems do not generally stop at the third trophic level, we also consider responses of hyperparasitoids to floral resources. We thus provide an overview of floral compounds as semiochemicals from a multitrophic perspective, and we focus on the remaining questions that need to be addressed to move the field forward.

1. INTRODUCTION

Conservation biological control (CBC) consists of a set of tactics and approaches that aim to sustain arthropod natural enemies of insect pests and improve their efficacy in crop habitats through modification of the biotic environment (70, 95, 100). In recent decades, considerable research has focused on how the interaction between landscape structure and the behaviors of both insect pests and their natural enemies can influence CBC (52). In the compositional complexity of agroecosystems, which include multiple types of crops and/or noncrop vegetation with different phenologies, natural enemies of arthropods need two broad categories of resources to carry out their life cycles: shelter and food. These two resources are often lacking in simplified agricultural landscapes, so pest suppression may be less effective than its full potential. Predators and parasitoids consume non-host-derived nutrients such as nectar from flowers and extrafloral nectaries and/or hemipteran honeydew, with positive effects on longevity, fecundity, foraging activity, parasitism rate, and female sex ratio. Thus, the introduction of flowering plants in or around cultivated fields should enhance the impacts of natural enemies on insect pests (54, 100). Although it is generally accepted that increasing heterogeneity by enriching agroecosystems with noncrop vegetation, at both local and landscape levels, can have positive effects on the abundance and richness of natural enemies of crop pests (98), the goal of reducing pest populations below economic threshold levels is frequently not achieved (66). In fact, even if flower-produced resources enhance attraction of natural enemies, they may also serve as resources for pests and hyperparasitoids, which potentially can aggravate the pest problem (122). Therefore, the identification of flowering plants that selectively attract natural enemies would likely enhance the efficacy of biological control. Such plants should be highly attractive and receive frequent visits from parasitoids, while also increasing the fitness of these parasitoids (10, 43, 63, 120).

Chemical ecology could help identify plants that attract natural enemies into cultivation systems and provide nutrient sources. Over the past two decades, most research on exploiting chemical ecology for CBC has focused on the attraction of natural enemies mediated by insect-produced kairomones (7) and herbivore-induced plant volatiles (HIPVs) (41, 85, 112). Floral odors have received much less attention despite their expected relevance to CBC. The main ecological function of floral odors is to attract pollinators, with the floral scent carrying information about the identity of the flower and the quality of the nectar reward (91). Similarly, floral odors can play a role in attraction of parasitoids. In fact, model simulations indicate that it is more profitable, in terms of longevity, nectar feeding, and parasitism levels, for parasitoids to visit highly attractive flowers with limited nectar accessibility than poorly attractive flowers that provide easy nectar access (12).

The interplay between flowering plants and natural enemies should not be simply considered as bipartite interactions because microbes can alter the sugar and amino acid composition of nectar (72), as well as the odors of flowers, by producing microbial volatiles (92, 104). Microbes are ubiquitous in flowers (115), and, because they can modify the intrinsic properties of plants used in CBC, they can act as hidden players mediating interactions between flowering plants and parasitoids. Additional levels of complexity that should be considered are added by top-down effects imposed by hyperparasitoids, which are specialized natural enemies of parasitoids (89). The potential benefits of CBC practices may be counteracted if they also enhance the fitness of hyperparasitoids. These fourth-trophic-level organisms are abundant in many agroecosystems, and due to their shared evolutionary origins and developmental lifestyle with third-trophic-level parasitoids, it is not surprising that they can also take advantage of flower resources.

In this review, we provide an overview of the progress and prospects for the chemical ecology of floral resources to enhance CBC, with a focus on hymenopteran parasitoids. The purpose of this review is threefold: (*a*) to evaluate the influence of floral odors in attracting parasitoids, (*b*) to assess the impact of nectar-inhabiting microbes associated with floral resources on parasitoids, and (*c*) to suggest implementations of potential conservation strategies that selectively favor third-trophic-level parasitoids over fourth-trophic-level hyperparasitoids.

2. INFLUENCE OF FLORAL ODORS IN ATTRACTING NATURAL ENEMIES

2.1. The Importance of Elucidating Parasitoid Foraging Behavior for Floral Resources

The foraging behavior of insect parasitoids has been intensively studied in the past decades (16, 124). It has been shown that parasitoids can exploit several types of cues, among which chemical stimuli play a major role in host location (19, 35, 65). While it has been clarified which long- and short-range chemical cues parasitoids exploit when searching for hosts, the ways in which parasitoids search for nutrients has received less attention, despite their predicted importance in CBC. Searching for hosts and searching for food sources are tightly linked behavioral activities because the foraging decisions of insect parasitoids often depend on their nutritional state. For example, starved females of the larval parasitoid *Cotesia vestalis* preferred the odors of inflorescences compared with nonflowering stems of wild turnip, *Brassica rapa* (69). However, nonstarved parasitoids did not display any olfactory or visual preferences between the flowering and the vegetative parts, suggesting that well-fed parasitoids focus on foraging for hosts (69). Furthermore, host searching is decreased when parasitoids are deprived of energy resources because starved parasitoids display a general reduction in foraging activities (108).

The ability of parasitoids to locate and exploit suitable flowering plants is particularly important in modern agriculture. Cropping systems largely dominated by monocultures provide limited food resources for parasitoids, and the lack of nutrition can compromise their efficacy as biocontrol agents. By analyzing the sugar profile of field-collected insects in monocultures, researchers have shown that parasitoids are starved, in all probability because of the lack of flowering vegetation (82, 107). Furthermore, noncrop habitats with flowering plants must be tailored for the specific needs of the biocontrol agents because not all flowering plants are suitable for parasitoids. For example, edge vegetation designed for bird conservation did not satisfy the energetic needs of parasitoids in adjacent agricultural fields, whereas addition of a single plant, the Cahaba White hybrid common vetch (*Vicia sativa* x *Vicia cordata*), greatly increased gut sugar content in field-collected parasitoids in the same agricultural landscape (82). It is thus important to augment cropping systems with flowering plants that are suitable for supporting actively foraging parasitoids. To date, the efforts of biocontrol practitioners have been primarily directed toward the identification of wildflower species that enhance the survival and fecundity of parasitoids, usually in simple laboratory or field cage experiments (11, 59, 62, 125). Nonetheless, as emphasized above, to exploit such flowering resources effectively, parasitoids must be able to locate them in the agroecosystem.

2.2. Parasitoid Olfactory Responses to Floral Resources Used in Conservation Biological Control

It has been hypothesized that, to maximize the chances of finding flowers, and thus food, in an unknown environment, parasitoids should respond to common floral volatile compounds shared among different flowering species (10, 120) (**Figure 1**). This is because the chemical diversity of volatile compounds released by flowers is high (68), and it is thus unlikely that parasitoids have evolved specific innate preferences. Instead, parasitoids are expected to fine-tune their ability to recognize suitable flowers through experience gained while foraging (**Figure 1**). In particular, it has been shown that associative learning is a key mechanism driving parasitoid decisions in

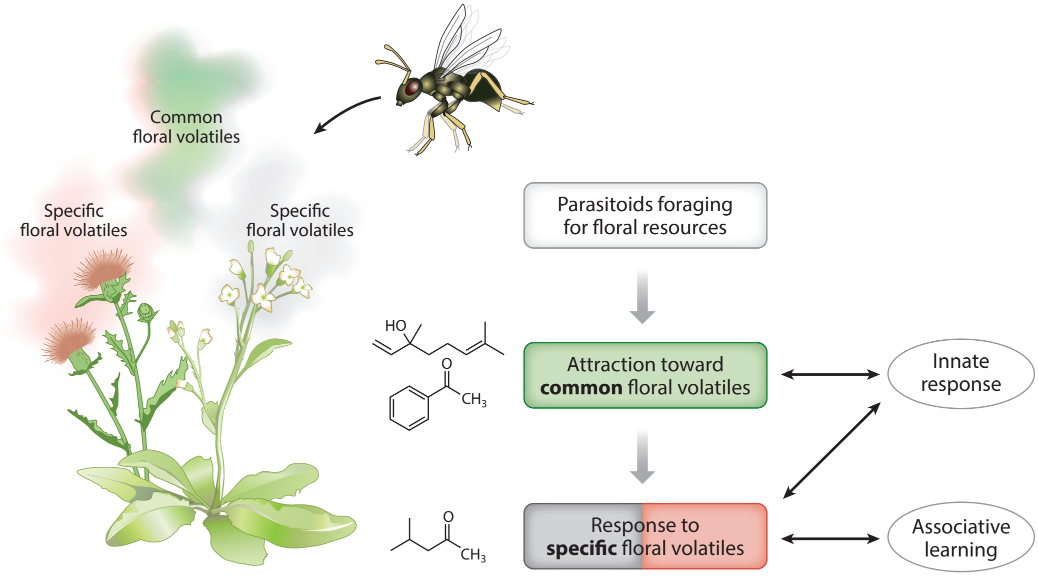

Figure 1

Conceptual framework for the attractiveness of flower volatiles to insect parasitoids foraging for floral resources. In an innate response, naïve parasitoids should be attracted by common floral volatile compounds (e.g., acetophenone, linalool) shared among several different flowering species to maximize the chances of finding flower resources in an unknown environment. In associative learning, experienced parasitoids are able to associate specific volatile compounds (e.g., 3-methylbutanoic acid) with food positive rewarding events.

foraging for nutrients, with wasps being able to associate a plethora of volatile compounds with sugar-rich resources (109, 121). There is some support for the hypothesis of parasitoid attraction to general flower odors (10, 17, 94, 120). For example, naïve *C. vestalis* parasitoids responded to odors emitted by flowering sweet alyssum, *Lobularia maritima* (17). The scent of sweet alyssum flowers is dominated by acetophenone, which is a common component of floral odors (68) and a known attractant for the braconid parasitoid *Diachasmimorpha longicaudata* (94). Although the attraction of *C. vestalis* to synthetic acetophenone has yet to be tested, an innate response to acetophenone seems likely. In another study, the parasitoids *Cotesia glomerata* and *Heterospilus prosopidis* innately responded to floral odors of oregano, *Origanum vulgare* (120). In this case, the major compound is the monoterpene linalool, another common floral volatile (68), which constitutes almost 40% of the total volatile blend of oregano (42). Thus, linalool may be a key compound attracting *C. glomerata* and *H. prosopidis* to oregano flowers (120), and it has also been reported as an attractant for the parasitoid *Aphidious ervi* (31).

Flowers and vegetative plant parts both emit several major classes of odorants, such as components of green leaf volatiles and terpenoids, although flower odors are generally more diverse than those of foliage or fruits (29). Such different odors likely play a role in the ability of naïve parasitoids to respond to suitable flowers (9, 38). Foti et al. (38) tested responses of the egg parasitoid *Trissolcus basalis* to four common flowering resources: sweet alyssum (*L. maritima*), buckwheat (*Fagopyrum esculentum*), French marigold (*Tagetes patula*), and sweet basil (*Ocimum basilicum*). When inflorescences were compared with vegetative shoots, only buckwheat flowers attracted naïve *T. basalis* females. Buckwheat flower odor is not characterized by a typical sweet floral scent, as it is dominated by two short-chain carboxylic acids not found in the foliage, 3-methylbutanoic acid and 2-methylbutanoic acid, which smell rather unpleasant to humans (38). Electroantennographic investigations confirmed that the parasitoids detected these carboxylic acids and that the antennal responses were similar to those in response to the sesquiterpene β-caryophyllene, a commonly released plant volatile that increases in abundance in the presence of feeding and oviposition activity by *Nezara viridula*, which *T. basalis* uses for host location (20, 21). It remains unclear why *T. basalis* females specifically respond to the odor of buckwheat flowers. However, the fact that the egg parasitoid *Telenomus leaviceps* is also innately attracted to buckwheat flower odor (9) may suggest that egg parasitoids in the Platygastridae have evolved an innate, but hard to explain, specific response to buckwheat volatiles, given that there is no chemical similarity between methylbutanoic acid and β-caryophyllene.

The olfactory responses of insect parasitoids to buckwheat flowers deserve particular attention because this flowering plant is widely used in CBC. Buckwheat flowers offer high-quality nectar that is easily accessible, and numerous laboratory and field studies have demonstrated its value for enhancing parasitoids' performance (6, 71, 77, 126). Nonetheless, because of the uncommon scent of buckwheat flowers, it is not surprising that studies have shown that naïve parasitoids do not respond to this flowering resource, as predicted by the general hypothesis of parasitoid attraction to common flower volatiles. For example, the parasitoid *C. vestalis* does not respond to buckwheat odors, whereas it is attracted to odors of sweet alyssum (17), and the parasitoid *Ooencyrtus telenomicida* is even repelled by buckwheat flower odors (37). However, wasp responses can be modified by experience, as demonstrated with *C. glomerata*, which does not innately respond to buckwheat odors but does respond after a rewarding feeding experience under laboratory conditions (34). This plasticity in olfactory responses by experienced parasitoids is reassuring for CBC because it facilitates visitation to highly rewarding, but poorly attracting, floral resources. Nevertheless, the buckwheat flower odor components that the wasps learn to associate with a reward have not yet been defined.

2.3. Parasitoid Attraction to Flowering Resources in Relation to Nectar Accessibility

The examples discussed above indicate a context-dependent effect in terms of parasitoid olfactory responses to flowering resources. The most striking outcome, elucidated by studies that focused especially on buckwheat floral volatiles, is that highly rewarding plants may not necessarily be innately attractive (17, 34, 37). The opposite is also true, in that flowering species can be highly attractive without providing any food rewards (10, 120). For example, the parasitoid *Microplitis mediator* is attracted by floral volatiles of candytuft, *Iberis amara*, although the flowers do not provide any apparent reward (10, 44). Similarly, the parasitoid *H. prosopidis* was attracted to odors of false baby's breath, *Galium mollugo*, and ground elder, *Aegopodium podagraria*, without gaining any fitness benefit (120). The emerging pattern is that innate flower preference is not always a good predictor of floral resource suitability for parasitoids.

The attractiveness of a flower resource may depend on other flowers that are present in the flower strip. The parasitoid *M. mediator* has been shown to display an olfactory preference for flowers of buckwheat, candytuft, and cornflower (*Centaurea cyanus*) when tested against vegetative odors from the same plant species. However, when plant species' attractiveness was compared in dual choice conditions, the wasp strongly preferred cornflower and candytuft over buckwheat (10). The fact that odors of a nonrewarding plant (i.e., candytuft) are preferred to odors of a highly rewarding plant (i.e., buckwheat) was counterintuitive, particularly as buckwheat resources are beneficial for *M. mediator* in terms of enhanced longevity and fecundity (44). However, associative learning is expected to buffer against apparently maladaptive responses of insect parasitoids, through rewarding and nonrewarding experience events (34, 103) (**Figure 1**).

3. IMPACT OF NECTAR-INHABITING MICROBES ASSOCIATED WITH FLORAL RESOURCES ON PARASITOIDS

3.1. Flower-Associated Microbes as Third Players in Plant–Insect Interactions

Microbes colonize virtually all animals and plants, and in terrestrial food webs, microbes have gained considerable attention because they can modulate plant–insect interactions (28, 30, 45, 101, 128). For example, plant growth–promoting bacteria and fungi not only enhance plant growth, but also can induce systemic resistance toward a wide range of attackers, including pathogens and herbivores (87). Conversely, microbes associated with herbivorous insects can manipulate plant defense-signaling pathways or disguise insect attack as pathogen attack and elude plant defenses (18). More recently, it has been shown that parasitoid-associated symbionts can have cascading effects at the plant–insect interface (24). For example, parasitoids can inject symbiotic viruses into caterpillar hosts; these viruses have been shown to alter the herbivore phenotype and, in turn, the way in which plants respond to feeding damage by viral-infected herbivores (25).

Even as microbes are increasingly recognized as hidden players in the interaction between plants and insects, the potential ecological effects driven by microbes on CBC have rarely been considered (73). As discussed above, floral resources added to agroecosystems for CBC purposes can enhance the performance of parasitoids, but nectar is also a suitable substrate for a wide variety of microbial organisms, among which fungi and bacteria are the most common (67, 115). This suggests that the effects of introducing flowering plants are not simply due to the intrinsic properties of plants, as microbes can modulate such effects (**Figure 2**). For example, nectar-associated microbial metabolism can lead to the formation of fructose-rich nectar, modifying the sucrose-dominated nectar originally produced by the plant (15, 56). Thus, we need to expand from a bipartite plant–parasitoid perspective to a more realistic, tripartite plant–parasitoid–microbe

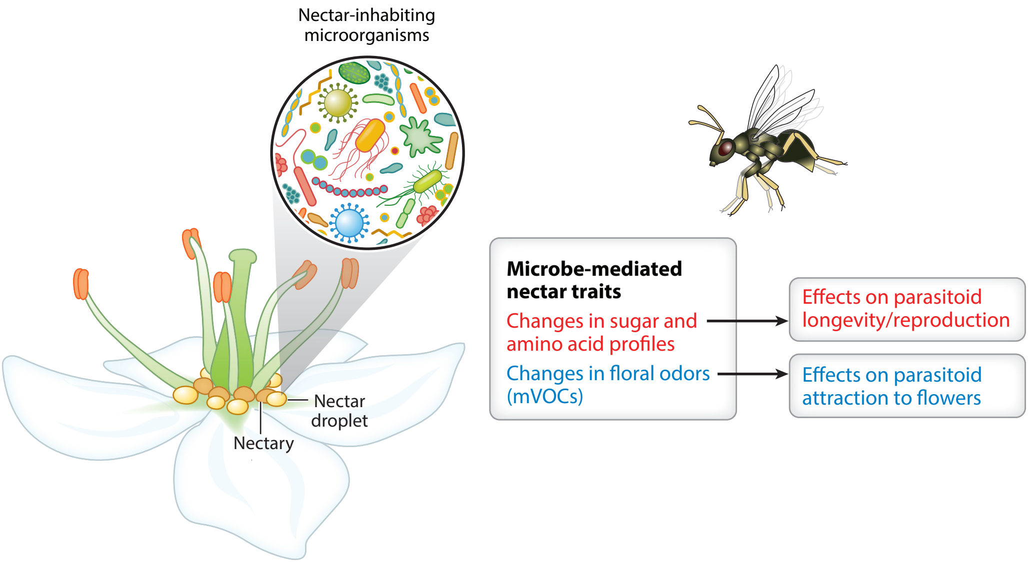

Figure 2

Overview of the effects of nectar-inhabiting microorganisms on floral nectar and consequences for parasitoids. The metabolic activity of nectar-inhabiting microorganisms modifies some nectar traits. Nectar is modified in terms of sugar profile and concentration, as well as amino acid composition affecting parasitoid longevity and reproduction, and microbial volatile organic compounds (mVOCs) affecting parasitoid olfactory responses to flowers.

perspective. Bacteria and fungi are the most-studied microbes associated with floral nectar, but other microorganisms associated with floral resources, e.g., those associated with pollen (26, 27), could also be of interest for CBC.

3.2. Bacteria and Fungi Associated with Floral Nectar

The microbial ecology of nectar-associated organisms is a rapidly growing area of research (67, 115). From an ecological perspective, flowers and their nectar represent an open habitat (22, 83) capable of sustaining high levels of microbial diversity (75, 115). The resources contained in nectar are generally only available for limited times, as they may rapidly disappear due to flower senescence or consumption by flower visitors. Although microbes can colonize flowers very early, even before anthesis (99, 118), floral nectars represent ephemeral habitats for microbes that function as metacommunities (i.e., a group of local communities that interact via species exchange) with frequent colonization–extinction dynamics (75, 115). Microbial biomass in nectar can reach high cell densities of $>10^5/\text{mm}^3$ for yeasts (55) and even $>10^7/\text{ml}$ for bacteria (40), but species richness within individual nectar samples is frequently low (90). This is because competition for the limited resource can be strong, and the order of colonization and growth rate capacity of the microbes are key features that affect the microbial community composition of floral nectar (84, 111).

Microbes exploiting floral nectars have diverse ecologies because they originate from the environment, the plant phyllosphere, and other vegetative tissues, or because they can be adapted to colonize flower nectar (115). The latter include specialist microbes, such as ascomycetous yeasts in the genus *Metschnikowia* (class Saccharomyces), which can be very abundant in flower nectar and dominate the microbial communities. Other yeasts in the basidiomycete class Tremellomycetes are common nectar-associated microorganisms. In addition, bacteria in the phyla Actinobacteria, Firmicutes, and Proteobacteria can be frequent colonizers of nectar (3, 40, 60, 61). However, the list of nectar-associated microorganisms is fragmentary and expected to rapidly increase as more plant species are sampled. Because nectar-inhabiting microbes can alter nectar traits, they can play crucial roles in the interactions among flowers, pollinators, and parasitoids.

3.3. Effect of Bacteria and Fungi on Nectar Traits and Consequences for Parasitoids

The most abundant sugars found in floral nectar are sucrose, glucose, and fructose, with traces of melibiose, maltose, and raffinose (8). Mono- and disaccharides dominate the biochemical composition of nectars, while amino acids and other compounds such as lipids, minerals, vitamins, and secondary metabolites are present in much lower concentrations (80). As a result of the metabolic activity of microorganisms, the quality of the sugar-rich nectar resource for parasitoids may drastically change as sugar profiles and concentrations are altered, amino acid composition is shifted, nectar pH is modified, and ethanol is produced (75). Furthermore, parasitoid attraction to flowers may change due to the production of microbial volatile organic compounds (mVOCs), which alter the scent of nectar (49, 92, 104). The nectar of a given flower type is typically dominated by a few taxa of fungi or bacteria due to priority effects (i.e., the first microbes that arrive in the nectar preclude the establishment of subsequent colonizers) (111). Microbial communities dominated by either fungi or bacteria can exert contrasting effects on nectar traits (116, 117). For example, experimental inoculation of the sticky monkey flower, *Mimulus aurantiacus*, with the yeast *Metschnikowia reukaufii* reduced amino acid concentrations without affecting sugar composition, whereas inoculation with the bacterium *Gluconobacter* sp. increased amino acid concentrations and enhanced the proportion of monosaccharides in nectar (116). Due to these modifications of nectar chemistry, parasitoids may experience taxon-specific effects when feeding on nectar fermented by microorganisms (72, 104). Longevity of the parasitoid *A. ervi* increased when individuals were given nectar fermented by the bacterium *Lactococcus* sp., whereas a detrimental effect was observed when nectar colonized by the bacterium *Asaia* sp. was tested versus synthetic nectar (72). In another study focused on yeasts, *A. ervi* longevity and survival were not affected by alterations to nectar chemistry caused by *M. reukaufii* and *Metschnikowia gruessii*, whereas the wasps experienced decreased longevity and survival when fed synthetic nectar colonized by *Aureobasidium pullulans*, *Hanseniaspora uvarum*, or *Sporobolomyces roseus* (104). While studies such as these have shown that nectar-inhabiting microorganisms affect the longevity of parasitoids, we are not aware of any studies that have investigated fitness-related proxies directly related to parasitoid reproduction. Because microbes affect the amino acid composition of nectar (72, 104, 116, 117), thus potentially affecting resources required for egg maturation, it would be useful to investigate whether nectar-inhabiting microorganisms induce changes in nectar chemistry that affect parasitoid fecundity.

Microbes produce mVOCs that can alter flower scents. Production of mVOCs that attract flower-visiting insects, including parasitoids, may be particularly advantageous for specialist yeast species, such as *Metschnikowia* species, which are believed to depend on animal vectors for colonization of new environments (2, 14). In fact, microbial abundance often increases after visitation by flower-associated insects (2). Evidence suggesting that mVOCs can be involved in the foraging behavior of insects exists for diverse pollinators (51, 92, 93, 97, 117), but similar studies for parasitoids have lagged. One such study did show that mVOCs produced by the specialist yeasts *M. reukaufii* and *M. gruessii* altered the nectar scent and attracted *A. ervi*, whereas odors of nectar fermented by the generalist yeasts *H. uvarum* and *S. roseus* failed to elicit parasitoid attraction (104). It is not known which volatiles produced by yeasts elicit parasitoid attraction, although 3-methyl-1-butanol and 2-phenylethanol have been suggested to play a role (104). It also has not been demonstrated whether parasitoids respond to the scent of nectar naturally fermented by bacteria, although mVOCs produced by *Bacillus* strains isolated from flower nectar did elicit parasitoid responses when tested in pure cultures (48).

3.4. Nectar-Inhabiting Microbes and Parasitoid Associative Learning

Insect parasitoids, when foraging for food, may encounter a diversity of flower resources that differ in quality, and this variation can be further amplified by colonization by nectar-inhabiting microbes. Parasitoid foraging behavior can be refined by associative learning (53, 103). Parasitoids can even be trained to learn stimuli that are not ecologically relevant (81). Because flower nectar is colonized by a wide range of fungi and bacteria, it is not surprising that such microbes may mediate parasitoid learned responses toward floral resources, in much the same way that pollinators are influenced by mVOCs associated with floral rewards (96). The first evidence that parasitoid olfactory decisions are modulated by associative learning of mVOCs with flower nectar has been found for the aphid parasitoid *A. ervi*. This parasitoid displays innate olfactory preference for nectar fermented by the specialist yeast *M. reukaufii*, whereas the generalist yeasts *H. uvarum* and *S. roseus* elicit neutral and repellent effects, respectively. However, associative learning strongly affected the parasitoid's subsequent olfactory responses, because wasps that were trained with yeast-fermented nectar exhibited attraction up to 24 h after conditioning, regardless of the yeast species used for conditioning (105). Interestingly, cross-specific effects were found, because conditioning with one species of yeast reinforced the wasp's responses to another yeast species, although this effect was short-lived (2 h) (105).

It is clear that this area of research is still in its infancy, and several aspects remain to be addressed. For example, whether associative learning in parasitoids can be mediated by mVOCs emitted by nectar-associated bacteria, or whether parasitoids conditioned with nectar-associated yeasts exhibit stronger attraction for bacteria-fermented nectar, has yet to be investigated. In addition, it is important to consider that floral nectar is not the only nutrient available to parasitoids to sustain their energetic needs, because other sugar-rich resources, such as hemipteran honeydew, might also be encountered when foraging. This is particularly relevant for parasitoids that attack honeydew-producing herbivores such as scale insects or aphids. Parasitoids can be attracted by mVOCs emitted by bacteria in honeydew (33, 74); thus, in these systems, microbial-based cues may be associated with both nutrients and hosts.

4. HYPERPARASITOIDS: ORGANISMS THAT MUST BE CONSIDERED IN CONSERVATION BIOLOGICAL CONTROL

4.1. Impact of Hyperparasitoids on Biological Control

The importance of considering multitrophic frameworks in biological control is now generally recognized (1, 23, 39, 110), as food webs do not stop at the third trophic level; fourth-trophic-level hyperparasitoids are common components of natural and agricultural trophic webs (89). Hyperparasitoids occur in all types of food webs, including annual, perennial, forest, and greenhouse cropping systems (23). Several hyperparasitoid species can attack the same parasitoid host, compromising the efficacy of biocontrol agents (32, 50, 88). For example, the larval parasitoid *Cotesia melanoscela*, which parasitizes the gypsy moth, *Lymantria dispar*, is attacked by a complex of 16 species of hyperparasitoids, which inflict approximately 50% mortality (32). In citrus orchards, six different hyperparasitoid species have been found attacking *Binodoxys angelicae*, the key parasitoid of the green citrus aphid, *Aphis spiraecola*, inflicting up to 82% mortality (50). In pepper and eggplant greenhouses, hyperparasitoids can cause up to 100% mortality of aphid parasitoids (13, 78). In addition to causing direct mortality of biocontrol agents, hyperparasitoids may exert indirect effects, such as mediating apparent competition (i.e., interactions between parasitoid species mediated by a shared hyperparasitoid enemy) (113) or inducing dispersal of the parasitoid (57). For example, females of the parasitoid *Aphidius uzbekistanicus* show reduced attack rates on the English grain aphid, *Sitobion avenae*, and are more prone to flight in the presence of 6-methyl-5-hepten-2-one, a pheromone produced by its hyperparasitoid *Alloxysta victrix* (57, 86). Nonetheless, in a few cases, hyperparasitoids can also have beneficial effects by dampening extreme host–parasitoid oscillations, reducing overexploitation of the herbivore host by the parasitoid and thus preventing the local extinction of the biological control agent (58).

Because fourth-trophic-level organisms can have substantial effects on the success of biological control programs, hyperparasitoids must be taken into account when designing chemical ecology approaches in CBC. In particular, because hyperparasitoids are natural enemies of the primary parasitoids that attack herbivore pests, they can be considered as pests themselves in a crop protection context.

4.2. Managing Hyperparasitoids in Conservation Biological Control

Because hyperparasitoids share a common evolutionary history and developmental strategies with their parasitoid hosts, it is not surprising that they too can benefit from CBC strategies such as provision of floral resources. For example, adding a floral resource such as buckwheat in a food chain consisting of lucerne, *Medicago sativa*; the pea aphid, *Acyrthosiphon pisum*; the parasitoid *A. ervi*; and the hyperparasitoid *Dendrocerus aphidum* increased both parasitism and hyperparasitism rates (4, 5). This effect was mediated by the behavioral changes between starved and fed insects because access to buckwheat floral nectar enhanced the searching efficiency of both *A. ervi* and *D. aphidum* by reducing the resting time and increasing the attack rates (6). Thus, it can be crucial to implement CBC approaches that selectively favor primary parasitoids over hyperparasitoids. Although this appears to be challenging because parasitoids and hyperparasitoids often respond in a similar way to floral resources, some studies have shown that targeting a specific trophic level is possible. For example, melibiose is a sugar found in floral nectar (119) that enhances the longevity of the parasitoids *Aphidious matricarie* and *Aphidous colemani* more than their shared hyperparasitoid, *D. aphidum* (46). Therefore, flowering plants that provide melibiose-rich nectar could be used to augment sugar-deprived agroecosystems to provide selective fitness benefits for these two parasitoids. Although melibiose was not the sugar that had the largest effect on the longevity of the parasitoid, it had the best trade-off when both the third and the fourth trophic levels were taken into account (46).

Ideally, flowering plants should selectively attract parasitoids rather than hyperparasitoids: Promising results for CBC have been found for natural enemies of the southern green stink bug, *N. viridula*, because its main egg parasitoid, *T. basalis*, is attracted to buckwheat floral scent, whereas the facultative hyperparasitoid *Ooencyrtus telenomicida* is repelled (37). Further indirect evidence suggesting differential attraction of parasitoids and hyperparasitoids toward flowering plants arises from studies showing that floral resource implementation can cause a shift in the relative abundances of parasitoids and hyperparasitoids. When buckwheat was added to plots of leek, *Allium porrum*, the community composition of natural enemies associated with pupae of the leek moth, *Acrolepiopsis assectella*, changed, with the facultative hyperparasitoid *Conura albifrons* becoming much more abundant, likely because this species particularly benefited from the addition of the floral resource (76). However, the overall parasitism rates at the pest population level were not affected by buckwheat introduction (76). Comparative olfactory experiments are needed to elucidate whether such shifts in the community of parasitoids and facultative hyperparasitoids can be explained by differential responses to floral volatiles.

Semiochemicals that could potentially be exploited in CBC to selectively target primary parasitoids over hyperparasitoids include HIPVs (88) and mVOCs (47), although these are not directly related to floral scent. The obligate hyperparasitoid *Lysibia nana* is a specialist attacking cocoons of *C. glomerata*, a parasitoid of cabbage white caterpillars, *Pieris* spp. *Lysibia nana* is attracted by HIPVs emitted by cabbage plants attacked by *Pieris* caterpillars in which *C. glomerata* larvae are developing (88, 127). In contrast, foraging females of *C. glomerata* avoid such HIPVs, likely to reduce levels of intraspecific competition (36, 64). Similarly, mVOCs may have potential applications in CBC, considering that bacterial volatiles induced contrasting responses in olfactometer assays with the parasitoid *A. colemani* and its hyperparasitoid *D. aphidum* (47). Significantly higher amounts of alcohols and ketones in the mVOCs from the tested bacterial strains were correlated with repellence of *D. aphidum*, whereas higher amounts of limonene, linalool, and geraniol in mVOCs were correlated with hyperparasitoid attraction (47).

To conclude, even if it is challenging to implement chemical ecology tactics that selectively favor parasitoids over hyperparasitoids, the results from the few examples discussed above show promise. Overall, it is clear that a better understanding of the ecological interactions among four trophic levels is needed to use flowering plants effectively to augment sugar-deprived agroecosystems.

5. CONCLUSIONS AND SUGGESTED FUTURE WORK

Habitat management in agroecosystems has largely relied on the provision of flowering resources to enhance the efficiency of natural enemies of insect pests. However, our current understanding of the mechanistic processes by which flowering resource implementation translates into successful or failed biological control is limited. As a consequence, management of noncrop habitats to promote insect parasitoids has obtained mixed results (54). Understanding how insect parasitoids locate flowering resources, and which chemical compounds they exploit, will provide mechanistic insights for improvement of CBC strategies.

Simulation models have shown that flower attractiveness is an important component that should be considered among the selection criteria when screening flowering plant species (12). Ideal plant species for CBC should enhance not only parasitoid longevity and fecundity, but also parasitoid attraction to ensure high visitation rates. However, there is increasing awareness that nectar accessibility and flower attractiveness do not always correlate (114, 123). Nonetheless, even when flowering plants are highly attractive but poorly rewarding, they can still be useful in designing flowering mixtures because frequently visited plant species can be complemented with less attractive but highly rewarding plants, whose cues parasitoids can learn as they visit them. Overall, the chemical ecology underlying how parasitoids forage for floral resources remains largely unknown. Although there is a growing body of empirical literature on parasitoid attraction to floral scents, few studies have investigated which chemical compounds mediate attraction. A concerted effort is needed to specifically identify which floral odor components serve as predictors of floral resource suitability by testing parasitoid responses to individual compounds or blends of compounds, particularly in field bioassays under natural conditions. Identification of bioactive compounds that play a role in parasitoid attraction to flowers could open new possibilities in biological control, for example, in the attract-and-reward context (102).

Although the ecological importance of flower-inhabiting microorganisms has been recognized based on the limited case studies to date, it is not possible to generalize about whether microbe-mediated effects in nectar are beneficial or detrimental to parasitoids. It could be argued that, because microbes deplete sugar resources, nectars lacking certain sugar types or having lower sugar concentrations may be less effective in boosting parasitoid fitness. However, microbial modifications go beyond the simple alteration of sugar profiles and concentrations (79), and positive effects on parasitoid fitness due to bacteria-mediated effects on floral nectar chemistry have been documented (72). Clearly, much more needs to be done, in part because most studies to date have tested nectar fermented by bacteria or yeasts after removal of the microorganisms, whereas microbes themselves are naturally ingested by parasitoids in the field while feeding on floral nectar. This microbial biomass may provide additional nutrients and energy that affect also the performance of parasitoids. Microorganisms specialized to inhabit flower nectars, such as yeasts of the genus *Metschnikowia*, have been found in the internal organs of field-collected parasitoids (106), so they should be considered in the nutritional ecology of biocontrol agents. Unraveling the complexity of the ecological interactions between nectar-inhabiting microorganisms and parasitoids could provide novel tools for enhancing biological control in cropping systems. The available evidence already suggests that mVOCs can attract parasitoids toward sugar-rich resources and could potentially be used as behavior-modifying semiochemicals. Selection of flowering plants based on the likelihood of their hosting beneficial nectar-inhabiting microbes could be an additional variable to consider when choosing flowering plant species to be tested in biological control programs.

Finally, it has become clear that, to implement floral resources for augmentation of sugar-deprived agroecosystems, the nontarget effects on pests and hyperparasitoids must also be part of the equation. In particular, there is almost nothing known about the semiochemical cues that hyperparasitoids use when foraging for nutrients. This is a crucial but largely overlooked topic in biological control, particularly as it may be challenging to selectively attract parasitoids versus their hyperparasitoids because both guilds share a common evolutionary history and a need for energy-rich nutrients and thus may respond to floral resources in a similar manner. In this context, comparative olfactory experiments that unravel which flower volatiles selectively attract insect parasitoids more than hyperparasitoids are very much needed to design successful chemical ecology tactics for CBC.

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Errata

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