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Microbe-mediated alterations in floral nectar: consequences for insect parasitoids

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Floral nectar is frequently colonized by microbes among which bacteria and yeasts are the most abundant. These microbes have the ability to alter nectar characteristics with consequences for the whole community of flower-visiting insects. Recent research carried out on natural enemies of insect herbivores has shown that microbe-mediated changes in nectar traits can influence the foraging behavior and life history traits of parasitoids. The production of microbial volatile organic compounds can affect the attraction of parasitoids to nectar, while changes in sugar and amino acid composition can impact their longevity. Future research should focus on understanding the effects of nectar microbial colonization on parasitoid reproduction, with a specific emphasis on the interactions among different microbial taxa known to co-occur in floral nectar. Overall, this review highlights the importance of considering the role of nectar-inhabiting microbes in shaping the interactions between parasitoids and their food resources.

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Introduction

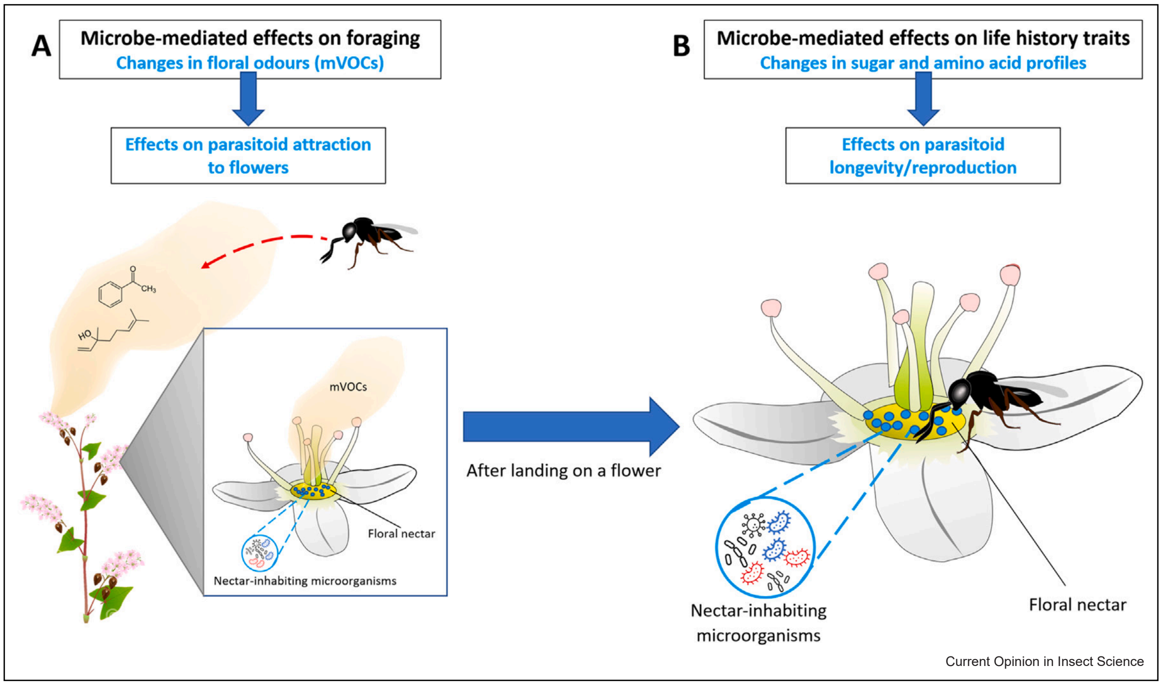
Insect parasitoids at the adult stage rely on sugar-rich resources for their energetic and nutritional needs. Such resources can be either plant-derived (e.g. floral nectar, extrafloral nectar, pollen, and plant guttation) or they can be acquired from other insects such as hemipterans that produce honeydew [1–3]. In particular, floral nectar is widely utilized by a diverse range of parasitoids that are, in addition to pollinators, well-known flower-visiting insects [4,5].

Floral nectar is not only exploited by flower-visiting insects such as pollinators and parasitoids. It is also ubiquitously colonized by specialized microorganisms that are adapted to its high osmotic pressure, low nitrogen availability, and presence of defensive metabolites [6–8]. Unraveling how microbial colonization of nectar affects floral traits is crucial for parasitoid ecology because the metabolic activity of nectar-inhabiting microbes can potentially impact the benefits that flowering plants provide to parasitoids. For instance, the presence of nectar-inhabiting microbes can lead to shifts in the sugar composition of nectar, such as a transition from sucrose- to fructose-dominant nectars [9,10]. Thus, the interplay between flowering plants and parasitoids should not be simply considered as a bipartite interaction but instead it should be viewed in the framework of a tripartite interaction among plants, insects, and microbes [11]. The emerging pattern is that microbial communities in floral nectar can act as important 'hidden players' in parasitoid nutritional ecology.

Microorganisms found in floral nectar can be categorized into two groups: occasionally present microbes and stably associated microbes [8,12]. Occasionally present microbes may come from the environment or the plant phyllosphere, but they are not well-adapted to survive and reproduce in nectar. By contrast, stably associated microbes are specialized to thrive in sugar-rich environments such as flower nectar. Among these specialist microbes, ascomycetous yeasts of the genus *Metschnikowia* are often the most commonly observed and dominant in floral nectar [6,8]. Also, bacteria from the phyla Actinobacteria, Bacillota, and Pseudomonadota are frequently associated with floral nectar [6,8]. For more comprehensive information about the diversity of nectar-inhabiting microbes as well as how microbial communities are established in nectar, see [13].

This review aims to explore the role of nectar-inhabiting microbes in parasitoid ecology. We will explore how the chemical composition and nutritional value of nectar can be modified by microbial metabolic activity, potentially altering nectar attractiveness and suitability as a food source for insect parasitoids. Specifically, we will tackle the following questions: 1) how do nectar-inhabiting

Figure 1



Impact of nectar-inhabiting microbes on insect parasitoids. **(a)** Nectar-inhabiting microbes can affect parasitoids' foraging behavior by altering nectar scent. This is likely to occur when parasitoids are far from their food resources, because microbial metabolic activity can result in the production of mVOCs. **(b)** Once a flower has been located, nectar-inhabiting microbes can affect parasitoids' performance (i.e. longevity and/or reproduction) when feeding on microbe-contaminated nectar. Microbe-induced changes of nectar chemistry include alteration of sugars and amino acid composition.

microbes affect localization of food resources by insect parasitoids? and 2) how do nectar-inhabiting microbes affect the quality of the food resources exploited by insect parasitoids?

Studying the role of microbes in floral nectar is not only important for unraveling the ecological dynamics of parasitoids in their search for food but also holds strong implications for biological pest control. Many parasitoids serve as excellent natural enemies of agricultural pests, but their use is still applied on a limited scale and more improvement is required [14]. Thus, understanding how microbial colonization of floral nectar affects the performance of insect parasitoids can pave the way toward the development of more effective sustainable pest management strategies. Although the focus of this review is on nectar-inhabiting microorganisms, it is worth noting that microbial colonization of food resources also extends to other food sources encountered by insect parasitoids such as pollen [15–18], insect honeydew [19,20], and extrafloral nectar [21]. However, little to virtually nothing is known about the impact of microorganisms associated with pollen, insect honeydew, and extrafloral nectar on parasitoids, despite the potential significant role that these additional food sources may play in satisfying the energetic and nutritional needs of foraging parasitoids.

Microbe-mediated effects on nectar traits and consequences for parasitoids

Effects on foraging behavior

The foraging behavior of insect parasitoids has been the focus of several studies in the last decades (see reviews by [22–25]). However, while foraging for hosts has been intensively investigated, how parasitoids search for food resources has received limited attention. One key aspect of parasitoid foraging behavior is the ability to detect and respond to floral cues that indicate the presence of nectar [1,11]. These cues include visual cues such as the color and shape of flowers, as well as olfactory cues emitted by the flowers. The olfactory stimuli, often in the form of volatile organic compounds (VOCs), play a crucial role in attracting parasitoids to the flowers [11]. These VOCs can act as long-range attractants, guiding parasitoids toward potential food sources. To increase their chances of finding floral resources in unknown environments, it has been suggested that parasitoids respond to common floral volatile compounds shared among different plant species [1,11]. This is because the chemical diversity of flower-associated volatile compounds is extensive [26,27], and it is rather unlikely that parasitoids have evolved innate preferences for specific compounds. Instead, it is expected that parasitoids refine their ability to recognize suitable flowers through experience gained during foraging [28].

There is increasing evidence that fermentation by yeasts and bacteria can alter floral nectar odors [29–32] (Figure 1a). Nectar-inhabiting microbes have a dual effect on the composition of VOCs associated with floral nectar. First, they can modify the constitutive blends of VOCs emitted by sterile floral nectar. Second, microbial metabolic activity can result in the production of *de novo* volatiles in nectar, also known as 'microbial volatile organic compounds' (mVOCs). In a study focused on comparing parasitoid responses under controlled laboratory conditions to nectar fermented by yeasts with a different degree of specialization, it was found that the specialists *Metschnikowia reukaufii* and the congeneric *M. gruessii* modified the scent of nectar substantially, attracting the aphid parasitoid *Aphidius ervi* [31,33] (Supplementary Table 1). Among the generalist yeasts — that are associated with a wide variety of habitats — only *Aureobasidium pullulans* induced a strong parasitoid attraction, whereas the odors of nectar fermented by *Hanseniaspora uvarum* or *Sporobolomyces roseus* did not elicit a response or even repelled the parasitoid [31,33]. The specific volatiles produced by yeasts that trigger parasitoid attraction are still unknown, although 3-methyl-1-butanol and 2-phenylethanol have been suggested to play a role [31].

In another study, the foraging behavior of the egg parasitoid *Trissolcus basalis* was investigated in response to mVOCs emitted by bacteria isolated from the floral nectar of buckwheat (*Fagopyrum esculentum*), a plant known to produce high-quality nectar and largely used in conservation biological control to support pest natural enemies [34–37]. Behavioral assays indicated that the egg parasitoid was attracted to odors of nectar fermented by four bacterial strains (identified as *Staphylococcus epidermidis*, *Terrabacillus saccharophilus*, *Pantoea* sp., and *Curtobacterium* sp.), out of the 14 strains isolated from buckwheat nectar (Supplementary Table 1). Although chemical analysis revealed qualitative differences in the volatile blend composition of the bacteria-fermented nectars, mVOCs such as butanediols are surprisingly unlikely to play a role because they were emitted by strains that failed to elicit egg parasitoid attraction. Instead, this finding implies that *T. basalis* is mostly guided by quantitative changes in nectar odor composition induced by bacterial fermentation [32].

So far, only a handful of studies have been carried out to investigate how mVOCs associated with microbe-fermented nectar affect parasitoid foraging decisions, which makes it difficult to draw general conclusions. Despite the paucity of studies available now, the emerging pattern is that both yeasts and bacteria have the potential to impact parasitoids' olfactory responses, leading to enhanced attraction [31–33].

Effects on fitness-related traits

To fulfil their nutritional and energetic demands, adult parasitoids rely on floral nectar as an essential food resource [5]. Nectar serves as a rich source of energy, providing sugars and other nutrients that are crucial for the survival and reproductive success of parasitoids [38,39]. By consuming nectar, parasitoids can replenish their energy reserves and increase their longevity that can in turn increase the performance of parasitoids as biological control agents [34,40]. The sugars in floral nectar, primarily sucrose, glucose, and fructose, provide parasitoids with resources that can sustain energy-demanding activities such as flight and foraging. Nectar also contains amino acids, organic acids, vitamins, and minerals, which supplement the parasitoids' diet and support their physiological processes [49].

Previous studies have shown that yeasts and bacteria can alter the quality of floral nectar. Microbe-mediated changes in nectar traits can include changes in sugar concentration and sugar profiles, shifts in amino acid concentration and composition, alteration of nectar pH, and production of secondary metabolites [41] (Figure 1b). Interestingly, bacteria and yeasts may have contrasting effects on nectar quality. For instance, in nectar of the sticky monkey plant (*Diplacus aurantiacus*), fermentation by the yeast *M. reukaufii* decreased amino acid levels without affecting sugar composition, whereas the bacterium *Gluconobacter* sp. increased amino acid concentrations and led to a higher proportion of monosaccharides [42]. Owing to contrasting microbe-mediated alterations of nectar chemistry, parasitoid performance may vary, depending on both parasitoids' specific nutritional needs and on which microbial taxa are dominant in the consumed nectar. Studies carried out on yeasts and bacteria using *A. ervi* as model parasitoid species have shown that parasitoid longevity can be enhanced, decreased, or remains unaffected when parasitoids are fed microbe-fermented nectar [31,43] (Supplementary Table 1). In the case of bacteria, the longevity of the parasitoid *A. ervi* was increased when adult wasps were offered *Lactococcus*-fermented nectar, while a negative effect was displayed when *Asaia*-fermented nectar was consumed [43]. In the case of yeasts, changes in nectar chemistry caused by specialist yeasts (*M. reukaufii* and *M. gruessii*) did not affect *A. ervi*'s longevity, whereas the wasps showed a reduction in longevity when fed nectar previously colonized by generalist yeasts (*A. pullulans*, *H. uvarum*, and *S. roseus*) [31].

As such, it is clear that there is emerging evidence indicating that bacteria and yeasts affect nectar quality with important consequences for parasitoid longevity. Nonetheless, how other fitness-related traits such as fecundity are shaped by microbe-fermented nectar is still largely unknown and should be explored in future studies. This is especially important from an application point of view, taking into account that the performance of insect parasitoids as biological control agents largely depends on their reproductive abilities.

Conclusions

In this review, we raise awareness about the importance of nectar-inhabiting microbes as hidden players that can shape olfactory responses and life history traits of insect parasitoids. Nevertheless, this is just the 'tip of the iceberg' as it is also imperative to broaden our understanding of the impact of microorganisms occurring in other parasitoids' exploited food sources, including honeydew, extrafloral nectar, pollen, and plant guttation.

To date, whether nectar-inhabiting microbes are beneficial for parasitoids is still debatable. Because microbes thriving in nectar can be seen as parasitoids' competitors that deplete sugar-rich resources, microbial activity can result in a reduction of nectar quality. Consequently, microbial colonization might be detrimental for parasitoid species, especially for those that mature yolk-rich eggs and thus have high nutritional demands. On the contrary, microbial fermentation may result in *de novo* production of nutrients, including essential amino acids and vitamins, which could be beneficial for parasitoids. Research efforts should be made to extend the number of case studies in order to understand under which conditions microbes act as competitors or mutualists of parasitoids. Based on the work done with aphid parasitoids (and pollinators [44]), it can be hypothesized that specialist microbes such as *Metschnikowia* yeasts are beneficial. Because such yeasts largely depend on flower visitors to disperse and colonize novel habitats, they should attract parasitoids toward rewarding flowers without impairing nectar quality in order to maximize the chance of dispersion [31,45].

In addition of being important for fundamental studies on parasitoid ecology, understanding how nectar-inhabiting microbes affect parasitoid performance as pests' natural enemies is highly relevant in conservation biological control. In order to sustain resident natural enemies, one of the most common practices in conservation biological control consists of introducing flowering plants into agro-ecosystems [51,52]. Such flowering resources are generally selected based on classical plant traits such as nectar accessibility and quality, flowering time, and duration [53]. Nonetheless, we should also consider the microbial perspective as an additional plant selection criterion. For example, it may be beneficial to select plants based on their likelihood to host microbial consortia known to be beneficial for parasitoids [54]. Alternatively, we could explore the possibility of spraying plant flowers with natural or synthetic microbial communities in order to enhance parasitoid efficiency in biological pest control [55]. Further research is needed to investigate the potential value of such scenarios.

Future research

To further advance our understanding of these plant–insect–microbe interactions, future research should be conducted under more realistic ecological conditions. We foresee three lines of research, which are highlighted below:

(1) Currently, our knowledge about the role of nectar-inhabiting microbes in parasitoid ecology is based on experimental work carried out with cell-free fermented nectar, so only indirect microbe-mediated effects have been studied. However, in natural conditions, parasitoids ingest both nectar and the associated microbial cells. For example, it is known that some nectar specialists (e.g. *Metschnikowia* spp.) have been detected inside the parasitoids' body [46]. Whether ingested microbial cells can have probiotic effects on parasitoids' gut microbiota is not known and should be explored in the near future.
(2) Studies on the effects of nectar-inhabiting microbes on insect floral visitors have often been conducted with isolated strains of bacteria or yeasts. However, it is important to recognize that these two taxa often co-occur in nectar [7]. Therefore, future research efforts should focus on understanding how interactions between yeasts and bacteria shape parasitoid nutritional ecology.
(3) The effect of microbial activity on parasitoid performance has been tested with simplified synthetic nectar solutions composed of a mixture of sugars and amino acids. However, natural nectar is much more than a simple feeding reward [47], as it also contains secondary metabolites such as phenolics and proteins that can have antimicrobial properties [48–50]. How secondary metabolites affect colonization and activity of nectar-inhabiting microbes and whether these compounds further modulate microbe-mediated effects on parasitoid fitness remains to be tested.

Data Availability

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

Declaration of Competing Interest

The authors declare that the content of this paper was not affected by any financial, commercial, legal, or professional interest. No conflict of interest.

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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.2023.101116.

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