New
Phytologist

Research review

Tiny but mighty? Overview of a decade of research on nectar bacteria

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Received: *29 September 2024*
Accepted: *9 December 2024*

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New Phytologist (2025) **245:** 1897–1910
doi: 10.1111/nph.20369

Key words: bacteria, floral nectar, plant–microbe–animal interaction, pollination, yeast.

Summary

An emerging focus of research at the intersection of botany, zoology, and microbiology is the study of floral nectar as a microbial habitat, referred to as the nectar microbiome, which can alter plant–pollinator interactions. Studies on these microbial communities have primarily focused on yeasts, and it was only about a decade ago that bacteria began to be studied as widespread inhabitants of floral nectar. This review aims to give an overview of the current knowledge on nectar bacteria, with emphasis on evolutionary origin, dispersal mode, effects on nectar chemistry and plant–animal interactions, community assembly, agricultural applications, and their use as model systems in ecological research. We further outline gaps in our understanding of the ecological significance of these microorganisms, their response to environmental changes, and the potential cascading effects.

Introduction

The role of floral nectar in plant–animal interactions has long attracted attention from physiologists, biochemists, and ecologists (Lorch, 1978; Roy *et al.*, 2017). More recently, floral nectar has also been recognized as the natural habitat of diverse microorganisms, that is the nectar microbiome, which can modify the amount and quality of nectar and volatile emission (Vannette, 2020). The nectar microbiome can act as a 'silent third partner' in nectar-mediated plant–animal interactions (Steffan *et al.*, 2024), adding complexity to the ecological network of plants and their floral visitors (Nepi, 2017; Barberis *et al.*, 2024).

Studies of the composition and ecological significance of the nectar microbiome have tended to focus on unicellular fungi, also known as yeasts, whose presence in flowers was already described > 140 yr ago (Boutroux, 1884). Floricolous yeasts have been the subject of intense research since the late 1980s, when a large number of new species were described (Lachance *et al.*, 2001; Rosa & Péter, 2006; Kurtzman *et al.*, 2011). Most of those studies were based on samples from whole flowers or the 'nectary region' of these and did not specifically consider floral nectar as a source of yeasts. Actually, it was not until the beginning of this century that studies in Germany (Brysch-Herzberg, 2004), Spain and Mexico (Herrera *et al.*, 2008, 2009), South Africa (de Vega *et al.*, 2009), and the United States (Belisle *et al.*, 2012), specifically started focusing on floral nectar as a yeast habitat. The abundant research on nectar yeasts has been the subject of some recent reviews (Chappell & Fukami, 2018; Klaps *et al.*, 2020; Fenner *et al.*, 2022), and it will not be covered in detail in this article.

By the end of the last century, bacteria had been occasionally detected in floral nectar (Gilliam *et al.*, 1983; Ehlers & Olesen, 1997). However, their prevalence and diversity in this habitat remained virtually unknown until Fridman *et al.* (2012) showed that bacteria were frequent in the floral nectar of cultivated trees in Israel. Around the same time, other studies reported the widespread presence of bacteria in the floral nectar of diverse wild plants from South Africa (Álvarez-Pérez *et al.*, 2012), Spain (Álvarez-Pérez & Herrera, 2013), and Belgium (Jacquemyn *et al.*, 2013a,b). Since then, many studies have demonstrated that bacteria can use nectar as an ecological niche, showing that nectar bacteria are ubiquitous in different terrestrial biomes (see Supporting Information Table S1 for an overview of published studies on this topic). However, the study of these prokaryotes still lags behind that of nectar yeasts. Most research on nectar bacteria has focused on taxonomic description or agricultural applications (to be described later). By contrast, the effects of nectar bacteria on plant–pollinator mutualisms remain poorly understood. In this article, we review the current knowledge on nectar bacteria and discuss some research areas that, in our view, require more attention to further characterize the ecological significance of these microorganisms.

Bacteria as frequent inhabitants of floral nectar: who are they and what do they do?

Floral nectar harbors specialized bacteria that can tolerate the challenging conditions of nectar, including high osmotic pressure, low oxygen level, low nitrogen content, and the presence of hydrogen peroxide and secondary metabolites (Álvarez-Pérez *et al.*, 2012; Nicolson, 2022; Landucci & Vannette, 2024).

Unlike nectar yeasts, which have the Metschnikowiaceae (Ascomycota) as the main family in nectar communities and their insect visitors (Pozo *et al.*, 2011; Belisle *et al.*, 2012; de Vega *et al.*, 2021), there is no obvious dominance of a specific bacterial group in floral nectar. However, several studies reported relatively low diversity and high specificity. The genus *Acinetobacter* (Gammaproteobacteria: Pseudomonadales) ranks among the most frequent bacterial inhabitants of this habitat in many regions (Fridman *et al.*, 2012; Álvarez-Pérez & Herrera, 2013; Sharaby *et al.*, 2020; de Vega *et al.*, 2021; Luizzi *et al.*, 2024). Other bacterial groups commonly present in floral nectar are the genus *Rosenbergiella* (Gammaproteobacteria: Enterobacterales), other Gammaproteobacteria such as *Pseudomonas* spp., *Pantoea* spp., and *Enterobacter* spp., and some acetic acid bacteria (Alphaproteobacteria: Rhodospirillales) (Morris *et al.*, 2020; Sharaby *et al.*, 2020; de Vega *et al.*, 2021; Chappell *et al.*, 2022). Repeatedly finding the same species in nectar communities, whether through cultivation-dependent or cultivation-independent methods, suggests adaptive traits. Nevertheless, except for the members of the *Acinetobacter nectaris*/*Acinetobacter boissieri* clade (often referred to as the 'nectar acinetobacters'; Álvarez-Pérez *et al.*, 2013, 2021a) and *Rosenbergiella* spp. (Halpern *et al.*, 2013; Lenaerts *et al.*, 2014; Álvarez-Pérez *et al.*, 2023), which seem to be mostly found in floral nectar and to be part of the microbiota of floral visitors, the degree to which other nectar bacteria are specific to nectar as opposed to other potential habitats remains uncertain.

It must be noted that most previous culture-based studies searching for nectar bacteria have used a limited selection of general-purpose, nonselective culture media (typically, trypticase soy agar and/or Reasoner's 2A agar, with or without sugar supplementation; see details in Table S1), which might introduce a source of bias against microorganisms that require more specific media, including nutritional supplements and/or preventing the growth of competitor species, to form colonies. For example, lactic acid bacteria of the genera *Lactobacillus*, *Apilactobacillus*, and *Fructobacillus* (Bacilli: Lactobacillales), and acetic acid bacteria of the genera *Asaia* and *Neokomagataea* (formerly *Gluconobacter*) that are found in insects can be frequently found colonizing floral nectar and might affect pollinators (Crotti *et al.*, 2010; Endo & Salminen, 2013; Rokop *et al.*, 2015; Russell & McFrederick, 2022a,b; Cecala *et al.*, 2024). To our knowledge, however, specific media for the cultivation of these two microbial groups have only been used by Anderson *et al.* (2013) and Jacquemyn *et al.* (2013b), respectively. Standardization of the procedures for isolation of nectar microbes might therefore contribute to a better characterization of specific bacterial groups.

While most previous research on nectar bacteria has focused on assessing their taxonomic diversity, the functional diversity of the nectar bacteriome remains mostly unknown. Some studies have revealed that nectar specialist bacteria such as *A. nectaris*–*A. boissieri* clade members and *Rosenbergiella* spp. display ample phenotypic diversity at both the inter- and intraspecies levels in relation to nutrient acquisition and tolerance to different stressors (Lenaerts *et al.*, 2014; Álvarez-Pérez *et al.*, 2021a,c, 2023; Morales-Poole *et al.*, 2023). The wide phenotypic landscape explored by nectar bacteria might help them to cope with a vast array of nectar environments in nature and allow them to coexist with other nectar microbes, as demonstrated for nectar yeasts (Pozo *et al.*, 2016), but these hypotheses remain mostly untested. Future studies should also explore if the observed variability in bacterial phenotypes, especially in those related to the alteration of nectar physicochemical properties, affects pollinator foraging and plant reproduction and fitness.

Genomic insights from nectar bacteria: what is their evolutionary origin?

In contrast to the abundant research on the evolutionary origin of insect-associated bacteria such as the obligate endosymbionts of the genera *Buchnera* and *Wolbachia* (Kaur *et al.*, 2021; Perreau & Moran, 2022) and some lactobacilli that are common members of the microbiota of bees (Tamarit *et al.*, 2015; Heo *et al.*, 2020), limited research has been performed on the evolution of nectar bacteria. Detailed phylogenomic information is available only for the *A. nectaris*/*A. boissieri* clade and the genus *Rosenbergiella* (Álvarez-Pérez *et al.*, 2021a, 2023; Sanchez *et al.*, 2023).

The genus *Acinetobacter* is an ancient and heterogeneous group of bacteria that display high metabolic diversity, show resistance to a variety of environmental stressors, and dominate in a variety of habitat types like soil, water, and diverse animal and plant hosts (Jung & Park, 2015; Dahal *et al.*, 2023). These characteristics have led some authors to consider the genus *Acinetobacter* as a 'microbial weed' (Cray *et al.*, 2013). However, the specific traits and genome characteristics underlying habitat diversification of the genus *Acinetobacter* are still poorly understood (but see Garcia-Garcera *et al.*, 2017 for findings on this topic). Recent genomic work with the nectar acinetobacters suggests that the *A. nectaris*/*A. boissieri* clade, which currently includes six species (*A. nectaris*, *A. boissieri*, *A. apis*, *A. baretiae*, *A. pollinis*, and *A. rathckeae* (Álvarez-Pérez *et al.*, 2013, 2021a; Kim *et al.*, 2014)), underwent substantial habitat change by evolving from a soil-dwelling ancestor to those that thrive in floral nectar (Sanchez *et al.*, 2023). Moreover, the six members of the *A. nectaris*/*A. boissieri* clade show reduced genome size compared with most other *Acinetobacter* species (Fig. 1; Table S2).

These *Acinetobacter* species have experienced extensive gene losses following genome streamlining and gene gains during their diversification, resulting from both evolutionary divergence and

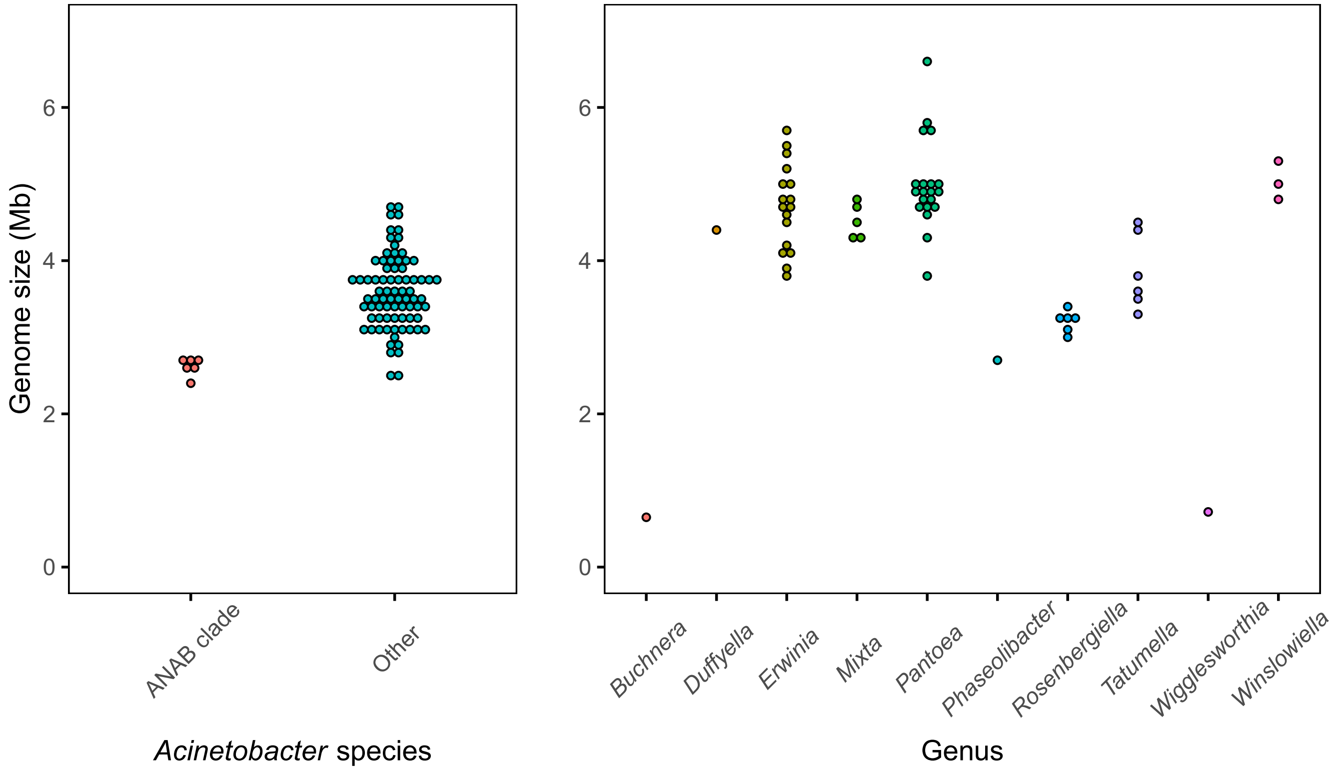

Fig. 1 Genome size comparisons of nectar specialist bacteria of the *Acinetobacter nectaris*/*Acinetobacter boissieri* (ANAB) clade (left) and genus *Rosenbergiella* (right) with their closest phylogenetic relatives (other *Acinetobacter* species and other genera of the Erwiniaceae family, respectively). These graphs were produced from the data included in Supporting Information Tables S2 and S3 using R v.4.3.1 (R Core Team, 2023) and the R library GGPLOT2 v.3.5.1 (Wickham, 2016).

horizontal gene transfer (Sanchez *et al*., 2023). For example, nectar acinetobacters seem to have acquired the ability to degrade pectin from necrotrophic plant pathogens and the genes underlying this ability have duplicated and are under selection within the clade (Sanchez *et al*., 2023). The ability to degrade pectin might be a key trait for adaptation to floral nectar that could improve access to limiting nutrients, such as nitrogen (e.g. through the induction of bursting of pollen grains that fall from the anthers to the nectary) (Christensen *et al*., 2021; Sanchez *et al*., 2023).

Furthermore, the presence of multiple copies of some *pgaABCD* genes of the poly-β-1,6-*N*-acetyl-D-glucosamine (PGA) operon in the genome of the nectar acinetobacters suggests that biofilm formation might represent another key trait of nectar inhabitants (Sanchez *et al*., 2023). Biofilms can protect the bacteria from extreme environmental conditions, provide an effective means of exchanging nutrients and metabolites, and facilitate horizontal gene transfer (Davey & O'toole, 2000), but the ecological and evolutionary significance of biofilm formation for nectar bacteria remains to be addressed in detail.

The genus *Rosenbergiella* is currently composed of six species (*R. nectarea*, *R. australiborealis*, *R. collisarenosi*, *R. epipactidis*, *R. gaditana*, and *R. metrosideri*) and five subspecies (*R. nectarea* subsp. *nectarea*, *R. nectarea* subsp. *apis*, *R. epipactidis* subsp. *epipactidis*, *R. epipactidis* subsp. *californiensis*, and *R. epipactidis* subsp. *japonica*). All of them seem to be mostly associated with floral nectar, pollen, and insects (Halpern *et al*., 2013; Lenaerts *et al*., 2014; Álvarez-Pérez *et al*., 2023). Farlow *et al*. (2023) described an additional putative species, *Rosenbergiella meliponini*, isolated from pollen pots of the Australian stingless bee *Tetragonula carbonaria* (Hymenoptera: Apidae), but this taxon remains to be formally validated. To date, the genus is classified within the family Enterobacteriaceae of the Gammaprotobacteria, even though its closest phylogenetic relatives were placed within the family Erwiniaceae (Adeolu *et al*., 2016). Reclassification of *Rosenbergiella* within this latter family was proposed by Soutar & Stavrinides (2020) based on phylogenomic data, but this proposal has not been accepted. As observed for the *A. nectaris*/*A. boissieri* clade when compared to other *Acinetobacter* species, genome size differs between *Rosenbergiella* (sub)species and most other members of the Erwiniaceae family, excluding obligate insect endosymbiots such as *Buchnera aphidicola* and *Wigglesworthia glossinidia* (Fig. 1; Table S3). Such genome size differences of the genus *Rosenbergiella* with respect to its closest phylogenetic relatives might be linked to niche specialization and an adaptation to inhabit floral nectar and/or the digestive tract of insects, but this hypothesis is yet to be tested.

Alternatively, it might be hypothesized that reduced genome size in nectar acinetobacters and *Rosenbergiella* spp. compared with other closely related bacteria allows them to proliferate faster in ephemeral nectar environments. However, studies have found little evidence for a positive correlation between generation time (or temperature-adjusted growth rate) and genome size, so these parameters are likely to be nearly independent dimensions of ecological variation (Vieira-Silva & Rocha, 2010; Westoby *et al.*, 2021). By contrast, short generation times are associated with the optimization of the translation machinery through codon usage bias, an increased number of rRNA and tRNA gene copies, and gene dosage of highly expressed genes under exponential growth (Vieira-Silva & Rocha, 2010). Genomic and transcriptomic comparison of those nectar specialists with habitat-generalist bacteria that are occasionally found in nectar and the nectar specialists' close phylogenetic relatives could help elucidate nectar adaptation.

Sources of nectar bacteria: how do they arrive at flowers?

Floral nectar is initially sterile upon anthesis. Generalist microbial species present in air, soil, freshwater, and the phyllosphere, including the anthosphere (Aleklett *et al.*, 2014), can get to floral nectar from the air or by contact with the floral surfaces (Pozo *et al.*, 2012, 2015b). In addition, some microbes might have the potential to move from the rhizosphere, the phyllosphere, and/or the endosphere to flowers (or vice versa) through the vascular systems of plants and the apoplast (Compant *et al.*, 2011; Donati *et al.*, 2018; Kim *et al.*, 2019) but this possibility has not been confirmed yet, to our knowledge. Notwithstanding these other dispersal routes, evidence suggests that nectar microbes depend predominantly on pollinators and other animal visitors of flowers for their dispersal (see Brysch-Herzberg, 2004; Herrera *et al.*, 2010; Pozo *et al.*, 2012; Hausmann *et al.*, 2017: on yeast dispersal; Vannette & Fukami, 2017; Vannette *et al.*, 2021; Luizzi *et al.*, 2024: on dispersal of both yeasts and bacteria). Herrera *et al.* (2010) demonstrated that although yeast's arrival to floral nectar via pollinators is not selective, the high osmotic pressure and other hurdles (e.g. presence of plant secondary compounds) of nectar restrict the type of yeast species that can inhabit nectar. Similarly, it has been demonstrated that plant identity and nectar properties can alter bacterial community assembly (Cecala *et al.*, 2024). Interestingly, plant host filtering may also depend on the origin of the bacterial communities. Warren *et al.* (2024) reported high compositional overlap between the nectar bacterial communities in the Japanese apricot (*Prunus mume*, Rosaceae) and those in the mouth of their main pollinators, namely *Apis mellifera* and *Apis cerana* (Hymenoptera: Apidae), which suggests limited habitat filtering of bacteria from bee mouth to floral nectar in this system. By contrast, most bacterial taxa found in the bees' crop (honey stomach) were absent from the bees' mouth and *P. mume* floral nectar (Warren *et al.*, 2024).

As flowers and pollinators share microbes, the following hypothesis was proposed (de Vega *et al.*, 2017): plants visited by different pollinator guilds show a distinct nectar microbiota signature (see also Ushio *et al.*, 2015). Not many studies have addressed the role of pollinators in shaping microbial communities, but certain trends are emerging. For example, Vannette & Fukami (2017) found that flowers accessible to hummingbirds and bees differ in bacterial species composition compared with those accessible only to bees. In a comprehensive study, de Vega *et al.* (2021) investigated the microbiome of 48 plant species from South Africa demonstrating that pollinator guild contributed to the maintenance of beta diversity and nectar-associated phylogenetic bacterial segregation. All isolates recovered from beetle-pollinated flowers belonged to the Alphaproteobacteria and Gammaproteobacteria classes (including members of the genera *Asaia*, *Enterobacter*, or *Rahnella*). Bird-pollinated plants did not have distinct bacterial communities as they were also visited by insects; however, communities isolated from fly-, bee-, and moth-pollinated plants contained exclusively Betaproteobacteria and Actinobacteria genera (de Vega *et al.*, 2021). More recently, Donald *et al.* (2025) found some differences in nectar bacterial communities between the bird- and possum-pollinated *Dactylanthus taylorii* (Balanophoraceae) and ship rat- and silvereye-pollinated *Phormium cookianum* (Xanthorrhoeaceae).

Floral visitors vectoring bacteria among flowers are not just limited to pollinators but also include nectar robbers, ants, thrips, and other animal groups that may not effectively transfer pollen. Zemenick *et al.* (2018) experimentally evaluated whether nectar bacterial communities were differently influenced by legitimate pollinators and nectar robbers in *Aquilegia formosa* (Ranunculaceae). They found increased bacterial diversity and a higher relative abundance of Gram-positive genera (*Enterococcus*, *Lactococcus*, and *Leuconostoc*) and Gram-negative (Enterobacteriaceae) when pollinators were allowed to access flowers. By contrast, nectar robbers had little effect on the alpha diversity but decreased the beta diversity of nectar bacterial communities (Zemenick *et al.*, 2018). Other studies testing the impact of pollinators and nectar robbers on nectar microbial communities have reported contrasting results. Morris *et al.* (2020) compared bacterial communities of *Epilobium canum* (Onagraceae) in flowers visited by legitimate pollinators (hummingbirds) or nectar robbers (carpenter bees). They reported that robbed flowers contained the lowest richness, but a greater abundance of the bacterial genera *Acinetobacter*, *Neokomagataea* (*Gluconobacter*), *Gluconacetobacter*, and *Acetobacter*. Furthermore, bacterial community functional profiles varied by visitation treatment: floral nectar visited by robbers exhibited convergent functional composition, and more genes relating to saccharide metabolism, osmotic stress, and specialized transporters (Morris *et al.*, 2020). These findings contrast with those observed in *Tecoma* (Bignoniaceae) flowers, in which the effects of nectar robbing compared with pollinator visitation showed no detectable differences in bacterial community composition, beta diversity, richness, or abundance (Luizzi *et al.*, 2024).

Despite these advances in the study of the bacterial communities of floral nectar and insects, published studies contain various biases. One source of bias is the choice of culture media used to study them, as we have pointed out above. There is also the geographic bias, which is currently skewed toward temperate regions (most studies are focused on Europe and North America, with tropical regions being underrepresented). Furthermore, the plant bias is skewed toward species pollinated by bees or hummingbirds. The role of other floral visitors in structuring nectar bacterial communities remains poorly known. Ants vector yeasts to nectar (de Vega & Herrera, 2012, 2013), but their role in bacterial vectoring has not been studied in depth. Aggressive ants can indirectly change nectar bacterial species richness and diversity by reducing the frequency and diversity of other floral visitors (Vannette *et al.*, 2017). Thrips are also important vectors of microbes in flowers (Vannette *et al.*, 2021). Lastly, male and female mosquitoes also visit many plant species and consume nectar, potentially vectoring microorganisms in their visits; however, their role in shaping bacterial communities remains unexplored (Sobhy & Berry, 2024).

Nectar bacteria as ecosystem engineers: how do they alter nectar chemistry?

Bacterial and yeast abundance in nectar is initially low, but in hours, it can reach high cell densities (up to 10^7 and 10^5 cells μl^{-1}, respectively; Herrera *et al.*, 2009; de Vega *et al.*, 2009; Fridman *et al.*, 2012). Nectar microorganisms can act as 'ecosystem engineers', profoundly altering floral nectar's chemistry (Fig. 2). For example, the metabolic activity of nectar-dwelling bacteria of genera *Asaia*, *Lactococcus*, *Rosenbergiella*, or *Neokomagataea* can modify sugar concentration, change the proportion of monosaccharides/disaccharides, reduce pH even up by 5 units, decrease H_2O_2 concentration, change the concentration of amino acids, increase the concentration of esters, aldehydes, and sulfur-containing compounds, and reduce the concentration of toxic metabolites of plant origin such as nicotine and aucubin (Vannette *et al.*, 2013; Good *et al.*, 2014; Vannette & Fukami, 2016, 2018; Lenaerts *et al.*, 2017; Rering *et al.*, 2020; Chappell *et al.*, 2022; Landucci & Vannette, 2024). Bacterial metabolism can also alter the floral scent profile by the emission of a wide variety of volatile organic compounds (VOCs) (Lenaerts *et al.*, 2017; Rering *et al.*, 2018; Sobhy *et al.*, 2018; Vannette & Fukami, 2018; Schaeffer *et al.*, 2019). Accordingly, microbial VOCs have been hypothesized to act as honest signals to flower-visiting insects, indicating the quality of the reward (Madden *et al.*, 2018; Crowley-Gall *et al.*, 2021). The extent to which bacteria modify the within-flower thermal microenvironment as occurs with yeasts (Herrera & Pozo, 2010) remains unexplored.

The metabolic activity of nectar-dwelling bacteria might have consequences on floral visitors' foraging behavior and fitness, altering plant reproduction as has been observed for nectar yeasts (Herrera *et al.*, 2013; Schaeffer & Irwin, 2014; Yang *et al.*, 2019; de Vega *et al.*, 2022). Bacteria of the genus *Neokomagataea* reduced pollination success, seed set, and nectar consumption by hummingbirds, weakening a plant–pollinator mutualism (Vannette *et al.*, 2013). Using synthetic nectar, it has been suggested that bumblebees partially avoid solutions inoculated with bacilli (Junker *et al.*, 2014) as do honeybees with artificial nectar colonized by *Asaia* and *Lactobacillus* (Good *et al.*, 2014). Based exclusively on volatile exposure, honeybees reduced the acceptability of nectar with *Neokomagataea* and *Asaia* (Rering *et al.*, 2018). By contrast, *Asaia astilbis* alone did not affect synthetic nectar removal by honeybees, but the effects changed when using co-cultures with the yeast *Metschnikowia reukaufii* (Rering *et al.*, 2020). Bumblebees preferred nectar solutions inoculated with the *A. astilbis* over the yeast *M. reukaufii* based on volatiles, despite this increase was not followed by higher nectar consumption (Schaeffer *et al.*, 2019). Taking all these findings together, we postulate that the extent of bacterial effects can vary among microbial species, plant species, pollinator guild, and experimental procedures. The extent to which modifications of nectar's traits depend on factors such as the microbial genotype (i.e. intraspecies variability) and the macro-environmental conditions remains understudied.

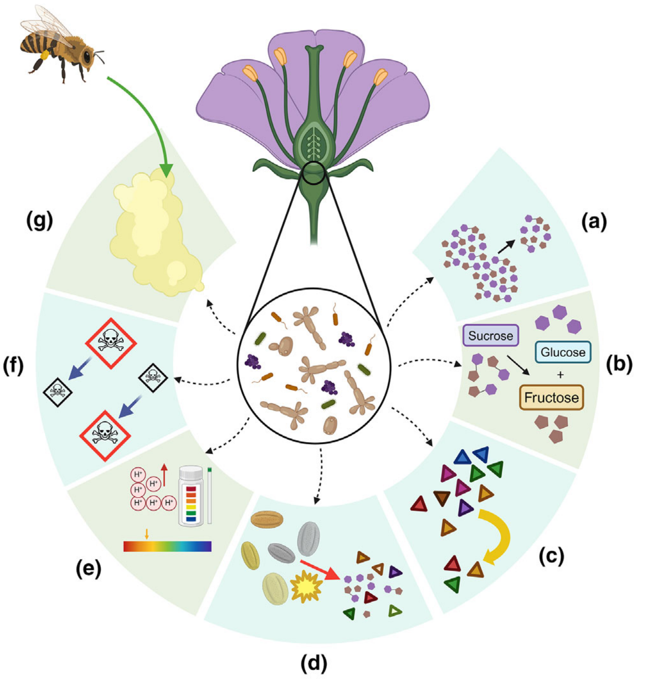

Fig. 2 Nectar microbes as 'ecosystem engineers'. As a result of their metabolic activity, nectar-dwelling bacteria and yeasts can alter floral nectar's physicochemical conditions in multiple ways. For example, these microbes can reduce the overall sugar content of nectar (a), alter its sucrose : hexose ratio (b), and consume the amino acids and other nitrogen sources (c). However, some nectar microbes including the members of the *Acinetobacter nectaris/Acinetobacter boissieri clade* may increase the nutrient content of nectar, for example by bursting the pollen grains that fall into nectaries (d). Additionally, nectar microbes typically acidify nectar (e), reduce the concentration of some toxic metabolites of plant origin, and might produce secondary metabolites that are toxic to other (micro)organisms (f). Finally, nectar microbes can alter the floral scent profile by releasing a wide variety of volatile organic compounds that elicit behavioral responses in pollinators and other plant-visiting animals (g). Created in BioRender: Álvarez-Pérez S. 2024. BioRender.com/s75h142.

Dynamics of microbial communities: bacteria vs yeasts?

The approach to studying plant–microbe and pollinator–microbe interactions has mostly focused on microbial monocultures. However, different species of yeasts and bacteria often coexist in nectar. Thus, monocultures are probably ineffective in understanding the impacts of complex microbial communities. Interactions between different co-occurring microbes can influence nectar chemistry and the resulting floral attractiveness in nonadditive ways (Rering *et al.*, 2020).

The modifications of nectar's physical and chemical conditions caused by nectar microbes seem to be species-specific (Vannette *et al.*, 2013; Lenaerts *et al.*, 2017; Vannette & Fukami, 2018; Landucci & Vannette, 2024), which may determine the relative impact of each microbial species on the growth of other nectar bacteria or yeast, thereby influencing community assembly in this habitat. In this regard, Pozo *et al.* (2016) demonstrated that the yeasts *M. reukaufii* and *Metschnikowia gruessii* differ in their phenotypic response to variation in nectar environmental conditions and suggested that niche differentiation and resource partitioning might explain the frequent co-occurrence of these species in natural nectar communities. The possibility of similar resource partitioning between different species of nectar bacteria, or between bacteria and yeasts, remains largely untested. However, several studies have reported that bacteria and yeasts co-occur in floral nectar more often than would be expected by chance, even after accounting for phylogenetic relatedness of the plant species surveyed (i.e. potential filtering effects due to similar nectar chemistry) (Álvarez-Pérez & Herrera, 2013) or the higher dispersal probability of nectar bacteria over yeasts via some common insect vectors such as thrips (Vannette *et al.*, 2021). In particular, Álvarez-Pérez & Herrera (2013) reported nonrandom co-occurrence between members of the *A. nectaris*/*A. boissieri* clade and the cosmopolitan nectar yeast specialists *M. reukaufii* and *M. gruessii* in the floral nectar of Mediterranean plants from Southern Spain. The hypothesis of co-occurrence facilitation via resource partitioning between nectar yeasts and bacteria was then postulated based on the different sugar assimilation patterns of *Metschnikowia* spp. and *Acinetobacter* spp., with the yeasts depleting glucose and enriching floral nectar in fructose and the bacteria preferentially consuming fructose (Álvarez-Pérez *et al.*, 2013, 2019). Rering *et al.* (2024) have recently reported a significant positive co-occurrence between *Metschnikowia rancensis* and *A. nectaris*, and between *M. rancensis* and *A. apis* in the floral nectar of *Vaccinium* (Ericaceae) plants from Florida, USA. Besides, in experimental pairings of nectar microbes across different growth-inhibiting compounds that are often found in natural nectars (e.g. deltaine, linalool, H_2O_2, and ethanol), neither the bacterial species *R. nectarea* nor the yeast *M. reukaufii* showed an altered viable cell count density (colony-forming units μl^{-1}) in coculture compared with growth in isolation (Mueller *et al.*, 2023).

Co-occurrence of nectar bacteria and yeasts has not been supported by some other studies (e.g. de Vega *et al.*, 2021; Chappell *et al.*, 2022). Given the ancient divergence between eukaryotes and prokaryotes, resource partitioning between nectar yeasts and bacteria seems more likely than the one observed between the more closely related *M. reukaufii* and *M. gruessii* (Pozo *et al.*, 2016). Nevertheless, species niche differences can sometimes be unrelated to phylogenetic distances, and phylogenetic niche conservatism in microorganisms is often blurred by convergent evolution, genetic recombination, horizontal gene transfer, and other genetic and nongenetic factors (Münkemüller *et al.*, 2015; Goberna & Verdú, 2016; Álvarez-Pérez *et al.*, 2021b). Therefore, the suggested nutrient resource partitioning between *Metschnikowia* yeasts and the nectar acinetobacters should not be assumed until experimentally demonstrated. In addition, niche partitioning is not the only mechanism that can determine the ease with which species can coexist in a habitat, and other mechanisms can be at play. For example, niche modification could also affect species coexistence. In some plants, yeasts may exclude bacteria by modifying nitrogen availability in nectar, whereas bacteria may exclude yeasts by modifying nectar pH (Tucker & Fukami, 2014; Vannette & Fukami, 2018; Chappell *et al.*, 2022).

Nectar bacteria to address ecological questions

Microorganisms provide manipulable systems, and their use can contribute to generating and refining ecological and evolutionary theories (Prosser *et al.*, 2007). Studies using microorganisms for this purpose have used protists, microalgae, yeasts such as *Saccharomyces cerevisiae*, and a few bacterial species such as *Escherichia coli* and *Pseudomonas* spp., for which abundant genetic resources are available (Jessup *et al.*, 2004; Altermatt *et al.*, 2015; McDonald, 2019).

The nectar microbiota is also a useful study system for testing ecological theory of processes affecting community assembly, including environmental filtering, competition, dispersal, metacommunity dynamics, and historical contingency (Chappell & Fukami, 2018; Klaps *et al.*, 2020; Fig. 3). Although much work on this topic was based on nectar yeasts (Herrera *et al.*, 2010; Peay *et al.*, 2012; Vannette & Fukami, 2014; Hausmann *et al.*, 2017; Letten *et al.*, 2018), nectar bacteria have also been increasingly used in this context. Specifically, several studies have used bacteria to elucidate the role of priority effects (i.e. phenomena in which the effects of species on one another depend on their arrival order into a local site and initial abundance; Stroud *et al.*, 2024), by themselves or in combination with other factors such as dispersal and/or environmental variability, in community assembly. For example, in microcosm experiments using two nectar-inhabiting yeasts (*M. reukaufii* and *Starmerella bombicola*) and two species of nectar bacteria (*Neokomagataea* sp. and *Asaia* sp.), Tucker & Fukami (2014) observed that when yeasts and bacteria arrive sequentially to floral nectar, multiple species can coexist under variable temperature, but not under constant temperature, and that temperature variability can prevent the extinction of late-arriving species that would be excluded due to priority effects under constant thermal conditions. By contrast, when yeasts and bacteria arrive simultaneously to floral nectar, both microbial types can coexist regardless of the temperature regime (variable vs constant) (Tucker & Fukami, 2014).

Also in microcosm experiments, Chappell *et al.* (2022) demonstrated that *A. nectaris* exerts a strongly negative priority effect against *M. reukaufii* by reducing nectar pH, which might explain the mutually exclusive pattern of dominance between nectar yeasts and bacteria found in natural populations of *Diplacus* (formerly *Mimulus*) *aurantiacus* (Phrymaceae) in California, USA. Furthermore, experimental evolution simulating pollinator-assisted dispersal between flowers revealed that *M. reukaufii* evolves rapidly to improve resistance against the negative priority effect if constantly exposed to *A. nectaris*-induced reduction in nectar pH (Chappell

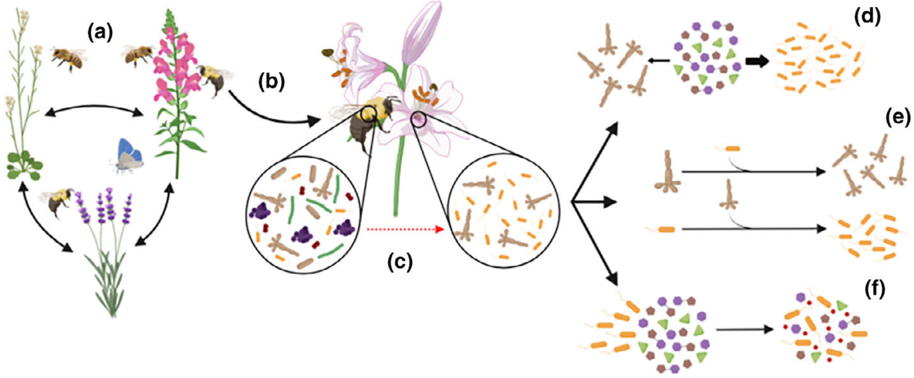

Fig. 3 Nectar microbiome as a model system in ecological research. Floral nectar microbial communities are powerful systems for ecological research due to the short generation times of most of their members, their relative simplicity compared with other natural microbiomes (e.g. rhizosphere and phyllosphere), and their organization in a well-defined hierarchical structure of increasing complexity (nectaries within flowers, flowers within individual plants, plants within populations, etc.), thus allowing multi-scale approaches. Initially sterile, floral nectar often receives various species of bacteria and yeasts via flower-visiting animals and by other means (a, b). The harsh physicochemical conditions of nectar (e.g. high osmotic pressure, scarcity of nitrogen sources, and presence of defensive compounds of plant origin) act as a filter of the incoming microbial community brought by pollinators and other floral visitors (c). Competition for nectar nutrients between nectar microbes (d), which can result in priority effects (e), and microbe-mediated changes in nectar chemistry that can affect the growth of other members of the community through niche modification (f) are some of the processes that may determine community assembly in the nectar microbiome. Created in BioRender: Álvarez-Pérez S. 2024. BioRender.com/p98m725.

et al., 2022). Taken together, these results put into question the putative nutrient resource partitioning between *A. nectaris* and *M. reukaufii* (as mentioned in the previous section) and suggest that pH acts as an overarching factor that governs the eco-evolutionary dynamics of priority effects in floral nectar (Chappell *et al*., 2022).

As demonstrated by Toju *et al.* (2018), priority effects between nectar bacteria and yeasts can persist across floral generations. In a field experiment, these authors manipulated the initial dominance of *Neokomagataea* sp. and *M. reukaufii* in the nectar of wild *D. aurantiacus* flowers and observed that bacterial dominance led to the exclusion of yeasts, and that such an effect persisted in time across multiple generations of flowers collected at different times during a flowering season (Toju *et al*., 2018). By contrast, inoculation of *D. aurantiacus* flowers with *M. reukaufii* did not result in the exclusion of *Neokomagataea* sp. from floral nectar (Toju *et al*., 2018). Therefore, even when local floral habitats are ephemeral, priority effects between bacteria and yeasts may influence multiple generations of local nectar microbial communities within metacommunities (Toju *et al*., 2018).

For the sake of brevity, we have mentioned here just a few representative studies of the use of nectar bacteria to test ecological theory, but further examples can be found elsewhere (e.g. Vannette & Fukami, 2017; Vannette *et al*., 2021; Francis *et al*., 2023; Cecala *et al*., 2024; McDaniel *et al*., 2024). We anticipate that future research in this field will benefit from possibilities offered by multi-omic approaches, as recently done for nectar yeasts (e.g. Chappell *et al*., 2024).

Use of nectar bacteria in agricultural applications

The last decade has seen an increasing interest in the use of nectar microorganisms to develop nontoxic alternatives to traditional chemical pest control (Cusumano & Lievens, 2023; Álvarez-Pérez *et al*., 2024). One factor motivating this work is the fact that microorganisms can alter the VOC profile of floral nectar, which, in turn, may deter pest insects and/or attract their natural enemies (Cusumano & Lievens, 2023; Álvarez-Pérez *et al*., 2024). The use of nectar microbes in biological control of phytopathogens has also been proposed (see, for example, Crowley-Gall *et al*., 2022; McDaniel *et al*., 2024) but will not be covered here.

Although earlier research on the use of nectar microbes against insect pests exclusively focused on yeasts (e.g. Sobhy *et al*., 2018, 2019), bacteria also have potential as biological control agents. For example, nectar bacteria may enhance or compromise (depending on the species) the longevity and survival of aphid parasitoids such as *Aphidius ervi* (Hymenoptera: Braconidae) (Lenaerts *et al*., 2017). Moreover, some nectar bacteria might alter the behavior and/or longevity of the egg parasitoids *Trissolcus basalis* (Hymenoptera: Scelionidae) and *Ooencyrtus telenomicida* (Hymenoptera: Encyrtidae), which are the main biological control agents of the cosmopolitan stink bug pest *Nezara viridula* (Hemiptera: Pentatomidae), via changes in the sugar composition and VOC profile of nectar (Cusumano *et al*., 2023; Sarakatsani *et al*., 2024). Synthetic nectar solutions fermented by four bacterial species isolated from floral nectar, including *Staphylococcus epidermidis*, *Terrabacillus saccharophilus*, *Pantoea* sp., and *Curtobacterium* sp., can significantly attract *T. basalis*. Five VOCs (namely 2-methoxy-*p*-cymene, glutaric acid dimethyl ester, methyl dihydro-jasmonate, 2,5-dimethylbenzaldehyde, and an unknown compound) might be responsible for this behavioral response (Cusumano *et al*., 2023).

Hymenopteran pollinators, such as the honey bee *A. mellifera* and the bumble bee *Bombus impatiens*, are also responsive, either positively or negatively, to bacterial presence in nectar and some bacterial VOCs (Good *et al*., 2014; Rering *et al*., 2018; Schaeffer *et al*., 2019). Accordingly, there is interest in exploring the use of bacteria and other nectar microorganisms to improve crop pollination (Álvarez-Pérez *et al*., 2024), but studies have so far yielded mixed results. For example, Colda *et al.* (2021) sprayed European pear blossoms with *A. nectaris*, either alone or in combination with *M. reukaufii*, observing that the yeast–bacterium mixture significantly increased the visitation rates of honeybees and hoverflies. By contrast, the spraying of pear blossoms with just *A. nectaris* or *M. reukaufii* did not affect flower visitation, and fruit set and seed set were not significantly influenced by any inoculation treatment (Colda *et al.*, 2021). Similarly, inoculation of almond tree flowers with *M. reukaufii* or the bacterium *Neokomagataea thailandica* had no significant effect on pollen germination and pollen tube number (Schaeffer *et al.*, 2023). Future research should aim to determine under which conditions the use of nectar bacteria in pest biocontrol or as pollinator enhancers is profitable and to evaluate the ecological, bioethical, and biosafety risks of these practices (Álvarez-Pérez *et al.*, 2024).

Remaining questions and perspectives

Despite the significant advances in the study of nectar-inhabiting bacteria achieved during the last decade, there are still many unanswered questions regarding the ecology and evolution of these microorganisms. Some of these understudied topics and knowledge gaps have been indicated in previous sections and are summarized in Table 1. We provide below a brief overview of future research on nectar bacteria that, in our view, deserve further investigation.

Is everything everywhere? Diversity and biogeographical distribution of nectar bacteria

There is growing empirical evidence that 'everything is not everywhere' and that the nectar microbiome is variable across geographic scales. However, these conclusions are mostly based on nectar yeasts. Our current knowledge of bacterial diversity in floral nectar is heavily biased toward some specific regions (mostly Western Europe and North America) (see Table S1), with some isolated reports available from other locations such as Argentina and Australia (Sharaby *et al.*, 2020), South Africa (Álvarez-Pérez *et al.*, 2012; de Vega *et al.*, 2021), Japan (Tsuji & Fukami, 2018; Tsuji, 2023), and New Zealand (Donald *et al.*, 2025). Most surveys of nectar bacteria have focused on bee-visited flowers, and only a few studies have dealt with the nectar bacterial communities associated with vertebrate pollinators (e.g. Vannette & Fukami, 2017; Donald & Dhami, 2022; Donald *et al.*, 2025; Table S1). Future research efforts should contribute to a better understanding of nectar bacterial communities in other underexplored biomes and evaluate the role of biotic and abiotic factors mediating variation patterns in the diversity of the nectar microbiome at small and large scales (de Vega *et al.*, 2021; Thiel *et al.*, 2024). Identifying potential sources of endemic bacterial taxa, as previously done for yeasts in Hawaii and South Africa (Lachance *et al.*, 2005; de Vega *et al.*, 2014), also deserves attention.

Additionally, intraspecies diversity has only been studied for a selected number of nectar bacteria, mostly in the context of new taxa descriptions (Álvarez-Pérez *et al.*, 2013, 2021a, 2023; Halpern

Table 1 Some knowledge gaps on nectar bacteria.

Topics	Underexplored research questions
Evolutionary origin	• Which specific traits and genome characteristics underly niche specialization of nectar bacteria? • What is the evolutionary reason for the reduced genome size of some nectar specialist bacteria when compared to their closest phylogenetic relatives?
Dispersal	• Can microbes arrive to floral nectar from other plant microbiomes via the vascular system of the host plant and/or the apoplast? • Have plants visited by different pollinator guilds a distinct nectar bacteriome signature? Do legitimate pollinators and nectar robbers differently influence nectar bacterial communities? • Do bacterial community functional profiles vary according to the visitor guild?
Impact on nectar chemistry	• How do nectar bacterial specialists vs habitat generalists alter floral nectar chemistry? • To what extent do bacterial modifications of nectar's traits depend on the microbial genotype and the macroenvironmental conditions? • Can nectar bacteria modify the within-flower thermal microenvironment?
Interaction with plants and animals	• How do nectar bacteria contribute to insect health and plant fitness? • Which consequences has the metabolic activity of nectar bacteria on floral visitors' foraging behavior? • How do different species of nectar bacteria interact with the immune response of plants?
Community assembly	• Which are the mechanisms allowing microbial co-occurrence in floral nectar? • Does floral nectar exert a similar habitat filtering effect on yeast and bacterial diversity? • Does co-occurrence facilitation via resource partitioning between yeasts and bacteria occur in floral nectar? Under what conditions? • Do bacteriophages and mycoviruses play any role in determining community dynamics in the nectar microbiome?
Diversity patterns	• How prevalent and diverse are nectar bacteria in underexplored regions (e.g. tropical and subtropical regions)? • Is the nectar bacteriome variable across geographic scales? • How do biotic and abiotic factors determine diversity variation patterns in the nectar bacteriome? • Are there endemic taxa of nectar bacteria associated to specific regions and/or plant hosts? • To what degree are different taxa of nectar bacteria specific to nectar as opposed to other potential habitats? • How phenotypically and genetically diverse are nectar bacteria at the intraspecies level?
Response to global change	• Do nectar microbial communities respond to anthropogenic environmental changes (e.g. climate warming, pollutants, and habitat fragmentation)? If yes, what are the potential short- and long-term effects for bacteria vs fungi? • What are the potential cascading effects on plant–microbe–animal interactions?

et al., 2013; Lenaerts *et al.*, 2014). An in-depth analysis of the phenotypic and genetic diversity of the main nectar bacterial specialists using large strain collections, as carried out for *M. reukaufii* and *M. gruessii* (Herrera *et al.*, 2011, 2014; Herrera, 2014; Pozo *et al.*, 2015a, 2016; Dhami *et al.*, 2018; Álvarez-Pérez *et al.*, 2021b), might help to elucidate the evolutionary origin and ecological significance of these microorganisms.

Biological interactions

Plant–insect–nectar microbe interactions are typically studied with a focus on a few pollinators, a few plant species, and a small set of microorganisms (typically yeasts) (Lignon *et al.*, 2025). While these simplifications have helped in the study of the ecological role of nectar microbes, it is important to analyze the complex multipartite biological interactions occurring in and around floral nectar within a wider scope.

Regarding the animal component, most attention has been paid to honey bees and bumble bees, but some studies have highlighted the role of other insect groups as solitary bees, flies, butterflies, ants, thrips, or moths as vectors of nectar yeasts (de Vega & Herrera, 2012, 2013), bacteria (Samuni-Blank *et al.*, 2014), or both microbial types (Vannette *et al.*, 2017, 2021; de Vega *et al.*, 2021). Different lines of evidence suggest that microorganisms can potentially contribute to insect health, for example by providing their host with digestive enzymes and essential nutrients that insects cannot produce by themselves, through the detoxification of toxic plant metabolites, and by suppressing potential pathogens (Douglas, 2009; Blackwell, 2017). Although these processes are still largely unexplored for the bacterial microbiome (Martin *et al.*, 2022), recent research is promising. For example, it has been demonstrated that *A. nectaris* and *R. nectarea* might have beneficial effects on *Bombus terrestris*' health and colony development, including faster egg laying, larger brood size, and/or increased production of workers (Pozo *et al.*, 2021). By contrast, supplementation of food provisions with yeasts or a combination of yeasts and bacteria has less impact on colony development, although this effect is species-specific (e.g. effects on colony development were strongest when a combination of *R. nectarea* and the ascomycetous yeast *Wickerhamiella bombiphila* was added to pollen) (Pozo *et al.*, 2021).

The questions regarding the direct and indirect effects of the nectar microbiome on plant fitness remain open. Most studies have focused on nectar yeasts (actually, just on *M. reukaufii*; Herrera *et al.*, 2013; Schaeffer & Irwin, 2014; Yang *et al.*, 2019; de Vega *et al.*, 2022). To date, only one study has tested the effects of the presence of a bacterium, namely *Neokomagataea* (*Gluconobacter*) sp., on the strength of a plant–pollinator mutualism, finding a reduction in the plant reproductive fitness (Vannette *et al.*, 2013). However, the results of all these studies testing the effects of nectar microbes on plant reproduction are inconclusive, as they reveal that, depending on the pollination context and/or experimental system, the nature of interactions may range from detrimental to neutral or positive to the plant, and that we cannot extrapolate the effects of these microorganisms from one plant species to another (see Klaps *et al.*, 2020; Vannette, 2020; de Vega *et al.*, 2022, for a detailed review). A broader focus considering factors such as phenology of the focus plant, geographic area, and other abiotic factors, pollinator community, microbial community assembly, and subsequent microbial alterations of nectar chemistry, is required to advance in the study of plant–microbe–animal interactions.

It is commonly regarded that plant immune responses can target both harmful and nonpathogenic microorganisms, affecting them in a way that helps shape their composition; avoiding or suppressing immune responses is a crucial trait of plant-adapted microbes (Mesny *et al.*, 2023). Microorganisms with disease-causing potential do not have strictly separated lifestyles but frequently occur in healthy plant and animal hosts, so there is a continuum between microorganisms acting as commensals, pathogens, or mutualists (Drew *et al.*, 2021; Mesny *et al.*, 2023). Nectar microbial communities can coexist with phytopathogenic bacteria such as the members of genus *Erwinia*, which use nectaries as their portal of entry to invade plant tissues (Bubán & Orosz-Kovács, 2003; Sasu *et al.*, 2010; McDaniel *et al.*, 2024). Previous research has shown that nectar bacteria can withstand (up to some degree, which largely depends on the compound, the dose, and the bacterial species) hydrogen peroxide and other toxic defensive metabolites of plants (Álvarez-Pérez *et al.*, 2012; Vannette & Fukami, 2016; Mueller *et al.*, 2023; Landucci & Vannette, 2024). We propose that further research is needed to elucidate how the different species of nectar bacteria interact with the immune responses of plants and fit within the parasite-mutualist continuum.

Finally, there is also increasing evidence that bacteriophages and mycoviruses play an extremely important role in determining horizontal gene transfer and community dynamics in diverse plant- and insect-associated microbiomes (Bonning, 2019; McLeish *et al.*, 2021). While viral sequences have been found in metagenomic studies of the nectar microbiome (Morris *et al.*, 2020) and the genomes of the nectar specialist bacteria *A. nectaris* (Sanchez *et al.*, 2023) and *R. nectarea* (Laviad-Shitrit *et al.*, 2020), the impact of viruses on the growth dynamics and genetic stability of nectar microorganisms remains vastly understudied. We propose that further research on the nectar viruses should not only focus on studying the prevalence and diversity of these agents but also on unraveling their potential impact on plant fitness and plant–pollinator interactions, as done for the pollen virome (reviewed in Fetters & Ashman, 2023).

Beyond the microcosm

Plant microbiomes are shaped by a complex network of positive and negative interactions, particularly between interactive species that act as 'hubs' (Mesny *et al.*, 2023). Metabolic interdependences, resource competition (e.g. the ability to rapidly utilize or sequester a limited resource), and antagonisms (e.g. growth suppression and predation between microbes) constitute key forces underlying the assembly of the plant microbiome (Mesny *et al.*, 2023). These same types of microbe-microbe interaction might affect the assembly of the nectar microbiome (Álvarez-Pérez *et al.*, 2019). However, most studies analyzing the interactions between different species of nectar bacteria or between nectar bacteria and yeasts have been conducted using microcosm experiments with a limited number of species (typically only two, with a single strain of each one) and under controlled conditions that do not fully mimic the factors that affect microbial growth in nature. Consequently, the mechanisms allowing microbial co-occurrence in this habitat remain poorly understood. Network analysis of high-throughput multi-omics data might help to dissect the interactions among nectar microbes, as already done in other systems (Liu *et al.*, 2021).

Response of nectar microbial communities to environmental changes

Plant-associated microbes can respond to anthropogenic environmental changes and affect plant ecological and adaptive responses to global change (Angulo *et al.*, 2022). While most research in this area has focused on the rhizosphere and phyllosphere of natural and crop plants (Trivedi *et al.*, 2022; Zhu *et al.*, 2022), some studies suggest that nectar microbial communities can also be impacted by global change, including climate warming. For example, Russell & McFrederick (2022a) reported that warming can affect overall bacterial density within nectar, subsequently affecting nectar sugar composition and pollinator preferences. Additionally, a naturally occurring extreme temperature event in California (43°C recorded air temperature) was found to have large effects on nectar sugars and the species composition of nectar-inhabiting microbial communities of *Penstemon heterophyllus* (Plantaginaceae) (Russell & McFrederick, 2022b).

Anthropogenic contaminants and fungicides, which can disperse and persist in the environment and potentially affect nontarget organisms, represent additional short- and long-term threats to nectar microbial communities. Cecala & Vannette (2024) have reported that neonicotinoids, widely used to combat insect pests, decreased the growth rate of the nectar bacterial species *Acinetobacter pollinis*, *Apilactobacillus micheneri*, *Neokomagataea thailandica*, *Pantoea agglomerans*, and *Rosenbergiella nectarea*. Different *in vitro* studies have shown that *Metschnikowia* spp. and other nectar yeasts are susceptible to agricultural and medical fungicides (Álvarez-Pérez *et al.*, 2016; Bartlewicz *et al.*, 2016b; Quevedo-Caraballo *et al.*, 2024). Furthermore, field application of fungicides leads to a significant decrease in fungal richness and diversity in exposed flowers but has no apparent effect on bacterial communities (Bartlewicz *et al.*, 2016b; Schaeffer *et al.*, 2017). So, humans can impact the diversity of nectar microorganisms differently for bacteria and fungi. In this line, the studies of Bartlewicz *et al.* (2016a) and Donald *et al.* (2022) have also suggested that human urbanization can shape nectar microbial diversity and community nestedness in contrasting ways for bacteria and fungi.

Concluding remarks

Much progress has been made over the last decade in the understanding of the nectar microbiome, but many studies are still biased toward yeasts. We expect that dissecting the complexities of nectar bacteria and their role in plant–animal interactions would reveal species-specific as well as general trends in multi-kingdom community dynamics, with practical applications in different areas. We hope that this article will help encourage further studies on the ecological and evolutionary significance of these tiny (but mighty?) organisms.

Acknowledgements

We thank two anonymous reviewers for comments. SA-P acknowledges the financial support of projects RYC2018-023847-I, CNS2022-135237, and PID2022-136719NB-I00 funded by MCIN/AEI/10.13039/501100011033 and by 'ESF Investing in your future', and a Complutense Del Amo travel grant. SQ-C acknowledges grant PIPF-2023/ECO-29442 from Consejería de Educación, Ciencia y Universidades, Comunidad de Madrid. Work in the laboratory of BL is financially supported by FWO, Vlaio, and internal KU Leuven funds. TF acknowledges support from US NSF (DEB 1737758). The funders had no role in the preparation of the manuscript or in the decision to publish.

Competing interests

None declared.

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Supporting Information

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

Table S1 Overview of previous studies on the prevalence and diversity of nectar bacteria.

Table S2 Genome size of representative strains of current members of the genus *Acinetobacter*.

Table S3 Genome size of representative strains of current members of the Erwiniaceae family and the genus *Rosenbergiella*.

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