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Review

Microbes, the 'silent third partners' of bee–angiosperm mutualisms

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While bee–angiosperm mutualisms are widely recognized as foundational partnerships that have shaped the diversity and structure of terrestrial ecosystems, these ancient mutualisms have been underpinned by 'silent third partners': microbes. Here, we propose reframing the canonical bee–angiosperm partnership as a three-way mutualism between bees, microbes, and angiosperms. This new conceptualization casts microbes as active symbionts, processing and protecting pollen–nectar provisions, consolidating nutrients for bee larvae, enhancing floral attractancy, facilitating plant fertilization, and defending bees and plants from pathogens. In exchange, bees and angiosperms provide their microbial associates with food, shelter, and transportation. Such microbial communities represent co-equal partners in tripartite mutualisms with bees and angiosperms, facilitating one of the most important ecological partnerships on land.

A mutualism that has shaped terrestrial foodwebs

Symbiotic (see Glossary) relationships are often the cornerstones of species success and evolutionary persistence in any ecosystem [1]. For plants and animals, evolutionary success has been carved from a world already occupied and dominated by microbes [2,3]. This may explain why microbes are increasingly revealed as key players in almost all eukaryotic symbioses [4]. The bee–angiosperm mutualism in particular is one of the most widely studied relationships in terrestrial ecosystems. The foundational role that this partnership has in supporting countless foodwebs (including human food systems) cannot be overstated. The mutualisms between communities of bees and angiosperms have facilitated the vast radiation of flowering plants, as well as the diversity and abundance of bees [5]. However, recent evidence suggests that there is a ubiquitous, yet inconspicuous group of organisms ('silent third partners') underpinning the bee–angiosperm mutualism (Figure 1). This third group is represented by the community of microbes associated with most global bee fauna and the flowers they visit [6–10].

Bee-associated microbial communities represent a remarkably diverse, abundant, and globally distributed group of organisms [11,12]. These microbial communities comprise **mutualists**, potential pathogens, and commensal (neither mutualistic nor pathogenic) taxa, all of which interact (e.g., facilitate or compete) with one another while providing a broad range of direct and indirect functions for bees and angiosperms [13–17]. The activities and services of these symbiotic microbes are often rendered within the floral arena, the nests of social bees, the guts of bees, and the brood cells of solitary bee species [5,6,11,13]. Increasingly, it is apparent that bees transport and introduce yeasts and bacteria to their **pollen provisions** [6,18], which often contribute to the digestion and transformation of the larval pollen provision (Table 1). These early studies established a basis to question the roles and impacts of the microbial

Highlights

Bee and angiosperm communities engage in myriad symbioses with microbial communities, conferring benefits, enduring costs, and exchanging fitness trade-offs.

Microbiota facilitate bee development by processing, protecting, and preserving the pollen provisions of young bees, while suppressing pathogen establishment. For angiosperms, microbes influence floral attractancy, increase fertilization, and antagonize pathogens.

Bee and angiosperm communities provide their microbial associates with vital resources, such as pollen, nectar, resins, transportation, and shelter. These microbial communities 'hitchhike' on bees and then feed upon the pollen–nectar provisions that bees curate within their hives/nests.

Such microbes contribute significantly to the enduring success of their tripartite (three-way) mutualisms with bees and angiosperms. This ancient relationship has been profoundly influential across the major terrestrial ecosystems on Earth.

Recognizing symbiotic microbes as true mutualists in this three-way partnership should recalibrate conservation strategies by widening the lens to include the vital, although inconspicuous, symbionts of bees and angiosperms.

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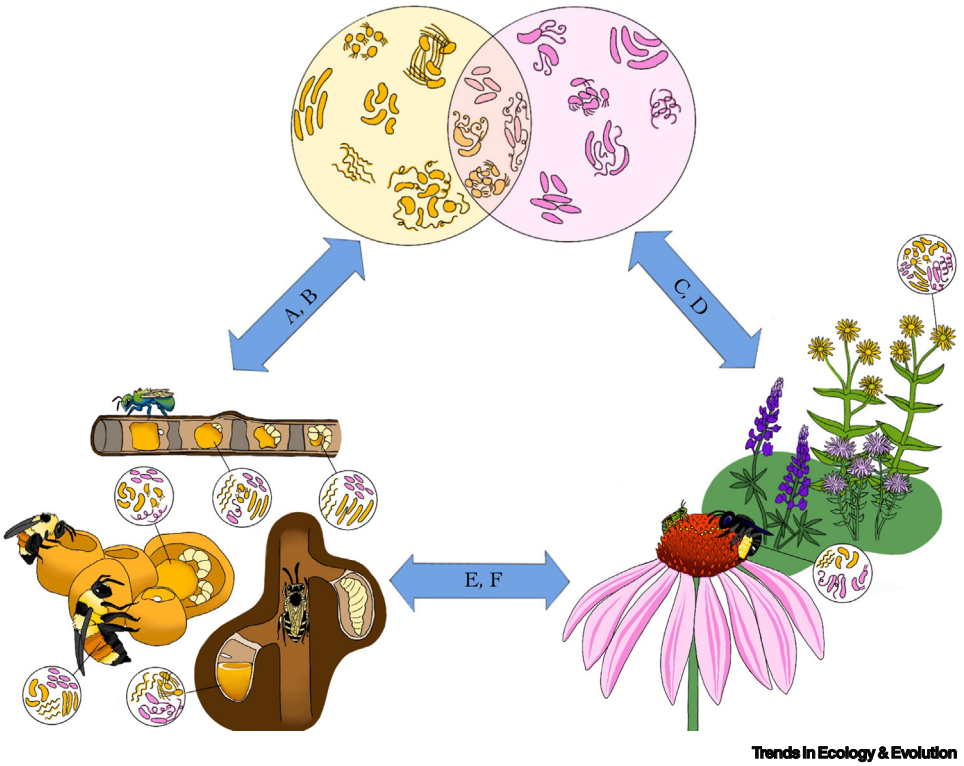

Figure 1. The proposed tripartite symbiosis. The three communities (microbes, bees, and angiosperms) are represented as points on a triangle. At the top of the triangle, the microbial communities associated with bees and flowers are presented with shared taxa indicating degrees of overlap. The overlapping microbial taxa represent the symbiont community supporting both bees and angiosperms. At the lower left, the community of bees and their associated microbes are depicted across a range of nesting habits (ground-nesting, stem-nesting, and social bee nests). At the lower right, the community of angiosperms and their associated microbes are presented. Links between communities are indicated by blue arrows. Within each arrow, bi-directional mutualisms between communities (denoted with letters A–F) correspond to specific relationships/services articulated in Table 1 in the main text.

symbionts associated with bees, especially those external to the bee gut [19,20]. Among the major bee families, recent evidence has shown that bees consume and assimilate significant quantities of microbe-derived amino acids during larval development [9]. Additionally, fungus-derived lipids appear to be important for healthy larval development among solitary bee taxa [15,21]. Microbes have also been known to aid pollen preservation [6,22], detoxification of harmful compounds [23], and defense against pathogens [24–26]. In exchange, bees provide microbes with sheltered spaces in which to grow [5], nutrient-rich pollen and nectar [27], and reliable transportation among flowers and nests/hives (microbes 'hitchhike' on bees) [11,12]. Bee-associated microbes also appear to advance angiosperm fitness by aiding in plant fertilization [28,29], mediating floral attractancy [29–31], and suppressing pathogen establishment [32–34].

The ubiquity, diversity, and impacts of the microbes associated with bees and angiosperms suggest that these microbial communities represent a true symbiont group within the canonical bee–angiosperm mutualism (Figure 1). As such, microbial communities can be examined empirically as integral players in the persistence of **tripartite** mutualisms between bees, microbes, and angiosperms (Table 1 and Figure 2). The ascendancy of this three-way relationship represents a singularly critical factor shaping the diversity and productivity of terrestrial food webs.

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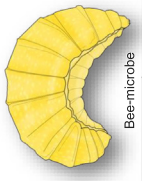
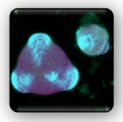
Table 1. Mutualisms between bees, microbes, and angiosperms

Pairwise interaction	Direction of mutualism	Nature of interactions
 Bee-microbe	A) Bee → microbe	• Bees create microhabitats in which to curate pollen-nectar provisions [5,8,27,36,37,38,41,56]. • Bees gather pollen and nectar, creating substrates on which microbes can grow [5-8,10,14-17,44-47]. • Bees transport microbes on/in their bodies, bringing them from flower-to-flower, from flower-to-nest, and/or from nest-to-flower [11,12,48,49,59,60].
	B) Microbe → bee	• Microbes are pollen-digesters [6,9,15,43,62,70-73] and become food themselves [9,15,39,42,75-80]. • Microbes may preserve pollen-provisions by preventing runaway growth by any single microbial community member [11,12,22,30,44,45,82,84]. • Microbes defend the provision by reducing its invasibility by pathogenic microbes [6,24,25,30,32,34,46,63,64,84,86]. • Some microbes break down plant toxins, sequester heavy metals, digest toxic sugars, and reduce oxidative stress from peroxides [8,47,73,80,87].
 Microbe-angiosperm	C) Microbe → angiosperm	• Microbes affect floral attractancy to pollinators, facilitating greater visitation [29,30,50–54]. • Microbes can aid in pollen germination [28,74]. • Microbes engage in fierce competition with other microbes, thereby reducing the likelihood of pathogen establishment [33,55,64,67,69].
	D) Angiosperm → microbe	• Angiosperms provide microbes with sugars, lipids, and amino acids [9,13,14,15,28,61]. • Angiosperms provide substrates that favor/disfavor microbial populations [11,55,63-69]. • Angiosperms create "hubs" for microbe dispersal by pollinators [11,12].
 Bee-angiosperm	E) Bee → angiosperm	• Bees transfer pollen from flower-to-flower, facilitating pollination [5,27]. • Bees deliver microbes to flowers on/in their bodies ("apivectoring"), some of which can be beneficial for angiosperms [11,12,59,60].
	F) Angiosperm → bee	• Angiosperms provide raw materials for bee growth (sugars, lipids, amino acids) [5,27] and self-medication [38,56]. • Angiosperms provide structural materials for nesting [5,11,36-38]. • Angiosperms create arenas in which bees pick up microbes [11,12].

Glossary

Aperture: in relation to pollen grain morphology, an opening in the exine layer (i.e., outer shell of the pollen) through which a germinating pollen tube may extrude.
Apivectoring: transfer of microbial propagules by bees, often from flower to flower.
Mutualist: organismal population that interacts significantly with another population, producing net positive outcomes for both.
Pollen provision: pollen–nectar blends created by adult bees and fed to progeny/siblings.
Symbiotic: type of relationship wherein two or more species (i.e., symbionts) interact significantly (canonically, in close contact) for sustained periods.
Tripartite: with regard to mutualisms, a significant relationship among three organismal groups (species or communities) in which the net effects of the interactions are positive for each group.

Bee–angiosperm mutualisms

Pollination, in exchange for food and building materials

Perhaps the most well studied of all mutualisms is that of bees and flowering plants. The global patterns of bee foraging among angiosperms facilitate gene flow via pollen transfer [27]. In return, bees are rewarded with sugar-rich (nectar) and proteinaceous (pollen) resources that they curate for their siblings or progeny. The bee–angiosperm partnership can be traced back to ~125 million years ago [8]; starting during the early Cretaceous, industrious and highly mobile animals (bees) facilitated the vast radiation of flowering plants, establishing a foundation on which foodweb productivity often rests. With over 300 000 angiosperm species and over 20 000 bee species, this partnership has transformed terrestrial habitats. However, not all bees pollinate and some may not commonly visit flowers (e.g., carrion-feeding bees [35]); nevertheless, most bees are reliable pollinators of the world's flowers, a service provided inadvertently as bees pursue their primary goal: collecting pollen and nectar to feed their progeny or siblings. Plants also provide the structural materials for bees to build their nests or hives. In addition to the hollow stems used by stem-nesting bees, some bee species masticate leaf material to use as the walls of brood cells within stems [5]. Other bee species harvest resins from leaf buds, twigs, or tree bark [36]. Resins can be used by bees to cement sand grains and plant materials together to fortify nests, establish partitions between brood cells, or to create waterproof and disease-resistant barriers (e.g., solitary bees in the genus *Heriades*) [37]. Various social and solitary bee species use the natural antimicrobial phytochemicals within resins as 'self-medication' to suppress pathogens within their nests [38]. When bees establish nests or hives near floral resources (or within

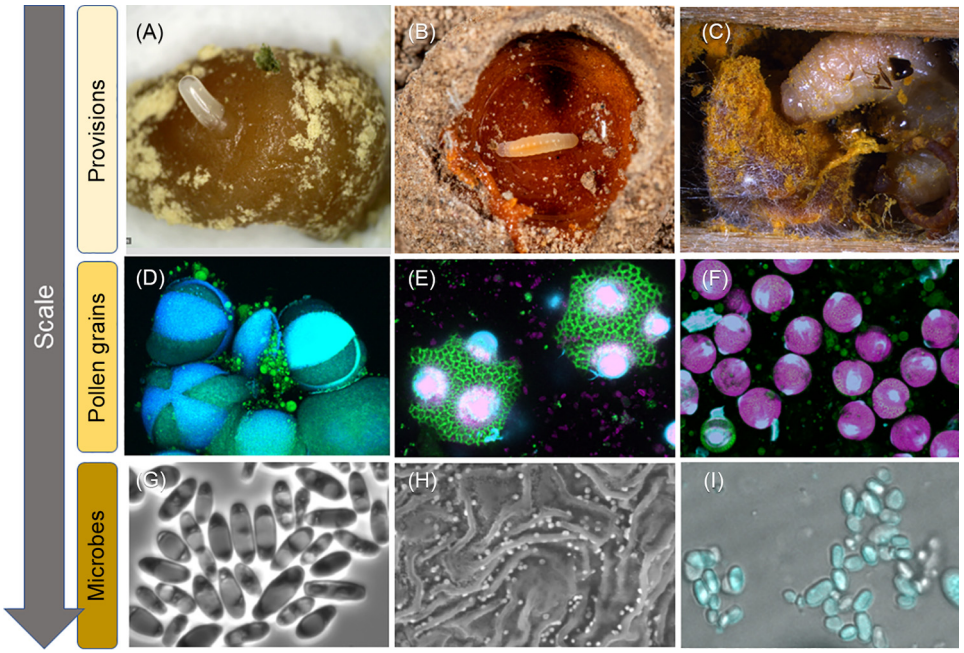


Figure 2. The inhabitants of a bee brood-cell. Young bees on pollen provisions (top row); microbes among pollen grains (middle row); microbes associated with bees/flowers (bottom row). (A) Blueberry bee (*Osmia ribifloris*) egg on a provision; (B) ground-nesting digger bee (*Centris pallida*) larva, feeding on its provision; (C) stem-nesting mason bee larva feeding on its provision; (D) yeast cells on/in pollen apertures; (E) bee (*Diadasia*)-collected pollen with intines herniating through pollen apertures; (F) bee (*Centris*)-collected pollen with bacterial colonies; (G) yeast (*Metschnikowia*) collected from nectar; (H) bacteria distributed across a flower petal; (I) yeasts from *Osmia*-collected pollen.

the structures provided by plants), it is likely that such localized nesting habits enrich the soil in which angiosperms are rooted. Future studies might examine whether there are pulses in soil fertility where bee cadavers, excrement, uneaten food, and/or microbial populations have been introduced to the soil by bees (see Outstanding questions).

Bee–angiosperm mutualisms derive from coevolved, interdependent communities: a community of angiosperms partnered with a community of bees [5,27]. The costs and benefits of these partnerships are distributed among the interacting species, and the net effects represent the emergent properties of the multi-community mutualism [1]. In a multi-community framework, not all species contribute equally to the mutualism, and the relationships may change over time. Given that angiosperms and bees coevolved in a world already occupied by microbes [3], the mutualisms among bees and angiosperms were likely mediated by interactions with ubiquitous microbial populations. To the extent that angiosperm and bee communities were able to exploit, host, or commandeer the services of microbes, such partnerships would have conferred benefits to those communities engaging in the partnerships [4]. Likewise, where microbes could exploit the benefits deriving from close associations with plants and animals (without exacting too high a cost from the host), phenotypes for collaboration would have emerged [1]. If the benefits of 'collaborator phenotypes' exceeded the costs, there would have been an increased probability that these populations would have persisted, facilitating more pathways for coevolution between partners.

Angiosperm–microbe mutualisms

Pollen and nectar represent food for microbes

Both fungi and bacteria can breach pollen defenses and consume the nutrient-rich cytoplasm, fueling their own growth [28,39]. Recent evidence demonstrates that microbes embedded within stored pollen provisions consume substantial amounts of pollen and assimilate the amino acids therein [9,15]. Within the bee gut, microbial communities also contribute significantly to pollen digestion [40]. The full breadth of enzymatic mechanisms by which microbes gain access to pollen cytoplasm is not well resolved, but current evidence suggests that microbial communities have a diverse molecular toolset to breach pollen structural defenses [13,28]. Therefore, the pollen–nectar provision is as much a diet for larval bees as the microbes within it.

Microbes influence plant fertilization

Microbes on floral substrates can affect pollination and plant fitness, either directly or via animal intermediaries [30,41]. Yeasts and bacteria growing in nectar or on petals (Figure 2) can shape olfactory or gustatory attractancy to pollinators [29], which can, in turn, alter their foraging patterns, in some cases increasing pollination [42] and seed set [43]. Additionally, epiphytic microbes on floral surfaces appear to have niches within the floral arena that favor certain microbes that 'sculpt' the phenotype of the flower itself [30]. Epiphytic microbes can reduce infection rates by plant pathogens [44] and are commonly used in agricultural applications [45]. Finally, certain bacteria (*Acinetobacter*) can induce germination of pollen grains [28], which could facilitate fertilization where pollen grain **apertures** (germination portals; Figure 2) do not make contact with the plant stigma.

Protection of angiosperms via microbe–microbe antagonism and plant 'filtering'

Microbes arrive at flowers via wind, rainsplash, and animal transport [11,46]. Microbial establishment in flowers is ubiquitous, but such communities are constantly 'filtered' by biotic and abiotic mechanisms [11,47,48], including microbe–microbe antagonism [49], UV radiation, floral volatiles [43], floral structures, such as petals and bracts [50], high sugar concentrations in nectar, and hydrogen peroxide production [51]. Indeed, angiosperms can create chemical niches for their epiphytic microbial populations, and these microbes can reshape the chemical phenotype of the plant [30]. Such flower-associated microbes are often adapted to environments with high osmotic stress [52], low pH, and antimicrobial compounds, such as peroxides [53]. Given the ubiquity and degree of interspecific antagonism among microbes [49,54], the pioneering microbes (earliest colonizers) of a floral structure or substrate may prevent later-arriving microbes from establishing [33], which likely confers a degree of protection to the plant.

Bee–microbe symbioses

Bee nutrition and development

Microbes as pollen digesters

The breakdown of the recalcitrant sporopollenin 'shell' (exine layer) of pollen grains is facilitated, at least in part, by microbes [55]. Pollen grains are protected by morphological and chemical barriers and, while bees are able to access (directly or indirectly) such nutrients [55], the mechanisms are poorly resolved. Pollen- and nectar-borne microbes deploy a molecular 'toolbox' replete with enzymes (e.g., proteases, lipases, amylases, aminopeptidase, and acid phosphatase) involved in protein, lipid, and carbohydrate digestion [6]. Bees are known to consume and assimilate the metabolic products (e.g., sugars, amino acids, and lipids) derived from the microbe-mediated breakdown of macromolecules within pollen [9,15].

To access the cytoplasm of pollen grains, microbes use a variety of biochemical strategies, such as lactic acid generation [56], pectinase production [57,58], and cellulose digestion [59]. *In vitro* studies suggest that certain floral- and pollen-associated microbes produce enzymes that mimic stigma-like environments and induce pollen germination [28,60]. A more diverse microbial community would be predicted to provide a broader enzymatic repertoire, increasing the variety of pollen types that can be accessed. Indeed, increased microbial diversity within pollen provisions confers benefits for certain solitary bees: it has been shown that, with increasing bacterial diversity [61] and microbial abundance [15], larval fitness can be enhanced.

Microbes as prey for developing bee larvae

Symbiotic microbes in fermenting pollen provisions often represent nutrition or prey for bees (Box 1). Microbes that feed on plant biomass are herbivores [62], and molecular evidence has consistently shown that the microbial populations feeding on pollen provisions represent prey to developing bee larvae [63,64]. Microbes are important direct sources of nutrition for young bees [65–67]. As consumers of microbial prey, larval bees are distinctly omnivorous [9,15]. While the individual microbes being consumed represent prey, their populations (i.e., at the species scale) derive a net benefit from the partnership with bees (Box 1). Removing, altering, or constraining such microbial prey can have adverse fitness consequences for both social [14,68] and solitary bee taxa [65,69].

Microbes as pollen preservers

To various degrees, pollen-borne microbes alter/tailor the substrate to not only maximize their own resource capture, but also constrain the resource capture of other microbes, either directly [22,30] or indirectly [70]. Specific physicochemical changes mediated by microbes include lowering of pH, increased abundance of free organic acids, decrease in the availability of simple sugars [71,72], and the breakdown of macromolecules, such as lipids and amino acids [9,15]. Transformation of the pollen substrate, via acidification, extracellular digestion, desiccation, and/or release of antimicrobial compounds, renders the substrate refractory to many microbes [11,12,30]. Constraining the capacity of other microbes to consume the substrate will tend to slow the digestion of the pollen provision. Among stingless bees (Meliponini), fermentation by microbes has been shown to be a means of preserving provisions during periods of food scarcity [22]. In spring, the pollen provisions of mason bees (*Osmia* spp.) are preserved (and partially consumed by microbes), while bee larvae consume the provision, which can last for 4 weeks [73]. Altogether, the combination of a refractory substrate and intense competition within the microbial community likely preserves the provision by moderating the magnitude of microbial digestion.

Microbes as defensive mutualists

Pollen-inhabiting microbes may have a role as defensive mutualists [24], deterring invading microbes that can cause disease and/or pollen spoilage. Given the intensity of interspecific competition among microbes [49], a more diverse microbe community likely presents a more competitive substrate and reduces the invasibility of pollen provisions [48,74], thereby decreasing the chance of pathogen establishment. In natural systems, microbes are commonly deployed by animals as their primary defense against unwelcome, invading microbes [75]. In agricultural systems, disease management strategies have, for decades, used microbes to defend plants from other microbes (i.e., pathogens), relying on the vigorous antagonism among microbes as a means to interfere with pathogen establishment [76]. Microbes isolated from nest-building materials, brood cell partitions [77], bee exoskeletons [78], and from the guts of social and solitary bees have been documented to suppress the proliferation of pathogens, induce the expression of antibacterial compounds, and support immune function [25]. Given that solitary bee larvae often require multiple

Box 1. Microbes eat pollen, and bees eat microbes

Developing bees consume a complex of plant and microbial biomass (Figure I). Tight associations between microbe-derived dietary subsidies and bee survival/fitness suggest that microbial biomass is not an ancillary constituent of the larval bee diet, but rather an indispensable component. While a subset of a microbial population may become food, the remainder of the population can persist, reproduce, and continue to benefit from their relationships with bees [4,67]. In this way, certain bee-associated microbes exemplify the classic ecological trade-off wherein the benefits of a mutualism exceed the costs.

As microbes consume the pollen substrate, they break down plant proteins, sequester amino acids, and reconstitute them as microbial proteins. Quite literally, the microbes feed on the pollen substrate, displacing plant proteins with their own proteins [62,63]. The microbes also create new lipids, consolidating them in their biomass (along with the proteins), making both nutrient groups more accessible to bee larvae [15]. Evidence suggests that the availability and quality of microbe-derived nutrients is as important to some bee species as the pollen itself [65]. Inconsistencies in bee performance on ostensibly 'appropriate pollen' may be explained by the absence of key microbial symbionts [69]. We hypothesize that the pairing of pollen composition and microbial community composition likely represents a 'lock-and-key' model of pollen nutrient extraction. Under this model, the functional diversity of a microbial community would affect the capacity of the microbes to access and extract nutrients from a pollen provision. With greater pollen diversity, greater microbial diversity would be required to effectively extract the nutrients. Therefore, nutrient availability could become highly idiosyncratic for bee larvae, depending on the capacity of the resident microbial community to access the variety of pollen types in a provision. Adaptive foraging strategies for the adult bee might converge on a narrower range of plant species that more reliably paired microbes with pollen types. Indeed, recent work showed that, by decoupling microbial and pollen sourcing (hetero- versus conspecific provisioners), conspecific sourcing of microbes and pollen was revealed to provide greater nutritional benefits to developing bee larvae. The larvae developed faster and became heavier pupae when the microbial community associated with their mother was present within their diet [65].

Figure I. Foraging and feeding patterns across the life stages of solitary bees (*Osmia*). (A) an adult female provisioning her progeny within a reed; (B) *Osmia* egg on a pollen provision; (C) older larvae feeding on provisions in a reed. Reproduced courtesy of Neil Losin (A,B).

weeks to consume a single provision before completing their development [5], there is the potential for greater reliance on microbes to preserve and protect the provision (Box 2).

Microbes as pollen and nectar detoxifiers

Many naturally occurring plant compounds, even certain sugars found in nectar, can be toxic to bees [79], and plants are known to coat pollen with both chemical and physical deterrents [80]. Furthermore, plants that grow on contaminated soils can translocate toxins, including heavy

Box 2. Shelter for bees and their symbionts: a unique challenge for animals with an external rumen

Pollen provisions can be divided into two major types: incremental and mass provisions [5]. Social bee species generally provision their larvae frequently and are considered incremental provisioners. Conversely, solitary species are mass provisioners, creating a single mass of pollen, nectar, and microbes for each of their young. The survival and fitness of a solitary bee larva is highly dependent on this single mass of food; thus, there is perhaps greater reliance on the microbes associated with their provisions.

There are unique challenges for animals relying on external symbiotic microbes for nutrient acquisition, which often necessitates sustained protection of the resource [73,88]. Since the food needs to ferment outside the body of the animal, the consumers (bees) sequester the resource within brood cells or nests (Figure I). While defending against predators, bees must also contend with opportunistic microbial colonizers. When an adult bee has created a nutrient-rich pollen–nectar blend for her progeny/siblings, this resource is already rife with microbes, and a subset of these microbes appear to transform and digest the pollen–nectar substrate. The pollen provision actively ferments, making it analogous to an external 'rumen' [64], and the resource is consumed simultaneously by both microbes and the developing bee larvae [9,15]. In feeding, the bee larva itself may alter this functional rumen, favoring/disfavoring certain microbial taxa over others [10].

A diversity of nesting structures is used by bees to safeguard their precious pollen resources from opportunistic colonizers (Figure I). Stem-nesting solitary bees seal their pollen–nectar provisions behind thick mud walls stashed within hollow plant stems (see Box 1 in the main text) [5,73]. Bees often create barriers to undesirable microbial colonists, such as the impermeable barriers common to the nests of cellophane bees [99], or the coatings of resin on the interior of hives and solitary bee nests [36,100]. The collective result of creating the nest space, curating the pollen provisions, and managing temperature/humidity is that a shelter for bee larvae also functions as a home for their microbial 'nestmates'. Within the nests of bees, there tends to be a resident microbiome associated with the various structures and substrates [77]. Colony-specific, idiosyncratic microbial communities can be found within these spaces [88], and propagules of the colony microbiome can follow the daughter queens into subsequent years [101].

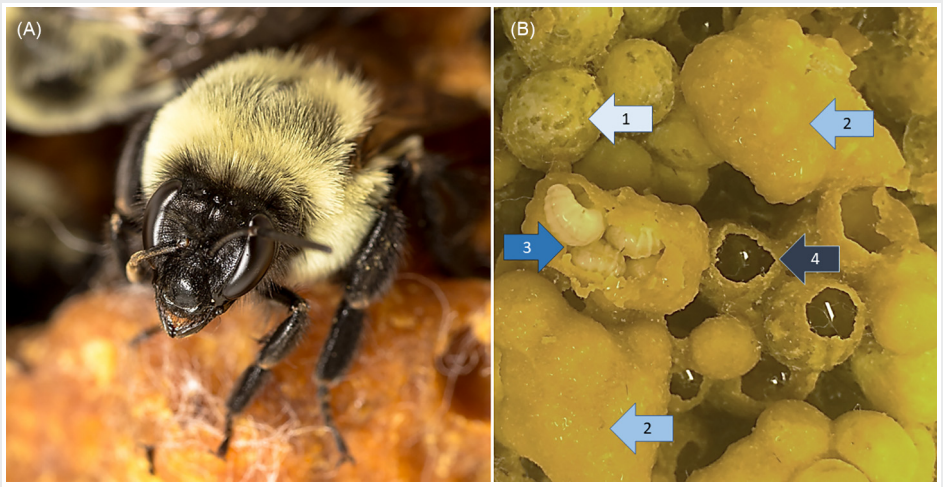


Figure I. A bumble bee nest (*Bombus impatiens*) is structurally different from honey bee hives or solitary bee nests. Within the protected space of the nest, the adult bumble bees (A) create waxen structures that protect eggs/larvae/pupae (B). The pupae complete their development in domed wax chambers (1), which are separate from the larger, irregularly shaped larval feeding chambers (2). Within the feeding chambers, eggs incubate and hatch, and the bee larvae [(3), larvae exposed here after tearing open the chamber] feed on microbe-rich, fermenting pollen–nectar blends. Colony 'honey pots' (4) provide sugar and water. Photos reproduced with permission from Don Parsons.

metals and pesticides, into pollen and nectar [81,82]. The core bumble bee (*Bombus* spp.) and honey bee (*Apis mellifera*) gut microbiomes have gene sequences involved in heavy metal transport and resistance, and several strains can accumulate metals from their surrounding

environment [83]. Indeed, bee-associated bacteria (*Apilactobacillus* spp.) commonly found in pollen provisions harbor genes involved in heavy metal detoxification [58]. Interestingly, a near-universal feature of lactobacilli is that they are catalase negative, yet the bee-, flower-, and provision-dwelling lactobacilli species have functioning catalase genes, suggesting they have a role in dealing with oxidative stress from nectar [58]. Given the common presence of peroxides in pollen and nectar [8], more work is needed to tease apart which microbes (or plants) are creating and neutralizing peroxides (see Outstanding questions).

Bees provide shelter, nutrition, and transportation for microbes

Bees engineer shelter for microbes

Bees serve as habitat engineers, architects, and home builders for their progeny/siblings [84] and, in the process, they provide protected, nutrient-dense, and humid microhabitats for the growth of microbes (Box 2). Indeed, entire bacterial (e.g., *Apilactobacillus*) and fungal lineages (e.g., *Starmerella*) are primarily bee associated, suggesting microbial dependence on bee-associated habitats and resources (Table 1). Intertwined with bee life histories/cycles are nesting habits (Figure 3), which differ structurally and functionally between social and solitary bees (Boxes 1 and 2). Inside any bee nest, there are different types of microbes, which interact not only with the adult female(s), but also their offspring and larval provisions [26]. At times, the bee itself may represent the safe space: microbes (yeasts, specifically) are known to rely on bumble bee queens as an overwintering habitat [85,86], which would simultaneously provide the microbes with a safe microhabitat while also allowing the overwintered queen bee to readily 'seed' its new colony (i.e., vertical, intergenerational transmission) with the microbes from its natal colony (Figure 3). The same may also be true for solitary bees, as well as certain stingless bee species, which move provisions and nest material after founding a new nest [5]. Eusocial bees (i.e., bee species with a queen, overlapping generations, cooperative brood care, and a division of labor between reproductive and non-reproductive siblings) that maintain perennial colonies may have a more conserved gut microbiome, attributable to vertical transmission. Recent work revealed microbial composition varied among closely related bee species [87] and even within a species [88], suggesting that perhaps plasticity and/or 'loose niches' (substitutable microbial species serving the same function) facilitate bee–microbe mutualisms among bee taxa with differing life-history strategies.

Bees deliver 'groceries' and make meals for microbes

Nectar–pollen ratios of pollen provisions are relatively idiosyncratic among bee taxa [5], which may be tailored, at least in part, to the microbes being cultured therein. For example, several diphaglossine bees create liquid provisions that harbor abundant lactobacilli that appear responsible for the distinct smell of fermentation emanating from these pollen provisions [89]. The genomes of these lactobacilli demonstrate signatures of highly specialized adaptation to the pollination landscape, including flowers, nest environment, pollen provisions, and the bee gut [58]. Given that the phyllosphere may influence the microbial community composition and distribution [30], certain microbes may similarly become optimized for nest conditions. Recent evidence reveals the nature and magnitude of microbial specialization at global scales, showcasing how microbial communities themselves can be distinctively constrained and converge upon functions or substrate types [90]. As habitat engineers, hosts, and resource gatherers, bees favor some microbes in their environment over others, which likely 'sets the table' for the fitness of all three symbiont groups (Boxes 1 and 2). The impact of the gut microbiome on bee health has been more extensively reviewed elsewhere [19,20]. We hypothesize that a nutritional symbiotic loop exists between larval bees and their gut microbiome: endosymbionts begin as external symbionts in the provision, then are hosted internally, are provided a steady stream of food, and in turn, the endosymbionts confer fitness benefits to the hosting larva.

Figure 3. Annual cycling and movement of bees, microbes, and angiosperms.

For a Figure360 author presentation of Figure 3, see the figure legend at https://doi.org/10.1016/j.tree.2023.09.001.

The symbiotic microbes associated with bees and flowers require transportation, food, and shelter. Adult bees commonly emerge in spring/summer (in temperate zones) from overwintering sites, labeled in the figure as 'Emergence'. Microbial propagules are known to spend the winter on adult bees, and newly pupated adults can acquire microbes upon emergence. Pie charts indicate hypothetical microbial diversity (colors within a chart denote microbial taxa) linked with bees, nests, hives, and/or flowers. As adult bees disperse in search of mates and nests ('Mating/Nesting'), the bees carry microbes with them. When bees visit flowers, they commonly slough microbes and pick up new ones, which may also facilitate pathogen transfer. The flowers become hubs for 'hitchhiking' microbes and, in this way, the community of foraging bees creates a community of bee-associated microbes within the community of angiosperms. Thus, the microbial community is physically embedded within the bee and angiosperm communities and, collectively, these three symbiont groups interact directly and indirectly. Here, three communities of symbionts (bees, microbes, and angiosperms) are linked and engaged in mutualisms. Note the increased microbial diversity represented in the pie chart linked to the flower community. As bees bring pollen and nectar back to their nests/hives, they bring a subset of the available microbes with them ('Foraging/Provisioning'). For most flower-associated microbes, it remains unclear how their propagules endure across seasons, when host flowers cease to be present ('Dormancy').

Bees as transporters of microbial propagules

Adult bees are particularly well suited as vehicles for pollen gathering and transport, given their morphological (e.g., hair-like setae, 'pollen baskets', and long tongues) and behavioral adaptations (e.g., 'buzz pollination' or repeated visitation of flowers) [27,91]. Of course, such adaptations also facilitate **apivectoring** of microbes [92–94], effectively transporting external microbes from bee hives/nests to flowers, from flower to flower, and back to hives/nests (Figure 3). The setae covering adult bees can accumulate microbial propagules, as evidenced by recent findings that bumble bee daughter queens carry yeasts and bacteria from their natal colonies [86]. Adult bees emerging from their winter shelters, particularly stem- or ground-nesting bees, may be analogous to a pipe cleaner being pulled through a tight space and, as the bees emerge from their overwintering sites, they likely bear some of the microbial propagules from their nest microbiome.

The repeated collection and deposition of microbes at flowers spreads microbial propagules across the floral landscape, potentially making the bee-associated microbial community broadly available to the resident bee community [11,12]. Flowers often serve as 'hubs' for microbial dispersal among pollinators [95,96], since bees slough some of the pollen and microbes at each flower they visit. It is reasonable to expect that microbial propagules on/within a bee would be commonly transported to and from their nests, where they could develop on a rich, curated resource (i.e., the larval pollen provision). Therefore, pollination is not merely a pollen-dispersal endeavor that benefits plants; it is also the primary means by which bee-associated microbes are transported across a landscape (Figure 3). These microbes then gain access to a high-quality, curated resource (Box 1) and are able to grow within a space protected from exposure to desiccation, temperature extremes, and opportunistic invaders (Box 2).

Bees can also vector plant pathogens [94] which means their foraging can contribute to the spread of plant diseases. However, as articulated earlier, antagonism among microbes is pervasive and tends to prevent runaway growth of a single microbial population (including pathogens) in diverse microbial communities (Table 1). For this reason, as well as plant defense responses, massive and chronic plant disease outbreaks in natural systems tend to be uncommon. Were such bee-vectored outbreaks common, the benefits of having pollinators would likely have been undercut, strongly selected against, and, over evolutionary time, dismantled.

Concluding remarks

Three organismal groups form the foundation of a dominant mutualism that has sculpted countless foodwebs in terrestrial ecosystems. Angiosperms fuel this tripartite partnership by supplying critical raw nutrients. In return, bees have become industrious pollinators, facilitating the diversification and global expansion of angiosperms. The enduring success of this collaboration has been facilitated and sustained via partnerships with symbiotic microbes. For bees, as well as other pollinators (indeed, most animal fauna), symbioses with microbes have facilitated remarkable diversification and proliferation through deep evolutionary time [97]. Tripartite mutualisms involving animals, microbes, and/or plants appear to be common in nature, as exemplified by leafcutter ant communities sprawling across the Neotropics [98] or the bee–microbe–angiosperm communities that exist wherever bees visit flowers. As microbial identities, functions, and symbioses are increasingly unveiled, it is likely that microbes will be revealed as 'silent third partners' within many communities, across most ecosystems.

It is important to consider that the mutualisms among bees, microbes, and angiosperms represent the emergent, adaptive effects of interacting communities. While numerous bee and plant species have been examined for their relationships with specific microbes, it is less common that microbes are examined as a dynamic, diverse community (see Outstanding questions). This underscores the need to examine explicitly how multi-community mutualisms may be driven by microbial partnerships. With this perspective, conservation strategies may be recalibrated to consider all partners, particularly the less conspicuous ones.

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Declaration of interests

None declared by authors.

Outstanding questions

Pollen dispersal also facilitates microbial transport. Do bees have particular morphological and/or behavioral adaptations, such as setae and mycangia, that exist to gather, harbor, and disperse (or avoid dispersing) microbial propagules?

While catalase-positive lactobacilli are relatively rare in nature, they are commonly found in the bee gut as well as within the pollen provisions of bee nests/hives. Do such bacteria use catalases to deal with oxidative stress while digesting pollen grains, and how common are peroxides or other strongly reactive oxygen species in pollen provisions?

Bee taxa, particularly solitary bee species, tend to mix pollen and nectar in idiosyncratic yet consistent ways, suggesting that the foraging females follow a 'recipe.' Does specialization in foraging derive from the need to create a pollen–nectar substrate conducive to particular microbes?

If bee species are catering to microbes, does this always provide nutritional/fitness benefits for their progeny?

Over time, microbes digest pollen provisions (see Box 1 and Figure 2 in the main text) and transform the substrate, potentially rendering the provision refractory to the development of other microbes. Are there successional stages in the microbial communities of pollen provisions and, if so, does each successive microbial community offer a new blend of pollen-processing potential?

Microbes exploit floral rewards for their own benefit while channeling floral gene flow and enticing bees to visit flowers (or avoid flowers). To what degree can microbes influence pollination, and are there particular microbial taxa that contribute disproportionately to floral attractancy?

Microbes compete fiercely with other microbes, which may preclude establishment of pathogens. How effective is microbe-derived disease suppression?

Bees and angiosperms are generally thought to simply trade pollination

services for raw nutrients. Are there other services that bees may be providing angiosperms? For example, do ground-nesting bee species enrich soil fertility, or potentially inoculate the soil with microbes important for plant health (i.e., nitrogen-fixing bacteria or pathogen-suppressing communities)?

In an era of climate change, the relationships between bees, microbes, and flowering plants may be changing. How might these partnerships evolve as the climate changes?

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