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Bees just wanna have fungi: a review of bee associations with nonpathogenic fungi

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Abstract

Bee–fungus associations are common, and while most studies focus on entomopathogens, emerging evidence suggests that bees associate with a variety of symbiotic fungi that can influence bee behavior and health. Here, we review nonpathogenic fungal taxa associated with different bee species and bee-related habitats. We synthesize results of studies examining fungal effects on bee behavior, development, survival, and fitness. We find that fungal communities differ across habitats, with some groups restricted mostly to flowers (*Metschnikowia*), while others are present almost exclusively in stored provisions (*Zygosaccharomyces*). *Starmerella* yeasts are found in multiple habitats in association with many bee species. Bee species differ widely in the abundance and identity of fungi hosted. Functional studies suggest that yeasts affect bee foraging, development, and pathogen interactions, though few bee and fungal taxa have been examined in this context. Rarely, fungi are obligately beneficial symbionts of bees, whereas most are facultative bee associates with unknown or ecologically contextual effects. Fungicides can reduce fungal abundance and alter fungal communities associated with bees, potentially disrupting bee–fungi associations. We recommend that future study focus on fungi associated with non-honeybee species and examine multiple bee life stages to document fungal composition, abundance, and mechanistic effects on bees.

Keywords: Anthophila, microbiome, provision, *Starmerella*, symbiosis, yeast

Introduction

Insects frequently host microbial symbionts, and although most work to date on these symbioses focuses on bacterial communities, insect–fungi associations are common and play important roles in insect nutrition and defense (Biedermann & Vega 2020, Vega and Blackwell 2005, Stefanini 2018). Fungal symbionts benefit insects in many ways, including acting as a direct food source (fungus-farming ants and termites, ambrosia beetles, Aanen et al. 2002, Beaver 1989, Mueller et al. 1998), provisioning limiting nutrients (yeast-like symbionts in planthoppers, Noda et al. 1979), detoxifying or digesting food resources (cactophilic fruit flies, bark beetles; Starmer and Fogleman 1986, Soto-Robles et al. 2019), and providing protection against pathogenic or saprotrophic microbes (fungus-farming ants, termites, and beetles; Florez et al. 2015).

Like many other insects, bees interact with microbes in symbioses ranging from beneficial to parasitic. Bees (superfamily Anthophila) are a large group of insects comprised of over 20 000 species (Orr et al. 2021). Bees are important pollinators, contributing to global services worth an estimated USD\$195–\$387 billion annually (Porto et al. 2020). While many of the bee species used for crop pollination services (such as honeybees and bumblebees) live in large social colonies, approximately 90% of all bee species are solitary (Danforth et al. 2013). Studies of microbial symbioses in bees have disproportionately focused on eusocial bee groups, which are known to have a small and well-conserved core bacterial gut microbiome that augments immunity and is transmitted across generations via the social hive environment (Kwong

et al. 2017). Emerging studies suggest that bacterial associations may also provide nutritional and protective benefits to solitary bees, though they lack a core microbiome (Voulgari-Kokota et al. 2019). Although the bulk of research to date has focused on bee-associated bacteria, there is growing recognition that bee microbiomes are complex and contain unicellular parasites, viruses, and fungi, which are the focus of this review.

Fungi associated with bees have typically been studied as pathogens (Evison and Jensen 2018), saprophytes of stored provisions, or indicators of poor bee health. The best studied bee-associated fungi are those in the genus *Ascosphaera*, which are specialized on bee-associated habitats and include species that are pathogenic to bee larvae (Aronstein and Murray 2010, Ravoet et al. 2014, Maxfield-Taylor et al. 2015) as well as those that grow saprophytically on stored pollen (Skou and King 1984, Vandenberg and Stephen 1983). In addition, fungi in the genus *Aspergillus* can be opportunistic pathogens of adult and larval bees (Becchimanzi and Nicoletti 2022) and can produce mycotoxins that are toxic to bees (Niu et al. 2011, Kostić et al. 2019). Microsporidians in the genus *Vairimorpha* (formerly *Nosema*), which are closely related to fungi, can infect a wide range of bee species and cause nosemosis (Martín-Hernández et al. 2018, Grupe and Quandt 2020). Outside of pathogenic interactions, the presence of fungi within bees has traditionally been regarded as a sign of stress; bees stressed by nosemosis, xenobiotics, or warm overwintering temperatures host a greater abundance of fungi within their gastrointestinal tract (Gilliam 1973, Gilliam et al. 1974, Rada et al. 1997, Borsuk

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et al. 2013, Ptaszyńska et al. 2016a, b, Maes et al. 2021). Within stored bee provisions, some fungi act as spoilage microbes and may contribute to larval bee mortality, especially in solitary bee species (Batra et al. 1973, Lunn et al. 2022, Pitts-Singer 2004). However, there is growing recognition that not all fungi associated with bees indicate disease or decay; some may be commensal or even mutualistic.

Bees host diverse communities of nonpathogenic fungi (Inglis et al. 1993a, Grabowski and Klein 2017, Echeverrigaray et al. 2021, Jacinto-Castillo et al. 2022). Over the last few decades, and with increased accessibility of DNA sequencing methods, these fungal symbionts have been characterized in association with a growing diversity of bee species, and their roles within bee health and ecology have started to be examined. Here, we synthesize the results of 148 studies of nonpathogenic bee–fungi associations. We summarize the fungal taxa which are most commonly associated with bees, differences in fungal communities between various bee species and bee-associated habitats, potential routes through which these fungi are acquired, and their effects on bee behavior, survival, and reproduction. We additionally discuss evidence for fungicidal disruption of these associations and identify current gaps in our understanding of bee–fungi interactions.

Review methods

To broadly assess which fungal taxa are found across bee species and habitats, we searched for studies that describe bee–fungi interactions using the Web of Science database, using the search term ‘*bee fung*’. Searches were carried out in July 2021, October 2022, and March 2023 using these parameters. These searches resulted in 1243 total studies, of which 127 were chosen for inclusion in this review. An additional search was carried out in June 2023 using the search term ‘*bee yeast*’, which resulted in the addition of 21 studies. Studies that only focused on fungicide or pathogen effects on bees were the vast majority of all results and were excluded from this review, as these disease interactions have been previously reviewed (Evison and Jensen 2018, Chen and Evans 2021). Of the chosen studies, 104 identified fungal communities associated with bees (Table S1, Supporting Information). For each of these 104 studies, we recorded the top three most prevalent fungal genera, determined by metrics such as relative abundance, frequency of isolation, or number of CFUs, depending on study design. For a small number of studies, four taxa were included in analysis, as two taxa both ranked at the third most abundant taxon. For characterization of these top fungal communities, potential pathogens such as *Aspergillus* and *Ascosphaera* were not excluded if they ranked as one of the most abundant taxa. The top three genera represented on average 84% of total fungi detected in studies using culture-based isolation of fungi (based on number of colonies or number of isolates), and 55% of fungal communities in studies that used direct sequencing approaches (based on read counts). For each study, we also recorded metadata including bee species, habitat, and detection method. Three broad habitats were considered: bee body (larvae, pupae, adult external, adult internal, and adult whole body), nest (corbicular pollen, pollen provisions, honey, and propolis), and flower (nectar, pollen, and whole flower). Methods to characterize fungal communities included culture-based isolation with morphological and physiological identification, culture-based isolation with DNA identification, and culture-independent direct sequencing approaches. Less common methods of fungal characterization included use of API test strips, RNA transcriptomics, and taxon-specific PCR. These methods yield taxonomic annotations that

vary in precision and employ different sampling depths and as a result generate very different types of data as we describe below. When studies examined multiple bee species or habitats, or used a combination of detection methods, the fungal community of each bee species/habitat/detection method combination was considered separately. To characterize floral fungal communities, a separate nonexhaustive search was carried out to supplement studies obtained using the above search parameters, resulting in 33 total studies on floral communities. We did not aim to comprehensively cover floral fungal communities, as these communities have been reviewed elsewhere (Vannette 2020).

We note that fungal taxonomy is complex and more recently, labile, posing challenges to comparing historical and current fungal community data. For example, most fungi were historically named in multiple phases including as an anamorph (asexual phase) and teleomorph (sexual phase) because they are morphologically distinct in these phases. However, recent conventions suggest identifying species with a single name (Taylor 2011). With the recent availability of gene or genome-based phylogenetic methods, many historical fungal names, including genus names, have been revised. However, many of the foundational descriptive studies of bee–fungi associations were performed prior to DNA sequencing availability. To accommodate these important historical studies, we have carefully compared fungal taxonomy and updated genus names to current where possible. We note that the common genus *Candida* is an artificial genus, as it is polyphyletic and has been split into multiple groups. When possible, we assigned *Candida* species to updated genera, but retain *Candida* as a genus name when this was not possible.

We used this dataset to: (1) assess the fungal genera most commonly detected in association with bees, including different bee species and bee tribes; (2) compare fungal communities across various bee-associated habitats; (3) assess gaps or biases in existing data, including taxonomic coverage of bee species and comparison among detection methods. We note that the existing data is extremely biased towards descriptions of honey bee-associated fungi (54% of studies on *Apis mellifera*) and by methods: 67% of studies employed culture-dependent methods followed by colony sequencing (Fig. 3B). Below, we integrate the results of our analysis with qualitative information from the literature to answer the questions: (1) which fungi associate with bees and how do they differ across habitats, (2) how are these fungi acquired by bees, and (3) how do these fungi impact bee behavior and health?

Who are the bee-associated fungi?

Fungi are a diverse group of organisms with about 150 000 described species (Species Fungorum 2023), and an estimated 2.2–3.8 million total species, most of which are undescribed (Hawksworth and Lücking 2017). Fungi associated with bees most commonly belong to the phylum Ascomycota (Fig. 1). Fungi can also be classified by their growth forms (yeasts or molds) rather than phylogenetic relatedness, and some have multiple growth forms, growing as yeasts under some ecological conditions and as filamentous fungi in other environments (Nadal et al. 2008).

The fungi most frequently associated with bees are yeasts within the genera *Starmerella*, *Metschnikowia*, *Zygosaccharomyces*, and *Candida*, which are detected across bee tribes and species (Fig. 1). Yeasts typically grow as single cells and primarily reproduce asexually. Ecologically, they are restricted to habitats that provide significant amounts of small molecular weight carbon, and their growth form makes them most competitive in liquid or high moisture substrates (Lachance and Starmer 1998). There-

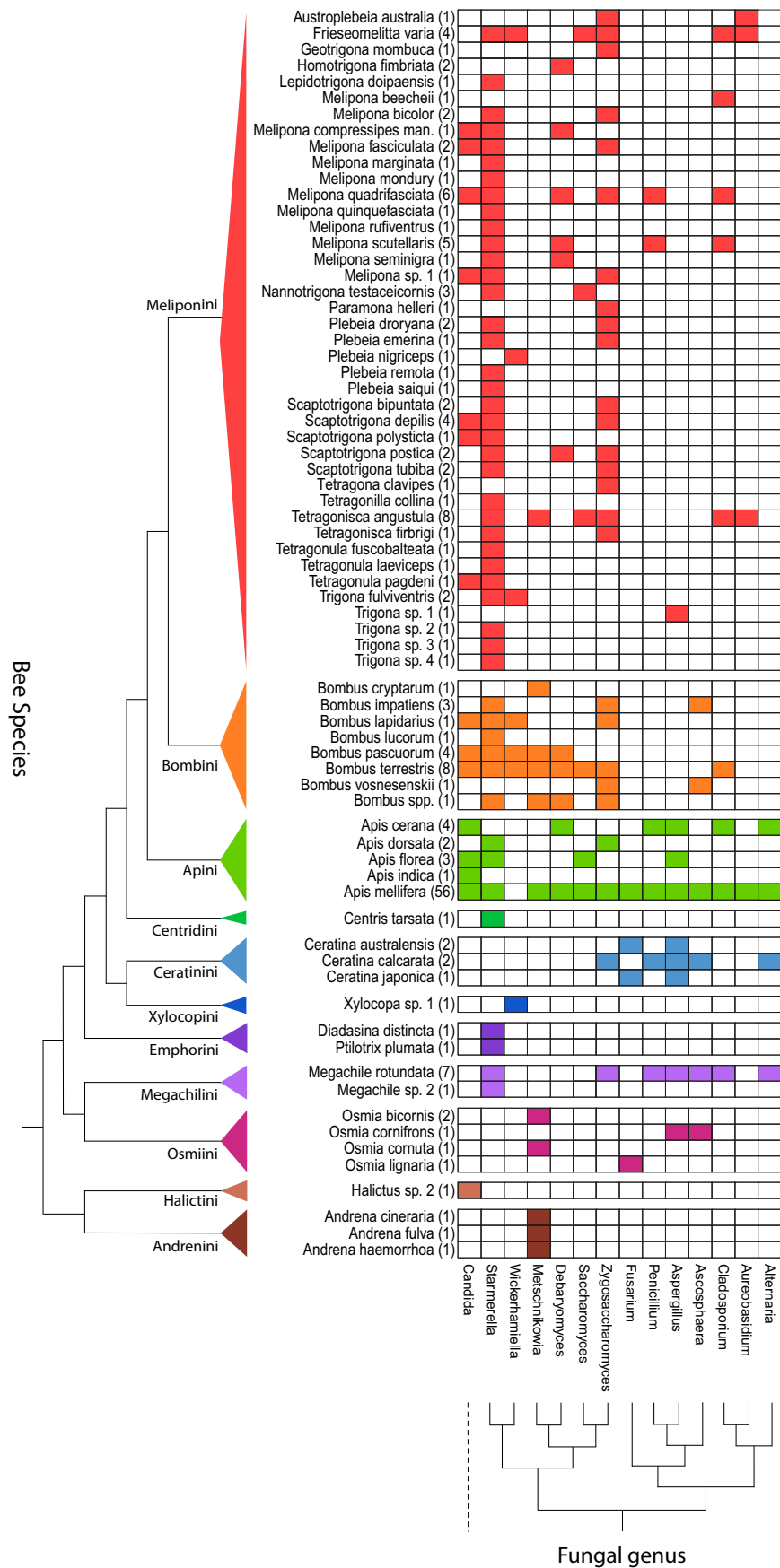


Figure 1. Occurrence of the top 14 fungal genera associated with bee species represented in this review, including fungi isolated in association with bee bodies or provisions. For each study, the top three fungal genera are represented. Fungal occurrence is represented as presence or absence, and so is biased toward bee species that are overrepresented in studies (*Apis mellifera*). The number of studies representing each bee species is included following species names.

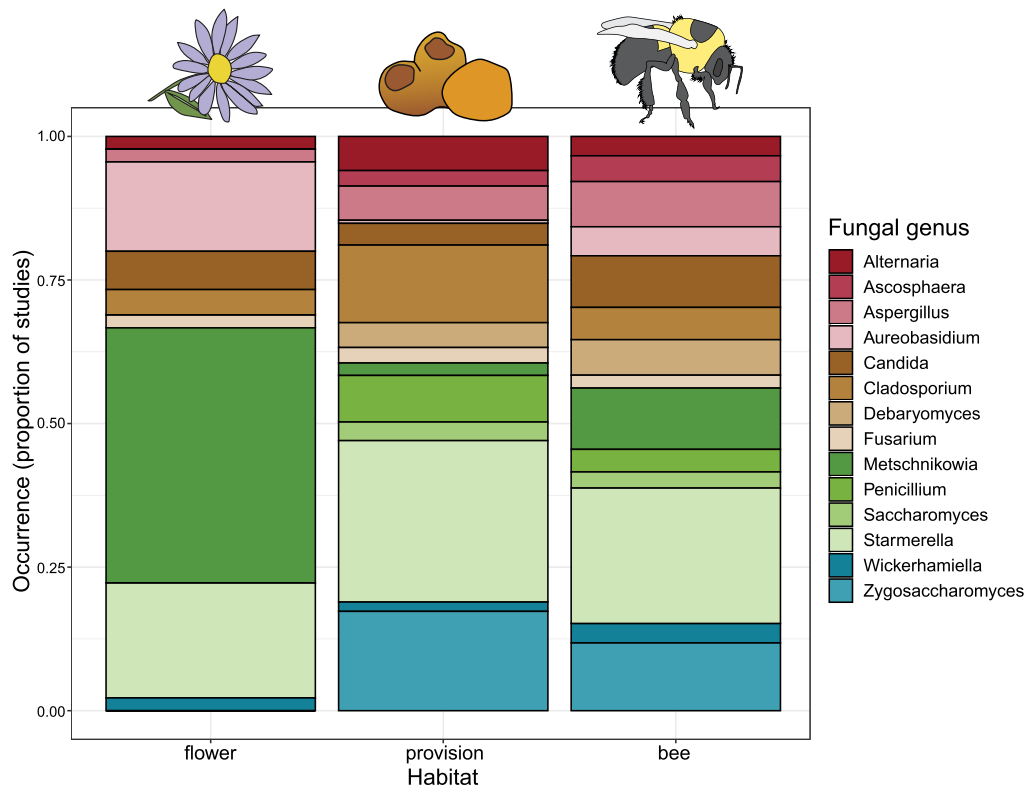


Figure 2. Composition of fungal communities associated with different bee habitats, including flowers (whole flowers, pollen, and nectar), bee nest provisions (stored pollen and nectar, propolis, and corbicular pollen), and the bee body [adult (external, whole body, and gastrointestinal tract), larvae, and pupae]. The top 14 fungal genera by frequency of detection are represented.

fore, it is not surprising that yeasts are common in sugar-rich habitats associated with bees, including floral nectar and stored provisions such as honey (Figure S1, Supporting Information). *Starmerella* yeasts have been noted for their specific interactions with bees and occurrence in bee-visited flowers (Lachance et al. 2001), suggesting a strong reliance of yeasts on bees as hosts and vectors. Bee-associated yeasts are generally osmotolerant, with *Zygosaccharomyces* yeasts exhibiting particularly strong osmotolerance, able to grow on media of up to 70% w/w glucose (Brysch-Herzberg 2004). This makes them well adapted to habitats like honey, which can reach similarly high sugar concentrations (Sohaimy et al. 2015). In addition to being osmotolerant, *Starmerella*, *Zygosaccharomyces*, and some *Wickerhamiella* yeasts also exhibit a preference for the sugar fructose as a carbon source (Leandro et al. 2014, Gonçalves et al. 2020). Fructophilia is uncommon among other yeasts and this trait may contribute to these groups' success in bee-associated habitats, which often contain high levels of fructose, in part due to conversion of sucrose to glucose and fructose by bees (Sohaimy et al. 2015, De-Melo et al. 2017, Cheng et al. 2019).

Bees also associate with molds, fungi that grow with spreading mycelia, which include the genera *Cladosporium*, *Aspergillus*, and *Penicillium* (Fig. 1). Unlike yeasts, molds are often less specialized in their habitats and can grow on a wide variety of carbon sources, including complex polysaccharides (Bennett 2009). Molds are commonly present in floral pollen and stored pollen provisions. Fungi within these bee-associated genera are diverse and inhabit a wide range of habitats and ecological roles, including plant pathogens (e.g. *Alternaria*), bee pathogens (e.g. *Aspergillus flavus*, Foley et al. 2014; *Ascospaera*, Evison and Jensen 2018), and saprotrophs.

How are bee-associated fungi acquired? Acquisition from floral resources

Floral resources are the main food source for most bee species, so the fungal species found in nectar and pollen directly contribute to communities in bee nests and bee gastrointestinal tracts. Many of the fungi most commonly isolated from bee nests and bodies are also frequent inhabitants of floral nectar and pollen, including *Starmerella*, *Metschnikowia*, *Aspergillus*, and *Cladosporium* (Fig. 2), and are likely sourced from plants. Indeed, changes in bee habitats (and presumably microbial species pools) such as exposure to novel floral communities, hive movement, or seasonal changes, are reflected by changes in the fungal community associated with bees (Kakumanu et al. 2016, Callegari et al. 2021, Hall et al. 2021, Ludvigsen et al. 2021, McFrederick and Rehan 2018, Rothman et al. 2019). Flowers also likely provide a hub through which commensal or mutualistic fungi may be spread between individual bees or bee species (Brysch-Herzberg 2004, McFrederick et al. 2012), as has been shown for fungal pathogen spread (Evison and Jensen 2018, Graystock et al. 2020).

Fungal communities in stored bee provisions diverge from floral communities over time, likely due to the addition of bee secretions, modifications to the stored food, and/or environmental conditions inside the nest. Provisions are stored in nests often lined with resin, glandular secretions, or other materials that are broadly antimicrobial (Chui et al. 2022, Hefetz 1987, Shanahan and Spivak 2021), filtering out nonadapted fungal species. In social bees, hive temperature is regulated and kept warmer than ambient temperature, around 35°C during the active summer months (Fahrenholz et al. 1989), which can additionally impact the composition of fungal communities in provisions (Friedle et al. 2021).

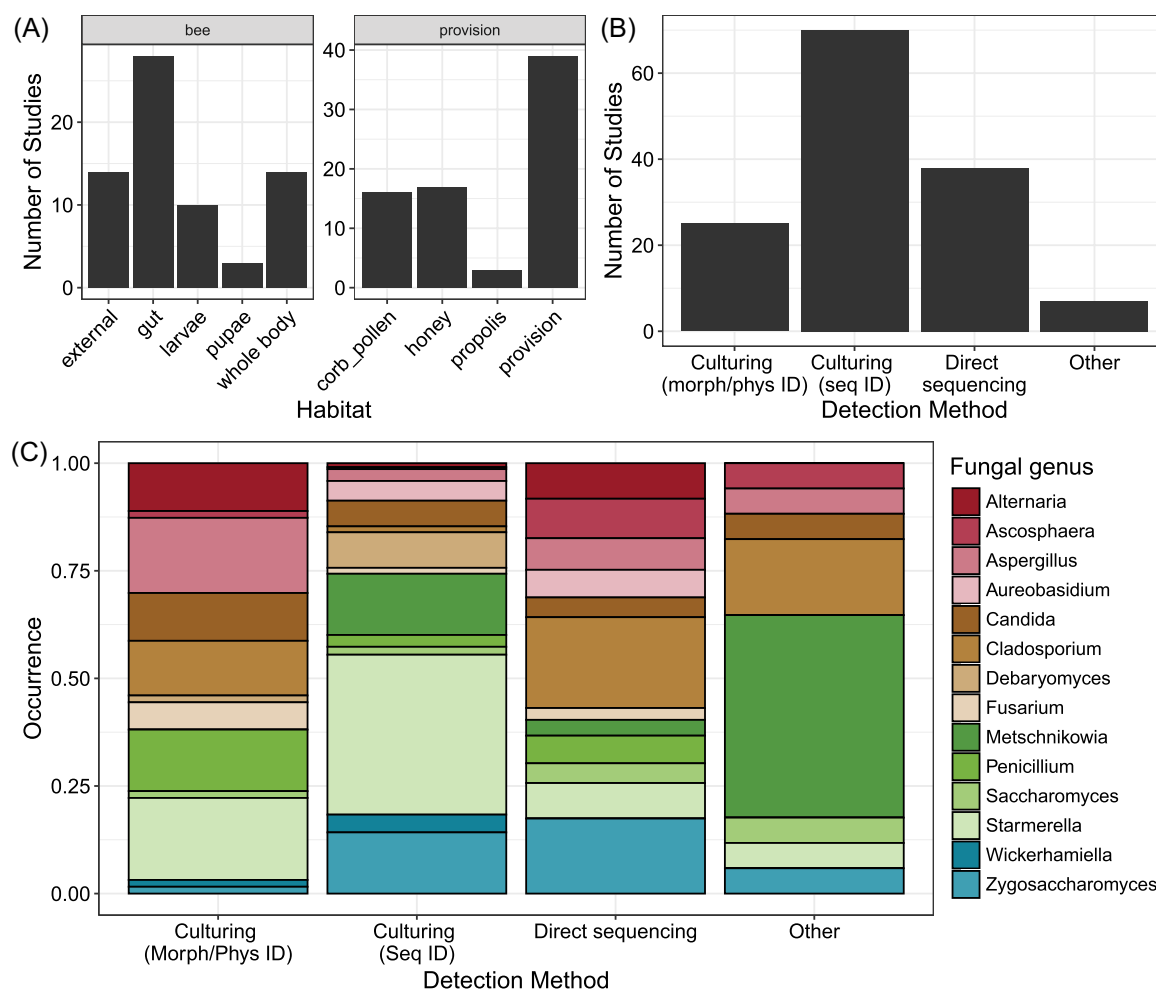


Figure 3. Plots showing variation in taxa recovered using different methods in current studies of bee–fungi associations. (A) Number of studies of specific habitats considered in this study in association with bees, (B) number of studies employing various detection and identification methods of fungal communities, and (C) differences in fungal communities across detection methods. Detection methods included are culture-based isolation followed by morphological and physiological identification, culture-based isolation followed by sequencing-based identification, and culture-independent community identification (amplicon sequencing). ‘Other’ detection methods include API test strips, RNA transcriptomics, microscopy, and taxa-specific PCR. The top 14 fungal genera are represented.

Modifications to the stored provisions themselves also reduce the risk of contamination by pathogenic or saprotrophic microbes. In honeybees, bumble bees, and stingless bees, floral nectar is modified to produce honey by reducing water content and adding glucose oxidases and antimicrobial peptides, resulting in a liquid with a high sugar content that can be upwards of 70% w/w (Souza et al. 2006, De-Melo et al. 2017) and general antimicrobial properties (Israili 2014, Suintiparapop et al. 2012). Other provisions, such as honeybee bee bread or many solitary bee nest provisions, are created by mixing nectar and pollen together, producing a provision, i.e. often (but not always) more solid than honey. These provisions are generally acidic (4–4.5 pH) due to the addition of glucose oxidase by worker bees and the proliferation of lactic acid bacteria, which produce gluconic acid and adds to the antimicrobial nature of these provisions (Herbert and Shimanuki 1978, Gilliam 1979, Sinpoo et al. 2017, Anderson and Mott 2023).

The impacts of these provision modifications on fungal community structure have been best illustrated by studies on the bee bread of *Apis mellifera* colonies. Fungal communities in bee bread initially closely resemble those found in floral resources, but decrease in diversity and abundance over time as provisions are altered and stored (Sinpoo et al. 2017, Detry et al. 2020, Disay-

athanoowat et al. 2020, Friedle et al. 2021). Many flower-associated taxa, such as *Metschnikowia*, decrease in abundance and are not normally isolated from stored provisions (Fig. 2). However, other fungal taxa, including *Starmerella* and *Zygosaccharomyces*, persist in these new conditions, and may even increase in abundance over time (Detry et al. 2020). Fungal community succession has not been as extensively studied in the provisions of other bee species, but bacterial communities of *Osmia* and *Megachile* nest provisions also change over time (Voulgari-Kokota et al. 2019, Kueneman et al. 2023), so it is likely that fungal communities also change with provision age in solitary bee species.

Vertical and social acquisition

In contrast to clear patterns of environmental acquisition, only limited evidence suggests that bee-associated fungi can be transmitted among individuals or between generations, in processes defined as social or vertical transmission. In the bumble bee *Bombus terrestris*, the yeasts *Starmerella bombi*, and *Wickerhamiella bombiphila* (but not *Metschnikowia reukaufii* or *M. gruessii*) persisted in daughter queens’ gastrointestinal tract through hibernation (Pozo et al. 2018), and thus could potentially be transmitted to

newly founded colonies. Fungal transmission to daughter colonies has also been suggested in stingless bees. Some evidence suggests that stingless bees carry their obligately symbiotic fungi within hive materials that are moved to new locations during hive splitting or swarming events (Menezes et al. 2015), though this has yet to be experimentally tested. To our knowledge, vertical transmission of fungal communities has not been documented in solitary bees. However, for spore-forming fungal pathogens of bees including *Ascosphaera* and *Aspergillus*, bee nest reuse or nest sharing is a primary mode of transmission (Evison and Jensen 2018); it seems likely that commensal or mutualistic fungi may be transmitted in a similar fashion, but to our knowledge this has not been documented.

Direct collection of fungi

Rarely, honeybees have been observed to directly collect spores of plant pathogens from plant surfaces, including the rust fungi *Melampsora*, *Uromyces*, and *Zaghouania*, powdery mildew in the genus *Podosphaera*, and other fungi within the genus *Cladosporium* (Shaw 1990, Shaw and McAlpine 1999, Eltz et al. 2002, Modro et al. 2009). The purpose of this behavior is unknown, but it has mostly been observed at the end of summer, when floral resources are scarce. Honeybees will not consume pure fungal spores (Parish et al. 2020a, Schmidt et al. 1987), but may mix these spores with provisions, potentially providing a nutritional benefit greater than pollen alone (Parish et al. 2020b). Multiple plant pathogens infect plants and produce fungal spores that mimic pollen (Slot and Kesson 2021 e.g. *Monilinia vaccinii-corymbosi* and others) and although multiple bee species visit such mimics, whether they ingest these spores is unclear.

Functions of bee-associated fungi

Despite extensive documentation that bees associate with fungi, the detection of fungi does not imply their importance in bee biology. Evidence from a few studies that manipulate fungal presence, abundance, or identity suggest that in some cases, fungi can influence bee behavior, development, health, and survival. We review these studies and potential mechanisms of fungal effects on bees below.

Flower-associated yeasts affect bee behavior

Perhaps the greatest number of studies of bee–fungi interactions have investigated fungal effects on bee foraging preferences or nectar feeding behavior. In many studies, fungi (most commonly yeasts) are applied to flowers or artificial nectar and the rate of bee visitation, pollen or nectar removal, or pollination are quantified. Of the studies considered here, most assessed responses of bumble bees (*B. impatiens*, *B. terrestris*, *B. vosnesenskii*, and *B. friseanus*). In all but one published instance, yeast-containing flowers or nectars increased visitation or consumption by bumble bees over uncolonized or bacteria-colonized nectars (Herrera et al. 2013, Schaeffer and Irwin 2014, Schaeffer et al. 2017a, 2019, Yang et al. 2019). As an exception, *B. vosnesenskii* did not prefer yeast-inoculated nectar volatiles over those of control nectar in a microcolony study (Rutkowski et al. 2022). In contrast to most bumble bee responses, honeybees show no attraction to nectar yeasts or even display reduced visitation to nectar colonized by floral fungi (Kevan et al. 1987, Rering et al. 2018, 2020, 2021, Crowley-Gall et al. 2022, Schaeffer et al. 2022). We are unaware of studies that quantify non-*Bombus* or *Apis* behavior in response to fungi-colonized flowers, although it has been hypothesized that yeast volatiles may act as

an honest cue of the presence or quality of nectar (Russell and Ashman 2019) for a variety of insect species, and are attractive to hoverflies as well as vespine wasps (Davis et al. 2012, Colda et al. 2021). It has been hypothesized that yeast volatiles could be used by insects as a cue of nectar presence (Crowley-Gall et al. 2021, Davis et al. 2012, Russell and Ashman 2019) so it is possible that bee species may differ in their use of such foraging cues. In addition, whether cues simply benefit foraging efficiency or the yeasts themselves are being actively collected is not understood.

Bee-associated fungi can benefit bee development

In addition to acting as resource cues, the ingestion of fungi or fungal metabolites can also affect individual bee and colony performance, though these effects differ by fungal and bee species. Inactivated yeasts (most commonly *Saccharomyces cerevisiae*) are common additives in artificial diets provided to social bee colonies, in some cases providing modest growth benefits over natural pollen diets (Fernandes-da-Silva and Zucoloto 1990, Dodoluglu and Emsen 2011, van der Steen 2015, Pavlović et al. 2022), though not always (Costa and Venturieri 2015, de Freitas et al. 2020). There is little evidence that these artificial diets have any impact on bee immunity and pathogen infection (Moliné et al. 2020, Canché-Collí et al. 2021, Hsu et al. 2021), though in one case yeast diets reduced *Nosema* spp. infection levels in honeybees (Škerl and Gajger 2022). In *Bombus impatiens*, consumption of the nectar yeast *Metschnikowia reukaufii* did not affect colony survival or brood production (Schaeffer et al. 2017a), but addition of the yeasts *Starmerella sorbosiivorans*, *Zygosaccharomyces rouxii*, and *Debaromyces hansenii*—which are typically present within the colony environment—improved worker survival and offspring production (Rutkowski et al. 2022). In the bumble bee *B. terrestris*, *M. gruessii*, and *W. bombiphila* increased colony development rates and the number of offspring produced, though other fungal species tested were not as beneficial (Pozo et al. 2019). In a separate study on the same bee species, addition of *W. bombiphila* and *Torulaspora delbrueckii* to colony provisions sped up colony development (Pozo et al. 2021). Interestingly, colonization by some yeasts decreased queen overwintering success, suggesting costs of hosting fungal symbionts (Pozo et al. 2019). Despite detailed work on the potential mechanisms by which yeasts benefit bumble bees (Schaeffer et al. 2017a, Pozo et al. 2019), evidence to date does not strongly support direct nutritional benefits of yeasts generally for bumble bees. Nevertheless, these studies suggest that consuming yeast can conditionally benefit bumble bees, and that yeast identity is important, with colony-adapted fungi potentially being more beneficial than yeasts from other environments.

The strongest evidence for mutualism involving bees and fungi has been documented in multiple stingless bee species. In *Scaptotrigona depilis*, native to Brazil, adult bees cultivate *Zygosaccharomyces* in brood cells, where larvae feed on fungal pseudohyphae. In the absence of this fungus, larval survival rate is low (8%), as the fungal tissue contains ergosterols necessary for pupation (Menezes et al. 2015, Paludo et al. 2018). The growth of this *Zygosaccharomyces* fungus is further regulated by other fungi (*Candida* sp. and *Monascus ruber*) in the larval cell, maintaining *Zygosaccharomyces* at a level beneficial to the developing larvae (Paludo et al. 2019). Similar filamentous growth forms of *Zygosaccharomyces* species have been isolated from brood cells of eight additional stingless bee species (*Scaptotrigona bipunctata*, *S. postica*, *S. tubiba*, *Tetragona clavipes*, *Melipona quadrfasciata*, *M. fasciculata*, *M. bicolor*, and *Partamona helleri*), suggesting similar nutritional roles in lar-

val development (de Paula et al. 2023). Additionally, larvae of the stingless bee species *Heterotrigona itama*, native to Malaysia, also show increased mortality (37% survival) when reared on sterile diet compared to natural diet (85%) or diet supplemented with the fungus *Panus lecomtei* isolated from provisions (57%, Razali et al. 2022). The mechanisms behind this effect were not examined but the authors hypothesize that nutritional benefits or pathogen protection may explain increased larval survival.

Potential mechanisms: fungi as nutrition, detoxification, or pathogen protection?

A few mechanisms have been hypothesized to explain the positive effects of fungal addition on bee health, including nutritional benefits from consumption of fungal cells and associated metabolites. Nutritional mutualism has been documented in other insects that associate with fungi, with fungi providing B vitamins, amino acids, or sterols to their insect hosts (Biedermann & Vega 2020). Fungi are known to produce developmentally necessary sterols in one stingless bee species, as discussed above (Menezes et al. 2015, Paludo et al. 2018). Fungi may also act as a direct food source. In pollen provisions and honey, fungi can reach densities of between 10^3 and 10^6 cfu/g for yeasts and $< 10^1$ and 10^3 for filamentous fungi (Inglis et al. 1992a, b, c, Rosa et al. 2003, Teixeira et al. 2003, Kačániová et al. 2004, Nardoni et al. 2015, Disayathanoowat et al. 2020, Echeverrigaray et al. 2021, Anderson and Mott 2023). These abundant fungal cells may constitute a substantial portion of bee diets. Isotopic analysis of amino acids sourced from bees of various families placed bees as omnivores instead of strict herbivores, potentially due to consumption of microbial matter (Steffan et al. 2019). In the solitary bee *Osmia ribifloris*, sterilization of pollen provisions to remove microbes reduced the rate of larval development and decreased the concentration of specific fatty acids compared to unsterilized provisions, further supporting a nutritional role of fungi in bee health (Dharampal et al. 2019). However, these beneficial effects were dependent on microbe identity, and were more pronounced when microbes were isolated from pollen of appropriate host plants for *O. ribifloris* (Dharampal et al. 2020). In other systems including bark beetles and cactophilic *Drosophila*, fungi mediate diet detoxification. Given that pollen is often high in plant secondary metabolites (Palmer-Young et al. 2019) and that pollen toxicity may influence host pollen use (Rivest and Forrest 2020), fungi could plausibly be involved in detoxification of pollen compounds for larval consumption, but to our knowledge this has not been documented.

Fungi could also benefit bees by reducing the growth of pathogens or spoilage microbes in provisions through microbe-microbe competition, though evidence for this is mixed. *Megachile rotundata* larvae fed yeasts including *Trichosporonoides* (*Moniliella*) *megachiliensis* were not more resistant to infection by the fungal pathogen *Ascosphaera* than those inoculated with the pathogen alone (Inglis et al. 1993b). In *in vitro* growth assays, *S. bombi*, *W. bombiphila*, and *M. reukaufii* reduced the survival of the bumble bee parasite *Crithidia bombi* (Pozo et al. 2019). Plate assays have found mixed evidence that pollen-associated fungi can reduce the growth of bee pathogens. For example, *Aspergillus*, *Cladosporium*, *Mucor*, *Penicillium*, *Rhizopus*, and *Talaromyces* isolated from honey bee provisions and guts inhibited the growth of *Ascosphaera apis* (Gilliam et al. 1988, Disayathanoowat et al. 2020). However, another study on fungi isolated from bumble bee guts, including *S. bombi*, *W. bombiphila*, and *Z. rouxii* found no evidence of inhibition of *Paenibacillus larvae*, *Melissococcus plutonius*, *C. bombi*, or *A. apis* in growth assays (Praet et al. 2018). It is possible that this variation in

inhibitory ability is due to strain-level differences among fungal species, as has been observed for different bacterial strains associated with bees (Praet et al. 2018). In addition to *in vitro* growth assays, several associational studies link the presence of fungi to greater disease resistance and lower pathogen loads. In honeybees, increased hygienic behavior of a colony and a lower abundance of *A. apis* was associated with greater non-*A. apis* fungal abundance (Gilliam et al. 1988). In *B. impatiens* pollen provisions, the abundance of yeasts in the *Wickerhamiella/Stammerella* clade was negatively associated with *Ascosphaera* abundance (Dharampal et al. 2020).

Fungi may also affect bee immunity, as has been documented for bacteria in the corbiculate bee gut microbiome (Bonilla-Rosso and Engel 2018). Immune stimulation has been demonstrated in the moth *Galleria mellonella*, where pretreatment with *Saccharomyces cerevisiae* protected larvae from subsequent infections of *Candida albicans* (Bergin et al. 2006). Similarly, *S. cerevisiae* augmented immune response to *Escherichia coli* in the social paper wasp *Polistes dominula* (Meriggi et al. 2019). In contrast, exposure of honeybee workers to *Wickerhamomyces anomalus*, a gut-associated yeast, lowered immune gene expression (Tauber et al. 2019). Overall, as all current studies of pathogen inhibition by bee-associated fungi have been either associational or based on *in vitro* growth assays, more research is necessary to determine if environmental or symbiotic fungi impact disease progression in living bees or colonies, and whether this is mediated through microbe-microbe interactions or bee immune response modulation. In particular, more research into fungal symbiont interactions with pathogens in nonmanaged and solitary bees, for whom fungal pathogens can be a significant cause of mortality, is necessary, as all studies to date focus on social bee species.

Impacts of fungicides on bees and associated fungi

Fungicide exposure can affect bee health, either through direct effects on bees or through effects on symbiotic fungi. The LD50 values for many fungicides tested on bees are significantly higher than most insecticides, indicating lower contact toxicity (Stoner and Eitzer 2013, Chmiel et al. 2020). However, multiple studies have found sublethal, long-term, or interactive effects of fungicides on bees. These detrimental effects may be due to fungicides acting on bees directly (Mao et al. 2017), interaction of fungicides with other pesticides (Elston et al. 2013, Sgolastra et al. 2017), or through suppression of beneficial fungi. While this last option has received little attention, emerging evidence suggests that fungicide application can change the composition of fungal communities associated with bees, with implications for bee health.

Fungicides reduce the growth of floral and bee-associated fungi (Alvarez-Perez et al. 2016, Bartlewicz et al. 2016, Schaeffer et al. 2017b), which may alter bee-fungi interactions. In bumble bees, exposure to the fungicides chlorothalonil and propiconazole reduced colony biomass, worker production, and worker survival (Bernauer et al. 2015, Steffan et al. 2017, Rutkowski et al. 2022). These effects on bee health were accompanied by changes in the fungal abundance and communities of nest provisions and bee guts, with a decrease in common bee associates like *Cladosporium*, *Aspergillus*, *Penicillium*, and *Zygosaccharomyces*, while other groups, including the pathogen-containing *Ascosphaerales*, increase in prevalence (Yoder et al. 2013, Steffan et al. 2017, Rutkowski et al. 2022). In one case, applying the azole fungicide propiconazole to *Bombus vosnesenskii* microcolonies reduced worker sur-

vival, but supplementation with bee-associated fungi (*Penicillium*, *Starmerella*, and *Zygosaccharomyces*) back into the nest following fungicide exposure eliminated negative effects of fungicide on survival, suggesting that fungicide effects could be mediated through disruption of nest fungi communities (Rutkowski et al. 2022). Alternatively, a study on *A. mellifera* found that although prolonged exposure to the fungicide azoxystrobin reduced gut fungal community diversity and altered community composition, bee survival was unaffected by exposure over 10 days (Al Nagar et al. 2022). We note that most research to date of fungicide impacts on bees does not consider changes in associated fungal communities, and more research on how fungicides impact bee health and associated communities in tandem is necessary to determine to what extent fungal community disruption is responsible for observed responses of bees to fungicides.

Limitations and future directions

Although we have outlined which fungi are detected in different habitats and in association with different bee species, we note that this summary is biased in a number of ways (Fig. 3) and is largely qualitative. In particular, we lack information on variation in fungal abundance among species and life stages. Some existing work reveals variation in fungal abundance associated with bumble bee queens from different habitats (Bosmans et al. 2018), and in some cases fungi are not detected in bumble bees (Hammer et al. 2022). In stingless bees, the presence of fungi in the gastrointestinal tract varied widely between bee species (Liu et al. 2023). These results highlight that fungi are likely not always abundant or important and we lack an understanding of when and where fungi may play important ecological roles. Below we discuss some additional limitations in the field of bee–fungi interactions as well as current gaps in our understanding of these relationships.

Detection methods

The studies included here span over a century of work, over which time new strategies for characterizing microbial communities have been developed. Many older studies of bee–fungi interactions were performed before DNA sequencing was accessible and relied on morphological and physiological identification. However, these methods of fungal identification may not be as reliable, as they can vastly differ from DNA sequencing results for the same fungal isolates (Rodrigues et al. 2018). In this review, the most common method for identifying fungal community members was culturing followed by DNA sequencing of isolates (67% of studies). More recently, studies implementing nonculture-based whole community sequencing methods (such as Illumina) have become more common. All detection methods have associated benefits and drawbacks. Culture-based work allows isolation and preservation of fungi associated with bees, but is limited to detection of fungi that are able to grow in the provided media and growth condition. Direct sequencing techniques better capture complete communities, including hard-to-culture microbes, but also introduce DNA extraction biases, amplification biases, and may include DNA from nonviable fungi (Boers et al. 2019, White et al. 2020). Only four studies summarized here used a combination of culture-based and culture-independent methods and illustrate how community composition (or species presence) depends on the methods employed (Sinpoo et al. 2017, Disayathanooawat et al. 2020, Callegari et al. 2021, Cui et al. 2022). We urge researchers to use a combination of methods to provide a comprehensive view

of fungal communities associated with bees and isolate cultures that enable experimental examination of fungal effects on bees.

Taxonomic and life stage bias in sampling of bees

The vast majority of all studies on bee–fungi interactions are performed on honeybees, specifically *A. mellifera*. Of the 104 bee-focused studies included in our analysis, 56 covered *A. mellifera*, while the next most commonly covered bee species were *B. terrestris* (eight studies) and *Tetragonisca angustula* (eight studies). Indeed, many of the most commonly studied bee species are those managed in some way for pollination, while nonmanaged bee species are less well represented. Additionally, though most bee species are solitary, the vast majority of current studies focus on eusocial species. Only 18 studies included noneusocial species, and most of these species were represented by only a single study. Greater coverage of more bee species including more nonmanaged species and spanning levels of sociality are needed to gain a full understanding of the breadth of bee–fungi associations, and how social living may impact associated fungal communities.

In addition, very few studies (11) characterize fungal communities associated with immature life stages of bees, despite the clear effects that fungal presence or supplementation can have on offspring development and survival. In studies that characterized both immature and adult bee microbiomes, there was strong overlap, though immatures tended to be more dominated by the plant pathogen *Alternaria* and the bee pathogen *Ascosphaera* (Shoreit and Bagy 1995, Tauber et al. 2021, Ye et al. 2021, Nguyen and Rehan 2022). In one case, the species *Starmerella batistae* was found associated with larvae and pupae of the solitary bee species *Diadasina distincta* and *Ptilotrix plumata*, while it was absent from adults (Rosa et al. 1999). Future experiments characterizing the fungal microbiome of immature bee stages, and their impacts on development, are needed to determine roles of these fungi throughout the bee life cycle.

Mechanisms behind fungal function

Currently, few studies have experimentally examined the effects of fungi on bees. As with most other studies of bee–fungi interactions, these have largely been restricted to economically important and managed pollinators, and the mechanisms behind many of the observed impacts of fungi are not understood. In addition to the mechanisms previously proposed in this review, bee-associated fungi may impact bees through a number of less well-studied mechanisms.

Interactions between fungi and the rest of the microbiome

The interactions between fungi and other microbiome members have received little study. Within the bee gut, abundance of fungal species is in some cases positively associated with the abundance of beneficial bacteria endosymbionts, like *Gilliamella* and *Snodgrassella* (Callegari et al. 2021). In other cases, fungal symbionts seem to replace bacteria symbionts as core members of the bee microbiome (Cerqueira et al. 2021). Increasing fungal richness in the gut of *M. rotundata* larvae was associated with lowered bacterial richness, suggesting competitive interactions between these groups (McFrederick et al. 2014). Within provisions, interactions between bacteria and fungi likely impact fungal community dynamics, as proliferation of lactic acid bacteria results in a more acidic pH, limiting the growth of many fungal species (Sinpoo et al. 2017, Janashia et al. 2018).

Table 1. Selected future research directions in the field of bee–fungi interactions.

1. How does the larval mycobiome compare with adults, and what impacts does it have on larval development and survival?
2. How do fungi interact with other members of the bee microbiome, including pathogens?
3. How do bee-associated fungi change the nutrient profile of stored bee provisions?
4. How does the mycobiome vary across gradients of sociality and diet specificity?
5. Are fungi in social colonies vertically transmitted between colonies and generations?
6. How do different pesticides impact the mycobiome, and how do these changes affect bee health?

Do fungi alter food resources?

The impact of nectar-dwelling fungi on nectar chemistry has been well-studied. Fungi often reduce total sugars present in nectar, shift sugar composition, and change the composition of floral volatiles (Herrera et al. 2008, Rering et al. 2018, 2021). Despite these clear effects on floral nectar, little is known about how fungi within bee nests alter the nutritional profile of pollen or nectar provisions that are provided to larvae. One study found that *Aureobasidium melangenium*, isolated from honeybee provisions, was able to degrade and ferment pollen provisions, which was associated with upregulation of nutrient genes in honeybees fed on this diet (Hsu et al. 2021). Intriguingly, bee-associated *Starmerella* species produce abundant sophorolipids which are used as commercial detergents and surfactants (Kurtzman et al. 2010, Van Renterghem et al. 2017, Van Bogaert et al. 2016). *Starmerella bombicola*, which has been isolated from the provisions of a number of bee species (Brysch-Herzberg and Lachance 2004, Inglis et al. 1993a, Echeverrigaray et al. 2021), is a particularly efficient producer of these compounds. These sophorolipids have antimicrobial properties, reducing the growth of other bacteria and fungi, including those also associated with flowers and bee nests (Hipólito et al. 2020, De Clercq et al. 2021, Alfian et al. 2022). These compounds may contribute to the preservation of bee provisions, which has been suggested as the main function of the provision microbiome in honeybees (Anderson et al. 2014). However, whether these surfactants are synthesized within bee provisions, and their impacts on provision microbiome and bee health have yet to be tested.

Conclusion

Overall, fungi are common associates of bees, with yeasts in particular exhibiting strong associations with bee bodies and provisions. Multiple bee species benefit from addition of these yeasts to their diets, and at least one stingless bee species obligately relies on fungi for larval development. However, fungal communities and abundance can substantially vary among bee species, populations, and life stages. This variation suggests that in many bee species, interactions with fungi may be more environmentally determined and, for bee hosts, facultative. We largely lack information on the mechanisms by which fungi affect bee hosts and on associations between fungi and different life stages of bees, and suggest more mechanism-focused research encompassing a wider variety of bee species and life stages so that we may expand our understanding of these associations and under which contexts they are beneficial to bee health (Table 1).

Authors' contributions

DR and RLV conceived the idea for the review and all authors compiled references for the review. DR created all figures. DR and RLV wrote the manuscript and contributed to revisions.

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Supplementary data

Supplementary data are available at [FEMSEC](#) online.

Conflict of interest. The authors have no conflict of interest to declare.

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