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Unfolding The Role of Nectar Mycobiome in Modulating Pollinator Preferences and Foraging Decisions - A Review

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ABSTRACT

Floral nectar, a primary attractant for pollinators, is a complex medium enriched with sugars, amino acids, and secondary metabolites. Traditionally viewed as a sterile reward, nectar is now recognised as a dynamic microfungal habitat, particularly for nectar-inhabiting yeasts. This review explores the multifaceted role of nectar mycobiomes in modulating pollinator behaviour and foraging decisions. We highlight how microfungi such as *Metschnikowia*, *Cryptococcus*, and *Rhodotorula* metabolise nectar sugars and amino acids and produce volatile organic compounds (VOCs), leading to significant shifts in nectar chemistry, pH, and sensory cues. These microfungal transformations influence pollinator olfactory and gustatory perception, ultimately affecting foraging efficiency, flower visitation patterns, and pollinator health. Furthermore, we examine how microfungal changes can have dual effects-enhancing pollinator attraction in some contexts while acting as deterrents in others. Importantly, this review discusses the bidirectional feedback loop in which pollinators shape microfungal community dispersal, creating a complex, co-evolved network between plants, microbes, and their mutualists. Despite increasing recognition of these microfungal influences, gaps remain in understanding their long-term ecological consequences on pollination success and plant fitness. We propose future research directions, including the functional profiling of nectar microbes and the potential for mycobiome engineering to enhance pollination services in agroecosystems. This review underscores the emerging paradigm of nectar mycobiomes as integral components of pollination ecology, warranting their integration into broader ecological and evolutionary frameworks.

Keywords: Floral nectar, Nectar-dwelling mycobiome, Altered nectar properties, Pollination impact

INTRODUCTION

Pollinators play a crucial role in the reproduction of many flowering plants, with their foraging decisions shaping plant-pollinator coevolution. Plants offer nectar as a primary reward to animal mutualists, facilitating these interactions. Two types of nectar exist: floral nectar (FN), which serves as a key nutritional resource for pollinators, and extrafloral nectar (EFN), which attracts defensive insects like ants and wasps to deter herbivores (Ananthakrishnan *et al.,* 1982). Both are secreted by specialised nectaries, differing mainly in their location on the plant (Schmitt *et al.,* 2021).

Nectar is primarily composed of sugars—glucose, fructose, and sucrose—which provide energy essential for pollinator flight, migration, and reproductive behaviours (Martin *et al.,* 2022). However, it also contains minor yet vital constituents such as amino acids, lipids, vitamins, and secondary metabolites. These components influence pollinator health, immune responses, and foraging behaviour (Martin *et al.,* 2022). Additionally, nectar's sensory attributes, including colour, scent, and taste, guide pollinator preferences and interactions (Rering *et al.,* 2018).

The plant–nectar–microfungi–pollinator relationship has evolved over millions of years. Initially a pollinator reward, floral nectar became a habitat for nectar-inhabiting microfungi, especially yeasts (Herrera *et al.,* 2008). Due to high sugar concentration, nectar-inhabiting microfungi are primarily subjected to high osmotic pressure and nutrient limitation. To cope with osmotic stress and nutrient limitation, microfungi alter their glycerol biosynthesis (GPD1), sugar transport (HXT genes), and invertase activity (Herrera *et al.,* 2008; Álvarez-Pérez *et al.,* 2012). Further, they resist plant antimicrobials with efflux pumps and detoxifying enzymes like cytochrome P450s, manage acid stress through H^+-ATPases, and enhance nitrogen uptake with amino acid and ammonium transporters (Pozo *et al.,* 2015).

With such metabolic reprogramming, nectarivorous microfungi alter nectar chemistry by metabolising sugars, modifying amino acid profiles, and producing volatile organic compounds (VOCs), which affect pollinator attraction and behaviour (Rering *et al.,* 2018; Schmitt *et al.,* 2021). These microbes, mainly yeasts, alter nectar chemistry by metabolising sugars, modifying amino acid profiles, and producing VOCs, which affect pollinator attraction and behaviour (Rering *et al.,* 2018). Some plants even contain antimicrobial substances in their nectar to regulate microfungal populations and deter nectar robbers—organisms that consume nectar without contributing to pollination (Schmitt *et al.,* 2021).

The ecological role of nectar-inhabiting mycoflora is a growing area of research as they must adapt to fluctuating environments, indicating broad ecological niches and phenotypic plasticity (de Vega *et al.,* 2021). Recent studies suggest that nectar inhabitants significantly influence plant-pollinator interactions, but their precise effects on pollinator longevity, reproduction, and plant fecundity remain unclear (Martin *et al.,* 2022). Understanding these interactions will provide deeper insights into the complex web of ecological relationships that govern pollination systems.

REVIEW METHODOLOGY

The selection of studies for this comprehensive review was guided by specific inclusion criteria developed to focus on the role of the nectar mycobiome in influencing pollinator preferences and foraging decisions. Studies published between 1980 and 2025 were retrieved from well-recognised databases and search engines, including PubMed, ScienceDirect, Web of Science, Scopus, the American Chemical Society, Google Scholar, Springer Link, and Wiley. The search terms employed for this purpose include “nectar microbiome,” “nectar inhabiting fungi,” “microbe-mediated nectar ecology,” “microfungal alteration,” and "foraging decision,” among others.

CHEMICAL COMPOSITIONS OF FLORAL NECTAR

The ratios of sucrose, glucose, and fructose vary widely among plant species, reflecting ecological adaptations that influence pollinator behaviour and preferences. Sucrose, glucose, and fructose are the dominant carbohydrates, though their relative proportions vary among plant species. Additionally, nectar contains low concentrations of amino acids, secondary metabolites, lipids, and micronutrients (Martin *et al.,* 2022). These constituents serve not only as nutritional resources but also as chemical signals that influence pollinator preferences.

MICROFUNGAL EFFECTS ON NECTAR COMPOSITION

Nectar chemistry is complex, with multiple layers of biotic interactions. The primary function of floral nectar is to attract and influence pollinators to maximise plant fecundity. Microfungal communities inhabiting nectar, especially specialist species (*Metschnikowia* yeasts), play a pivotal role in modulating nectar's nutritional composition. These microorganisms influence nectar quality through the utilisation of mono- and disaccharide sugars, thereby modifying their relative concentrations and inducing pH reductions via fermentation processes (Vannette *et al.,* 2013; Tucker and Fukami, 2014). Furthermore, nectar microbes possess the capability to metabolise, alter, or synthesise amino acids and secondary metabolites, leading to significant changes in nectar's flavour and scent profiles. Such biochemical transformations are detectable by pollinators and can consequently affect their foraging preferences (Herrera *et al.,* 2013; Rering *et al.,* 2018). Simultaneously, nectar maintains some toxicity to inhibit the growth of non-friendly microorganisms that could be deleterious to plant reproductive success while still limiting its distastefulness or toxicity to pollinators (Martin *et al.,* 2022).

Amino acid and carbohydrate availability in nectar is one of the determining factors of the health and fitness of foraging species. In nature, upon colonisation, microfungal communities can alter the plant-provisioned compositions of such essential biomolecules and simultaneously secrete metabolic by-products or antibiotics into the nectar environment, resulting in selective perception by distinct pollinators. Such distinct imprints on olfactory and gustatory cues further help in foraging decisions. Further, yeast and yeast-like fungi, such as *Aureobasidium pullulans*, *Citeromyces matritensis*, *Cryptococcus laurentii*, *Rhodotorula glutinis*, and *Sporobolomyces roseus,* produced antibacterial compounds that may directly limit the growth of bees’ pathogens (*Pseudomonas fluorescens* and

Staphylococcus aureus) in floral nectar, thereby improving pollinator health (Martin *et al.,* 2022).

In certain winter-blooming plants, such as *Helleborus foetidus,* yeast colonisation causes enhanced nectar temperature through metabolism and fermentation, which is preferred by specific pollinators for easier digestibility (Herrera and Pozo, 2010; Nicolson *et al.,* 2013). Apart from temperature, viscosity is another aspect of nectar that can influence pollinator foraging. It is well known that nectarivorous mycoflora consume sugar from nectar to meet their growth requirement, and while doing so, it made alterations to nectar sugars, thereby changing its viscosity (Martin *et al.,* 2022).

Sugar metabolism

Nectar microbes, particularly yeasts, significantly alter the sugar composition of nectar. For instance, *Metschnikowia* yeasts preferentially consume sucrose and glucose, leaving a higher proportion of fructose. This shift can benefit pollinators like hummingbirds, which exhibit a preference for fructose-rich nectars due to their rapid metabolization and energy yield. Other yeasts recorded include species of the genera *Rhodotorula, Cryptococcus, Sporobolomyces,* and *Candida,* although they generally occur in much lower frequencies. This metabolic activity not only alters the nutritional profile of nectar but also its palatability and energy value for pollinators (Martin *et al.,* 2022). Although yeast contamination rates of nectar samples can be high, nectar-associated yeast communities are generally species-poor (on average 1.2 culturable yeast species/sample) and dominated mainly by the insect- or bird-vectored yeast genus *Metschnikowia* (Saccharomycetales). Species of *Metschnikowia* can deal with sugar concentrations up to 50% (Pozo *et al.,* 2015). The high sugar concentrations in nectar leads to extreme osmotic pressure and high C:N ratios, both of which limit microfungal growth (Mueller *et al.,* 2023)

Despite these observed effects, the energetic consequences of microfungi-induced alterations in nectar foraging for pollinator health remain largely unknown. Eusocial bees are sensitive to changes in the identity and concentration of sugars in nectar. In honeybees, low nectar sugar (i.e. sucrose) concentrations are linked to a reduction in the number of foraging trips made by workers, likely communicated through social interactions (i.e. waggle dance) and potentially resulting in fewer resources for the colony. Bumblebees also exhibit a strong preference for sucrose in nectar and will adjust their foraging tactics in response to changes in concentration (Martin et al. 2022).

Production of Volatile Organic Compounds (VOCs)

Pollinators utilise visual, olfactory, and gustatory cues to inform their foraging decisions. Olfactory stimuli, often in the form of volatile organic compounds (VOCs), play a vital role in attracting pollinators to flowers. These VOCs can serve as long-range attractants, guiding parasitoids towards potential food sources. Thus, it may not be entirely surprising that microfungi-induced changes in nectar VOCs can influence pollinator foraging behaviour. For instance, nectar-specialist yeasts in the *Metschnikowia* genus reduce the concentrations of sucrose and glucose, resulting in an increased proportion of fructose in nectar. These alterations are associated with the production of volatile organic compounds (VOCs) such as n-hexanol, 2-ethyl-1-hexanol, and 2-phenylethanol, which are detectable by floral visitors such as bumblebees and honeybees. Additional compounds like 3-methyl butyl acetate and 2-nonane have also been noted for eliciting strong behavioural responses in pollinators. Electroantennography studies have shown that bumblebee and honeybee olfactory neurons are responsive to microfungal VOCs, including n-hexanol, 2-ethyl-1-hexanol, and 2-phenylethanol at low concentrations (0.4 µmol). (Martin *et al.,* 2022).

Alteration of amino acids and secondary metabolites

In addition to qualitatively and quantitatively modulating sugar concentration and composition, nectarivorous fungi can also alter the amino acid content in nectar (Peay *et al.,* 2012). They not only consume the amino acids found in nectar but are also capable of synthesizing or modifying these compounds, resulting in metabolic changes that may affect nectar flavor and, therefore, pollinator preferences. The nectar-dwelling yeasts *Candida floricola*, *Metschnikowia koreensis, M. kunwiensis,* and *M. reukaufii* have been shown to significantly reduce the concentration of non-essential amino acids, such as proline, glutamic acid, and aspartic acid, in the nectar of *M. aurantiacus* (Peay *et al.,* 2012). Furthermore, secondary metabolites produced by microfungal communities, including antibiotics, can further influence nectar's chemical composition. The preference for nectar with a higher amino acid concentration is likely linked to its nutritional value, as its metabolism can impact adult longevity and fitness, as seen in Dipteran and Lepidopteran species (Martin et al. 2022).

SENSORY MODULATION AND POLLINATOR BEHAVIOUR

Olfactory cues

Pollinators exhibit a highly sensitive response to volatile organic compounds (VOCs) produced by nectar-associated fungi, which can significantly influence foraging behaviour (Rering *et al.,* 2018; Schaeffer *et al.,* 2022). The extent of this sensitivity varies based on the pollinator species, their olfactory adaptations, and environmental factors such as floral density and microfungal diversity across habitats (Junker & Keller, 2015). Experimental studies using naive bumblebees (*Bombus impatiens* and *Bombus terrestris*) have demonstrated that these insects are capable of detecting microfungal VOCs and utilising them as olfactory cues to locate nectar sources (Rering *et al.,* 2018). Electroantennography (EAG) and gas chromatography-coupled electrophysiological assays have further confirmed that olfactory neurons of honeybees exhibit significant responses to fungal VOCs, even at low concentrations (Christensen and Hildebrand, 2002). This suggests a fine-tuned chemosensory adaptation that allows pollinators to detect fungal presence and possibly assess nectar quality before consumption (Shimizu *et al.,* 2014).

Besides nectar specialist yeasts from the genus *Metschnikowia*, several members of Ascomycota, including the species *Starmerella* and *Wickerhamiella,* are among the most abundant nectar-dwelling fungi found in nature. Furthermore, the genera *Aureobasidium* and *Cryptococcus* (belonging to Ascomycota and Basidiomycota, respectively) are widely distributed in nectar, though at lower densities. Due to the variability in fungal community composition within the nectar of various floral species, considerable variation in the production of microfungal VOCs is observed across different floral types. This variation is primarily linked to differences in the fermentation of sugars present in the medium (Cusumano and Lievens, 2023). Such uniqueness in the VOCs fosters plant-pollinator interactions and is increasingly recognised as a crucial component in pollination ecology (Álvarez-Pérez *et al.,* 2024).

Gustatory cues

Nectar microbiota significantly impacts nectar chemistry, modifying sugar composition, pH, and secondary metabolite profiles, influencing pollinator feeding behaviour (Vannette and Fukami, 2018). Nectarivorous yeast species, such as *Metschnikowia reukaufii*, preferentially metabolise sucrose and leave behind fructose, a sugar known to enhance feeding rates in artificial colonies of bumblebees (*Bombus terrestris*) (Herrera *et al.,* 2013; Rering *et al.,* 2020). These metabolic alterations create distinct taste profiles that can either attract or deter certain pollinators, thereby acting as an ecological filter for pollinator selection (Canto *et al.,* 2017).

Microfungal metabolism also leads to the production of organic acids and alcohols, which can further modify the gustatory properties of nectar (Vannette *et al.,* 2021). For example, ethanol concentrations as low as 0.5% have been shown to influence honeybee (*Apis mellifera*) feeding preferences and learning behaviours, potentially altering foraging dynamics in nectar-rich environments (Aleklett *et al.,* 2014). Additionally, floral yeasts affect the nutritional quality of nectar through consumption of mono- and disaccharide sugars, alterations of their relative proportions, and decreases in pH through fermentation (Vannette *et al.,* 2013). Nectar-specialist yeast *M. rekaufii* specifically reduces the concentrations of sucrose and glucose, leaving an elevated proportion of fructose in nectar. Such specialist fermentation of floral nectar by *M. rekaufii* has been found to reduce nectar pH by half a unit in 36 h and more than two units in a 5-day period, further complicating the interplay between nectar chemistry and pollinator foraging efficiency (Good *et al.,* 2014; Tucker and Fukami, 2014).

Integration of olfactory and gustatory cues

Pollinators integrate olfactory and gustatory cues to optimise foraging efficiency and resource selection. The interaction between microfungal VOCs and nectar chemistry suggests a sophisticated plant-microbe-pollinator dynamic, where microfungal modifications serve as indirect mediators of pollinator behaviour (Schaeffer *et al.,* 2022). Recent research highlights that pollinators respond differently to nectar-inhabiting microbes, particularly *M. reukaufii,* depending on the insect species and the type of behavioural assay used (olfactory, gustatory, or both) (Crowley-Gall *et al.,* 2021; de Vega *et al.,* 2022). The influence of microfungal cues on pollinator behaviour spans a spectrum: some studies report neutral or even deterrent effects on foraging preferences (Good *et al.,* 2014; Rering *et al.,* 2018), while others document increased feeding activity and attraction to flowers (Herrera *et al.,* 2013; Yang *et* *al.,* 2019). These microfungal interactions can affect plant fitness both directly, without involving pollinators, and indirectly, by altering the physicochemical characteristics of flowers. Such microfungal "footprints" may influence pollinator choices and modify the floral microenvironment, thereby impacting pollination and fertilisation outcomes (Herrera and Medrano, 2017; Cullen *et al.,* 2021).

CONCLUSION

The presence of nectar-inhabiting microorganisms significantly influences plant-pollinator interactions by modifying nectar chemistry and sensory properties. Initially sterile, floral nectar becomes colonised by yeasts dispersed through the air or by pollinators (Pozo *et al.,* 2015). These microfungal communities alter nectar composition by fermenting sugars, changing amino acid profiles, and producing volatile organic compounds (VOCs), collectively influencing pollinator foraging behaviour (Herrera *et al.,* 2013; Rering *et al.,* 2018). Notably, nectar microfungal metabolism reduces the pH and shifts the balance of mono- and disaccharide sugars, affecting nectar palatability and attractiveness to pollinators (Vannette and Fukami, 2018).

Importantly, reciprocal feedback exists between nectar-inhabiting microorganisms and pollinators. While microbes modify nectar chemistry in ways that shape pollinator preferences, pollinators themselves mediate microfungal dispersal among flowers, thereby influencing microfungal community composition and dynamics (Martin *et al.,* 2022). This bidirectional interaction underscores the ecological and evolutionary complexity of plant-microbe-pollinator networks. Future research exploring the consequences of microbe-induced changes in nectar traits on pollinator health and behaviour across diverse ecological settings holds substantial promise. Such investigations could not only clarify the nuanced roles nectar microbes play in shaping plant-pollinator interactions but also reveal context-dependent effects, where factors such as habitat type, plant species composition, pollinator community structure, and climatic conditions mediate microfungal influence. These dynamics may offer innovative pathways to enhance pollination efficiency. For instance, microfungal consortia that consistently promote desirable foraging behaviours or boost pollinator nutritional intake could be harnessed to engineer floral microbiomes, particularly in managed agricultural systems. Additionally, exploring the long-term effects of nectar microbes on pollinator physiology, immune function, and microbiome stability could uncover overlooked mechanisms by which microbes indirectly affect plant reproductive success. Ultimately, integrating microfungal ecology into pollination biology may lead to the development of microbe-informed crop management practices that simultaneously support pollinator health and optimise plant yield.

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STATEMENT OF INTEREST

The authors declared no competing interests.

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