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DERLEME /REVIEW

STRATEGIES AND MECHANISMS OF PLANT-MICROBIOME-POLLINATOR COADAPTATION

Bitki-Mikrobiyom-Polinatör Ko-adaptasyon Stratejileri ve Mekanizmaları

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ABSTRACT

Plant-pollinator interactions showcase mutualistic coevolution, but the role of microorganisms in these relationships is often overlooked. Nectar-dwelling microorganisms, mainly yeasts and bacteria, significantly influence floral chemistry, pollinator behavior, and plant reproduction. These microorganisms alter nectar's sugar content, amino acid profiles, pH, and scent emissions, shaping pollinator preferences. For example, the yeast *Metschnikowia reukaufii* produces fruity esters that attract bumble bees, while some bacteria lower pH, repelling honey bees. Pollinators spread these microorganisms between flowers, creating a feedback loop that shapes microbial communities and drives coevolution. Beyond nectar, microorganisms' impact on thermal regulation through metabolic heat, pollen health, and pollinator gut microbiomes. Specialized bacteria like *Rosenbergiella nectarea* and *Acinetobacter spp.* thrive in nectar's high-sugar environment, while pollinator microorganisms, such as *Lactobacillus kunkeei,* protect honey bees from pathogens. Microbial diversity varies by region, with tropical flowers hosting richer communities than temperate ones. This review highlights how microorganisms act as key players in plant-pollinator networks, boosting pollinator nutrition, immunity, and foraging efficiency. It explores microbial spread, competition, and chemical influence, calling for studies that blend microbiology, ecology, and evolution. Understanding these interactions is vital for predicting how climate change and habitat loss threaten pollination, affecting agriculture and biodiversity.

Keywords: Honey bee, Pollinators, Microbiome, Coadaptation, Coevolution

ÖZ

Bitki-polinatör etkileşimleri, karşılıklı faydaya dayalı ko-evrimi sergilemektedir; ancak mikroorganizmaların bu ilişkilerdeki rolü genellikle göz ardı edilmektedir. Başlıca mayalar ve bakterilerden oluşan nektarda yaşayan mikroorganizmalar, çiçek kimyasını, polinatör davranışını ve bitki üremesini önemli ölçüde etkilemektedir. Bu mikroorganizmalar, nektarın şeker içeriğini, amino asit profillerini, pH'ını ve koku emisyonlarını değiştirerek polinatör tercihlerini şekillendirmektedir. Örneğin, *Metschnikowia reukaufii* mayası, *bombus* arılarını cezbeden meyvemsi esterler üretirken, bazı bakteriler pH'ı düşürerek bal arılarını uzaklaştırmaktadır. Polinatörler, bu mikroorganizmaları çiçekler arasında yayarak, mikrobiyal toplulukları şekillendiren ve ko-evrimi yönlendiren bir geri bildirim döngüsü oluşturmaktadır. Nektarın ötesinde, mikroorganizmalar metabolik ısı yoluyla termal düzenlemeyi, polen sağlığını ve polinatör bağırsak mikrobiyomlarını etkilemektedir. *Rosenbergiella nectarea* ve *Acinetobacter spp.* gibi özelleşmiş bakteriler, nektarın yüksek şekerli ortamında gelişirken, *Lactobacillus kunkeei* gibi polinatör mikroorganizmaları, bal arılarını patojenlerden korumaktadır. Mikrobiyal çeşitlilik bölgeye göre değişmekte olup, tropikal çiçekler ılıman iklim çiçeklerine göre daha zengin topluluklara ev sahipliği yapmaktadır. Bu derleme, mikroorganizmaların polinatör beslenmesini, bağışıklığını ve besin arama verimliliğini artırarak bitki-polinatör ağlarında nasıl kilit oyuncular olarak rol oynadığını vurgulamaktadır. Mikrobiyal yayılımı, rekabeti ve kimyasal etkileri inceleyerek, mikrobiyoloji, ekoloji ve evrimi harmanlayan çalışmalara çağrı yapmaktadır. Bu etkileşimleri anlamak, iklim değişikliğinin ve habitat kaybının tozlaşmayı nasıl tehdit ettiğini tahmin etmek, tarımı ve biyoçeşitliliği etkilemek için hayati öneme sahiptir.

Anahtar Kelimeler: Bal arısı, Polinatörler, Mikrobiyom, Ko-adaptasyon, Ko-evrim

GENİŞLETİLMİŞ ÖZET

Giriş: Nektar, 1884 yılında Boutroux tarafından ilk kez belgelendiği gibi zengin ve az keşfedilmiş bir mikrobiyal habitattır. Çalışmalar, çiçek nektarının *Metschnikowia* gibi mayalar ve *Acinetobacter* ve *Pseudomonas* gibi bakteriler de dahil olmak üzere, öncelikle tozlayıcılar tarafından getirilen çeşitli mikrobiyal toplulukları desteklediğini ortaya koymuştur. Bu mikroorganizmalar nektar ekolojisinde merkezi bir rol oynamakta, bitki ve böceklerin davranış ve uygunluğunun yanı sıra nektarın tadı, aroması, şeker içeriği ve amino asit bileşimini de etkilemektedir.

Böcekler, özellikle de bal arıları, kovanla ilişkili türleri nektara bırakarak çiçekler arasında mikropların aktarılmasında önemli vektörler olarak hareket ederler. Bu mikrobiyal değişim nektarın mikrobiyomunu şekillendirir ve tozlayıcıların tercihlerini ve bitkilerin üreme başarısını etkileyebilir. Mikroorganizmalar nektara rüzgar veya yağmur gibi abiyotik yollarla girebilse de, tozlayıcı aktivitesi bu habitattaki mikrobiyal çeşitliliğin birincil itici gücü olmaya devam etmektedir. Bal arıları, çiçeklere yaptıkları tekrarlı ziyaretler ve kovandaki sabit mikrobiyotaları sayesinde, nektarı tozlaşma dinamiklerini etkileyecek şekilde değiştirerek ekosistem mühendisleri olarak hareket ederler. Çiçek mikrobiyal toplulukları genellikle tozlayıcı ziyaret modellerini yansıtır ve iklim ve coğrafya topluluk kompozisyonunu daha da etkiler. Bu derleme, nektarda yaşayan mikropların nektar kimyasını dönüştürerek tozlayıcı davranışını ve bitki-polinatör etkileşimlerini nasıl değiştirdiğine dair mevcut bilgileri özetlemektedir.

Bitki-polinatör birlikte evriminde çiçek adaptasyon stratejileri: Bitkiler, tozlayıcıların davranışlarını manipüle etmek için karmaşık çiçek adaptasyonları geliştirmiştir. Bunu esas olarak nektar salgılayarak yaparlar. Böceklerin ziyaretleri, genellikle mikroorganizmaların katılımı yoluyla nektarın kimyasını önemli ölçüde değiştirebilir. Örneğin, bal arıları bez salgıları ve polen biriktirme yoluyla nektardaki amino asit seviyelerini artırır. Bombus arıları ise muhtemelen ağız parçalarından maya transferi nedeniyle şeker konsantrasyonlarını azaltır. Yalnız yaşayan arıların nektar üzerinde çok az etkisi vardır. Tozlayıcılar tarafından getirilen mikroorganizmalar, özellikle de *Metschnikowia* gibi mayalar, şeker bileşimini, pH'ını ve uçucu emisyonlarını değiştirerek nektarı modifiye eder. Bu değişiklikler tozlayıcıların çekiciliğini ve yiyecek arama davranışını etkiler. Maya metabolizması ısı üreterek nektarın sıcaklığını 6 santigrat dereceye kadar yükseltir, çiçek kokusu salınımını artırır ve daha soğuk iklimlerde böcekleri çeker. *Nelumbo* *nucifera* gibi ısı üreten türler, tozlayıcı enerji maliyetlerini azaltarak ve ziyaret süresini artırarak fayda sağlar. Koku taklidi ve renk değişiklikleri gibi çiçek ipuçları, bitki çekim stratejilerini daha da geliştirir. Örneğin orkideler ve Ceropegia türleri, belirli tozlayıcıları çekmek için böcek ipuçlarını kimyasal olarak taklit eder. UV işaretleri ve anthesis ile bağlantılı renk değişimleri, yiyecek arama davranışını yönlendirir. Bununla birlikte, son derece uzmanlaşmış stratejiler, tozlayıcıların azalması karşısında üreme başarısını riske atabilir. Mikrobiyal uçucu organik bileşikler (VOC'ler) hem tozlayıcıları çekebilir hem de rakip mikroorganizmaları bastırarak ekolojik dinamikleri şekillendirebilir. Bu nedenle, mikroplar sadece nektar modülatörleri olarak değil, aynı zamanda bitki-polinatör iletişimini rafine eden ekolojik aracılar olarak da hareket eder.

Çiçek nişlerinde mikroorganizmaların uzmanlaşması ve adaptasyonu: Çiçeklerde yaşayan mikroorganizmalar hava, toprak, su ve bitki dokularından türetilen dinamik topluluklar oluşturur. Bakteriler ve mantarlar çiçek dokularını erken dönemde, hatta tomurcuklar açılmadan önce kolonize eder, ancak bollukları genellikle düşük kalır ve bu da geçici kolonizasyona işaret eder. Bu mikroorganizmaların kalıcılığı, UV radyasyonu, kuruma, rekabet ve sınırlı dağılma gibi çevresel stres faktörlerinin üstesinden gelme yeteneklerine bağlıdır. Tozlayıcılar gibi böcekler mikroorganizmaların yayılmasında önemli bir rol oynar, ancak yalnızca ozmotik strese toleranslı olanlar ve diğerleriyle rekabet edebilenler nektara yerleşebilir. Diğer yayılma şekilleri arasında rüzgar, yağmur sıçraması ve bazı mikroorganizmaların çiçek dokularına göç etmesiyle bitkiler içinde iç taşınma yer alır. Çiçeklerin taç yaprakları ve yapraklarındaki mikrobiyal topluluklar sıklıkla örtüşse de, çiçek mikrobiyomu tipik olarak daha az çeşitlidir ve eşit olmayan bir şekilde dağılmıştır. Bazı mikroorganizmaların çiçek ortamında oldukça uzmanlaştığı, çiçeklerde bol miktarda bulunurken diğer habitatlarda nadiren görüldüğü görülmektedir. Bu uzmanlar genellikle hızlı büyüme, nektar ozmolaritesine tolerans ve çiçeğe özgü bileşikleri metabolize etme yeteneği gibi özellikler sergiler. Çiçekler yaşlandıkça, özellikle nektarda ve pistillerde mikrobiyal bolluk artar. Tozlayıcılar, temas, dışkı veya tımarlama yoluyla mikroorganizmalar getirerek çiçek kısımlarındaki mikrobiyal çeşitliliği önemli ölçüde etkiler. Metodolojik zorluklara rağmen, mikrobiyal yaşam döngülerini izlemek ve konakçıya adapte olmuş türler arasında ayrım yapmak, çiçek nişlerindeki mikroorganizmaların uzmanlaşmasını ve evrimini anlamak için kritik öneme sahiptir.

Nektar ve bal mikrobiyal topluluklarının polinatör aracılı şekillendirilmesi: Nektar, özelleşmiş mikrobiyal toplulukları destekleyen dinamik bir mikrohabitattır. Bu topluluklar öncelikle tozlayıcılardan etkilenen bakteri ve mayalardan oluşur. Tozlayıcılar hem polen vektörleri hem de mikrobiyal dağıtıcılar olarak hareket ederek farklı çiçek türleri arasında nektar mikrobiyomunun bileşimini şekillendirir. Nektardaki mikrobiyal yoğunluklar, bir çiçeğin ömrü boyunca mikrolitre başına 105 maya hücresine ve 107 bakteri hücresine ulaşabilir. Nektardaki koşullar, yüksek ozmotik basınç ve düşük nitrojen mevcudiyeti ile sert olsa da, *Metschnikowia*, *Wickerhamiella*, *Acinetobacter* ve *Rosenbergiella* gibi ozmotoleranslı türler gelişebilir. Ilıman bölgelerde, nektar topluluğu sınırlı çeşitlilik nedeniyle genellikle tek bir tür tarafından domine edilir. Bununla birlikte, çiçeklenme mevsiminin daha uzun sürdüğü ve bitki çeşitliliğinin daha fazla olduğu tropikal bölgelerde, nektar daha çeşitli mikrobiyal topluluklar sağlar. Tozlayıcılar nektarın mikrobiyal bileşiminin şekillenmesinde önemli bir rol oynar. Böcekler tarafından ziyaret edilen çiçekler ascomycetous maya topluluklarına sahip olma eğilimindeyken, tozlayıcılar tarafından ziyaret edilmeyen çiçekler daha fazla basidiomycete türüne sahiptir. Bazı nektar mikropları bal arılarının bağırsaklarında da yaşar ve patojenleri engelleyen antibiyotikler ve organik asitler üreterek koloni sağlığını etkiler. Nektar ve balın yanı sıra arı bağırsaklarında da bol miktarda bulunan *Lactobacillus* ve *Bifidobacterium* laktik ve asetik asitler üreterek pH'ı düşürür ve patojenlerin büyümesini sınırlar. Bu etkileşimler nektarın kimyasını ve tozlayıcıların sağlığını geliştirerek, karşılıklı fayda sağlayan ve antagonistik etkileşimler yoluyla çiçekleri, mikropları ve tozlayıcıları birbirine bağlayan birlikte evrimleşmiş bir mikrobiyal ekolojiye işaret etmektedir.

Nektar mikrobiyom dinamikleri ve tozlaşma için işlevsel sonuçları: Çiçek nektarında yaşayan mikroorganizmalar, nektarın kimyasal bileşimini değiştirerek bitki-polinatör etkileşimleri üzerinde önemli bir etkiye sahiptir. Neokomagataea ve Rosenbergiella nectarea gibi özelleşmiş bakteriler ve *Metschnikowia reukaufii* gibi mayalar, metabolizmaları yoluyla sükroz seviyelerini düşürüp nektardaki glikoz ve fruktoz konsantrasyonlarını artırmanın yanı sıra amino asit konsantrasyonlarını ve asitliği modüle eder. Bu değişiklikler nektarın

lezzetini ve besin değerini etkileyerek tozlayıcı tercihlerini ve yiyecek arama davranışını doğrudan etkiler. Bazı mikroorganizmalar, tozlayıcıları çekebilen veya itebilen uçucu organik bileşikler yayar; *M. reukaufii* meyvemsi aroması nedeniyle özellikle çekicidir. Ayrıca, bu mikroplar nektar hacmini, şeker oranlarını ve çiçek kokusunu etkileyerek tozlaşma başarısını ve üreme verimini etkileyebilir. Bazı mikroplar nektar kalitesini veya polen canlılığını azaltabilirken, diğer mikroplar tozlayıcı sağlığını iyileştirir, bağırsak mikrobiyotasını modüle eder veya Crithidia bombi gibi patojenleri inhibe eder. Bu mikrobiyal ajanlar, çekici meyvemsi esterlerden itici asitlere kadar bir dizi bileşik üretir ve bu bileşikler böcek tozlayıcıların yiyecek arama tercihlerini doğrudan etkiler. Buna ek olarak, tozlayıcıların çiçekler arasında belirli mikrobiyal toplulukları dağıtmak için vektör görevi görmesi ve bağışıklıklarını, besin asimilasyonunu ve patojenlere karşı dirençlerini artıran bağırsak simbiyotik mikroorganizmalardan faydalanması ile ilişki çift yönlüdür. Tropikal ve ılıman ekosistemler farklı mikrobiyal bileşimler sergilediğinden, coğrafi ve ekolojik faktörler bu karmaşıklığa daha da katkıda bulunur. Bitkiler, mikrobiyal aktiviteye yanıt olarak kimyasal savunmalar geliştirmiştir. Bu savunmalar, nektarlarındaki mikropları kullanabilir ya da bastırabilir. Mikrobiyal metabolizma çiçek sıcaklığının düzenlenmesine bile yardımcı olabilir, bu da daha soğuk koşullarda tozlayıcı ziyaretini artırabilir. Son zamanlarda elde edilen bilgilere rağmen, özellikle pestisitler ve habitat parçalanması gibi insan etkilerine ilişkin hala önemli bilgi boşlukları bulunmaktadır. Polinatör popülasyonları azalmaya devam ederken, bitki-polinatör etkileşimlerinin mikrobiyal yönünü anlamak çok önemlidir. Bu, mikroorganizmaların bu hassas biyolojik ağlarda temel ekolojik oyuncular olarak kabul edilmesiyle, biyoçeşitliliği ve tarımsal üretkenliği desteklemek için hedeflenen probiyotiklerin geliştirilmesine yol açabilir.

Sonuç: Mikroorganizmalar, bitki-polinatör ilişkilerinin karmaşık ağında çok önemli bir rol oynar ve ekolojik sonuçları incelikli ancak derinden etkiler. Nektarda yaşayan mayalar ve bakteriler çiçek nektarında sadece pasif olarak bulunmaz, aynı zamanda kimyasal ve fiziksel özelliklerini aktif olarak yeniden şekillendirir. Bu durum tozlayıcı davranışını değiştirir ve nihayetinde bitkinin üreme başarısını etkiler. Bu mikrobiyal ajanlar, çekici meyvemsi esterlerden itici asitlere kadar, böcek tozlayıcılarının besin arama tercihlerini doğrudan etkileyen bir dizi bileşik üretir. Buna ek olarak, tozlayıcıların çiçekler arasında belirli mikrobiyal toplulukları dağıtmak için vektör görevi görmesi ve bağışıklıklarını, besin asimilasyonunu ve patojenlere karşı direncini artıran bağırsak simbiyotik mikroorganizmalardan faydalanması ile ilişki çift yönlüdür. Bu savunmalar, nektarlarındaki mikropları kullanabilir ya da bastırabilir. Mikrobiyal metabolizma çiçek sıcaklığının düzenlenmesine bile yardımcı olabilir, bu da daha soğuk koşullarda tozlayıcı ziyaretini artırabilir. Son zamanlarda elde edilen bilgilere rağmen, özellikle pestisitler ve habitat parçalanması gibi insan etkilerine ilişkin hala önemli bilgi boşlukları bulunmaktadır. Tozlayıcı popülasyonları azalmaya devam ederken, bitki-polinatör etkileşimlerinin mikrobiyal yönünü anlamak çok önemlidir. Bu, mikroorganizmaların bu hassas biyolojik ağlarda temel ekolojik oyuncular olarak kabul edilmesiyle, biyoçeşitliliği ve tarımsal üretkenliği desteklemek için hedeflenen probiyotiklerin geliştirilmesine yol açabilir.

INTRODUCTION

Nectar remains one of the least studied microbial habitats, despite over a century of research. As early as 1884, Boutroux documented yeasts in flowers, fruits, and insects, using morphological and physiological methods to assess their diversity. Subsequent studies have revealed that nectar from diverse plant species worldwide hosts bacterial and yeast communities, with *Metschnikowia* (Ascomycota, Fungi) being one of the most common genera (Boutroux 1884, Álvarez-Pérez and Herrera 2013, Aleklett et al. 2014).

Nectar, rich in carbohydrates and amino acids, attracts insect pollinators and supports dynamic microbial communities, including yeast and bacteria (Willmer 1980, Nicolson and Thornburg 2007). These microorganisms colonize floral surfaces, pollen, and nectar (Álvarez-Pérez et al. 2012, Aleklett et al. 2014, Manirajan et al. 2016) and are dispersed by both biotic and abiotic vectors. Although microorganisms exist in nectar before pollination, animals - particularly pollinators - play a key role in introducing and spreading microorganisms among flowers, enriching floral microbiome diversity (Boutroux 1884,de Vega and Herrera 2012).

Pollinating insects play a significant role in structuring the microbiome of nectar, pollen, and floral surfaces, with their visitation patterns directly shaping microbial composition (Aizenberg-Gershtein et al. 2013, Morris et al. 2020, Vannette 2020, de Vega et al. 2021, Hietaranta et al. 2022). Honey bees, for instance, act as microbial vectors, introducing nest-associated bacteria and fungi into floral resources (Keller et al. 2021), which can subsequently influence plant fitness and pollinator behavior.

Honey bees harbor a distinct in-hive microbiome that differs from environmental microbial communities (Santorelli et al. 2023). Their social structure reinforces microbiome stability, enabling intergenerational transmission (Canto et al. 2008). When deposited into nectar, these microorganisms can modify floral conditions, effectively acting as ecosystem engineers that mediate plant-pollinator interactions. Thus, nectar functions as a dynamic micro-ecosystem, linking macro- and microorganisms (Vannette et al. 2013).

Microbial communities in nectar can reduce sugar concentration (Herrera et al. 2008, de Vega et al. 2009,de Vega and Herrera 2012), alter carbohydrate and amino acid composition (Herrera et al. 2008, de Vega and Herrera 2012, Lenaerts et al. 2017, Vannette and Fukami 2018), induce floral heating (Herrera and Pozo 2010), and release volatile organic compounds (VOCs) (Rering et al. 2017, Schaeffer et al. 2019). These changes influence pollinator behavior and pollination success (Vannette et al. 2013, Herrera et al. 2013, Junker et al. 2014, Schaeffer and Irwin 2014, Vannette and Fukami 2017, Schaeffer et al. 2017).

Flowers are known to harbour a diverse array of microorganisms, which have the capacity to be passively dispersed by wind, rain, or soil (Zarraonaindia et al. 2015, Sharaby et al. 2020). However, microbial colonization of nectar also depends on animal vectors (Peay et al. 2011, Tucker and Fukami 2014, Álvarez-Pérez et al. 2019). Yeasts and bacteria in nectar are often introduced by birds, bats, beetles, butterflies, ants, flies, and honey bees (Sandhu and Waraich 1985, Lachance et al. 2001, de Vega and Herrera 2012, Canto and Herrera 2012, Vannette 2020, Keller et al. 2021, de Vega et al. 2021). Early work by Boutroux (1884) showed that honey bee-visited flowers contain more enzymatic yeasts than those not visited by honey bees (Boutroux 1884, de Vega and Herrera 2012).

Nectar hosts specific yeast and bacterial species commonly found in this ecological niche across plants worldwide (Brysch-Herzberg 2004, Pozo et al. 2011, Belisle et al. 2012, Fridman et al. 2012, Álvarez-Pérez and Herrera 2013, Jacquemyn et al. 2013, Canto et al. 2017). The bacterial community is often dominated by Proteobacteria, particularly *Acinetobacter*, *Rosenbergiella*, and *Pseudomonas* (Aizenberg-Gershtein et al. 2013, Álvarez-Pérez and Herrera 2013, Álvarez-Pérez et al. 2013, Morris et al. 2020, Sharaby et al. 2020), while the yeast community is frequently represented by *Metschnikowia* species (Brysch-Herzberg 2004, Belisle et al. 2012, Pozo et al. 2012, Schaeffer et al. 2019). Less common nectar-associated yeasts include *Cryptococcus*, *Papiliotrema*, *Rhodotorula*, and *Sporobolomyces* (Basidiomycetes), as well as *Aureobasidium*, *Clavispora,* *Debaryomyces*, *Hanseniaspora*, *Kodamaea*, *Starmerella*, and *Wickerhamiella* (Ascomycetes) (Klaps, 2019). Ongoing research continues to expand the known diversity of floral yeasts (Klaps et al. 2020), with over a dozen new species described in the past two decades (de Vega et al. 2017, Klaps 2019).

Pollinators act as biological vectors, facilitating the exchange of microorganisms between flowers and insects through the different microbial communities they carry (Brysch-Herzberg 2004, Keller et al.). It has been demonstrated that flowers visited by the same pollinator species possess compositionally similar nectar microbiomes (de Vega et al. 2017). Each pollinator species leaves a unique microbial signature on the flower it visits (Lachance et al. 2001, Ushio et al. 2015, Morris et al. 2020, de Vega et al. 2021), suggesting that the observed differences in floral microbiota are shaped not only by environmental but also pollinator-specific effects. Additionally, nectar microbial diversity varies with climate, with tropical plants typically supporting greater species richness than those in temperate regions (Álvarez-Pérez et al. 2012, de Vega et al. 2017, Canto et al. 2017).

This review explores how microorganisms mediate plant-insect pollinator interactions, focusing on their role in shaping pollination dynamics. Specifically, it examines how microorganisms alter the properties and chemical composition of nectar and honey, influencing the behavior and health of honey bees and other insect pollinators. The discussion highlights the mechanisms by which microorganisms modify nectar’s nutritional and chemical profiles, ultimately affecting pollinator activity.

Floral adaptation strategies in plant-pollinator coevolution

Plants have evolved mechanisms to interact with insect pollinators, primarily through nectar secretion, which functions to manipulate pollinator behavior (Pyke 2016). Insect pollinators can directly alter nectar chemistry, partly due to microorganisms they introduce (Aizenberg-Gershtein et al. 2013). For example, honey bee visits increase amino acid concentrations in nectar through mandibular gland secretions, cell wall damage, and pollen transfer (Corbet et al. 1979, Willmer 1980).

The impact on nectar composition varies by pollinator species. While solitary bees (*Andrena* and *Lasioglossum*) do not affect sugar content, bumble bees (*Bombus terrestris* and *B. pratorum*) reduce it (Canto et al. 2008). Honey bees and bumble bees actively modify nectar chemistry, altering acidity and fructose-to-sucrose ratios, likely due to yeast inoculation from their mouthparts (Aizenberg-Gershtein et al. 2013). Pollinator sociality may influence yeast transfer frequency, as bumble bee visits correlate with higher floral yeast densities, while solitary bee visits show an inverse relationship (Herrera et al. 2009).

Nectar-inhabiting yeasts can influence floral thermal microclimates by generating heat through sugar catabolism, elevating both nectar and internal floral temperatures. In nectaries with high yeast densities, this temperature gradient can reach up to 6°C (Herrera and Pozo 2010). For early-flowering plants such as *Helleborus foetidus*, this warming effect has significant ecological consequences, including enhanced pollinator attraction through increased volatile organic compound emissions and improved floral visibility to insects.

Thermogenic flowers, such as *Nelumbo nucifera*, use microbe-mediated heat production to maintain temperatures above ambient levels, attracting pollinators in cooler conditions (Seymour and Schultze-Motel 1998). This thermogenesis not only boosts scent dispersion but also reduces pollinators' thermoregulatory energy costs, increasing their foraging activity (Rands and Whitney 2008). Some species, like *Cistus ladanifer*, combine thermal cues with structural adaptations - such as sticky surfaces that deter predators - though larger flowers face a trade-off, as their size increases both pollinator attraction and susceptibility to herbivory (Teixido et al. 2016).

Chemical signals play an important role in plant-pollinator communication. Yeasts, as part of these mutualistic interactions, can have both beneficial and detrimental effects. While their metabolism of nectar sugars may seem parasitic - exploiting resources meant to attract pollinators (Herrera et al. 2008) - yeasts can also enhance pollination success. For example, they may raise nectar temperature or produce compounds like ethanol, which attract certain pollinators (Wiens et al. 2008, Herrera et al. 2010).

Floral volatile organic compounds (VOCs) act as long-range insect attractants. Some plants employ deceptive strategies, such as *Philodendron solimoesense*, which mimics the scent of decaying matter to lure dung beetles (Seymour et al. 2003). Similarly, *Ophrys* orchids imitate female honey bee pheromones, triggering pseudocopulation in males (Peakall et al. 2010). While these tactics reduce nectar production costs, they may also lower repeat pollinator visits (Jersáková et al. 2006). Nocturnal flowers often emit fungal or carrion-like scents, adapting to the preferences of night-active pollinators (Stökl et al. 2010).

Floral adaptations often involve color variations linked to geographic range and pollinator preferences. For example, *Gentiana lutea* displays flower colors ranging from yellow to greenish hues, corresponding to local honey bee activity (Sobral et al. 2015). Some Asteraceae species feature ultraviolet markings - invisible to humans but visible to insects - that guide pollinators to nectar (Miller et al. 2011). Additionally, color changes during the anthesis period, as seen in *Quisqualis indica*, indicate flower maturity. White blooms attract nocturnal moths, while pink ones attract diurnal honeybees and butterflies (Yan et al. 2016).

Some plants employ highly specialized pollination strategies. The South African *Ceropegia gerrardii* lures kleptoparasitic flies (*Desmometopa spp.*) by mimicking the scent of injured honey bees and offering nectar resembling honey bee hemolymph in protein and sugar content (Heiduk et al. 2023). While such adaptations demonstrate evolutionary plasticity, they also make plants vulnerable to declines in their specialized pollinator populations (Zariman et al. 2022).

Nectar microorganisms, such as yeasts and bacteria, play a significant role in plant-pollinator interactions. By colonizing nectar and changing its chemistry, they modify its nutritional value and attractiveness, ultimately influencing insect foraging behavior (Vannette et al. 2013, Martin et al. 2022). For instance, yeasts metabolize sucrose into fructose and produce volatile organic compounds (VOCs), such as alcohols and ketones, which pollinators can detect (Herrera et al. 2013, Rering et al. 2017). Although these changes reduce nectar's caloric content, they often enhance its appeal to bumble bees and honey bees (Schaeffer et al. 2017).

Critically, microbial VOCs not only attract pollinators but may also suppress competing microorganisms, creating a dynamic interplay between nectar microorganisms and plant chemistry (Good et al. 2014, Cullen et al. 2021). These volatiles can either increase or decrease nectar attractiveness, fine-tuning pollinator preferences (Rering et al. 2017). Thus, microorganisms act as both biochemical modifiers and ecological mediators, bridging plant and pollinator interactions (Table 1).

Table 1. Plant-pollinator-microbe interaction mechanisms and examples

Strategy	**Mechanism**	**Specific Microbial Taxa and Metabolite Involved**	**Effects on Nectar/Pollinators**	**Plant Examples**	**Citations**
Nectar Chemistry Modification	Pollinators introduce microorganisms that alter sugar composition and pH	*Metschnikowia reukaufii* (yeast), *Acinetobacter spp.* (bacteria)	Converts sucrose to fructose+glucose, reduces sugar concentration by 15-30%, lowers pH by 1-2 units	General across angiosperms	Herrera et al. 2008, Canto et al. 2008, Álvarez-Pérez and Herrera 2013
Thermal Microclimate Regulation	Microbial metabolism generates heat	*Metschnikowia gruessii* (yeast)	Increases nectar temp by 2-6°C, enhances VOC emission by 20-40%	*Helleborus foetidus*, *Nelumbo nucifera*	Herrera and Pozo, 2010, Seymour and Schultze-Motel, 1998
Volatile Organic Compound (VOC) Production	Microorganisms synthesize attractant/deterrent compounds	*M. reukaufii* (fruity esters), *Asaia astilbes* and *Neokomagataea sp.* (2,5-dimethylfuran)	Increases bumble bee visits by 25-50%, repulses honey bees at high concentrations	*Mimulus aurantiacus*	Rering et al. 2017, Schaeffer et al. 2017, Good et al. 2014
Nutritional Quality Modulation	Microbial consumption/transformation of nutrients	*Rosenbergiella nectarea* (reduces amino acids), *Neokomagataea sp.* (increases amino acids)	Alters pollinator foraging duration by 30-60%, affects colony growth rates	*Epilobium canum*	Lenaerts et al. 2017, Pozo et al. 2021
Antimicrobial Defense	Plant secondary metabolites regulate microorganisms	Callunene in heather inhibits the bumble bee parasite *Crithidia bombi*	Reduces *Crithidia bombi* infections by 70-90% in bumble bees	*Calluna vulgaris*	Koch et al. 2019, Carter and Thornburg,, 2004
Pollen-Nectar Microbiome Linkage	Gut microbiota acquisition from flowers	*Lactobacillus kunkeei*, *Bifidobacterium spp.*	Improves honey bee pathogen resistance (30-50% survival increase)	General across bee-pollinated plants	Arredondo et al. 2018, Vásquez et al. 2012
Specialized Pollinator Attraction	Co-evolved scent/chemical mimicry	*Saccharomyces spp.* (ethanol production)	Attracts kleptoparasitic flies (*Desmometopa spp.*)	*Ceropegia gerrardii*	Wiens et al. 2008, Heiduk et al. 2023

Specialization and adaptation of microorganisms in floral niches

The microorganisms inhabiting flowers form complex, dynamic communities derived from diverse environmental sources, including air, soil, and water. Both bacteria and fungi colonize flowers early in development, appearing on buds and petals as soon as they form (Shade et al. 2013, Morris et al. 2020). Notwithstanding their early presence, microbial abundance remains low, thus indicating transient colonization (Brysch-Herzberg 2004, Morris et al. 2020).

An important factor shaping nectar microbial communities is limited dispersal. Insects, such as pollinators, introduce yeasts and bacteria into nectar, but only those capable of tolerating high osmotic pressure and outcompeting rivals persist (Álvarez-Pérez et al. 2019, Vannette 2020). Since most flowers are short-lived, dispersal critically influences microbial species richness, composition, and function. Potential dispersal vectors - wind, water, plant tissues, and flower-visiting animals - each carry distinct microbial groups (Vannette 2020). However, not all arriving microorganisms successfully establish on floral surfaces. Environmental stressors, including UV radiation, desiccation, patchy nutrient availability, and microbial competition, limit colonization (Herrera et al. 2010). For instance, the bumble bee pathogen *Crithidia bombi* remains infectious on petals and sepals but survives only a few hours under environmental exposure (Figueroa et al. 2019), underscoring how abiotic and biotic factors shape floral microbial communities.

Microorganisms can colonize flowers not only from external sources but also from within the plant itself. Endophytes, microorganisms living within plant tissues without causing visible harm, along with surface pathogens and epiphytic microorganisms, can migrate into floral tissues. For example, fungal hyphae have been observed moving from vegetative tissues to flowers in grasses (Hinton and Bacon 1985). Bacteria can also travel through the plant's vascular system, moving between flowers and other tissues (An et al. 2020, Kim et al. 2019, Vanneste 2000). It is hypothesized that certain species of bacteria that are endemic to the xylem may be able to penetrate nectar through secreted droplets. Nevertheless, this assertion is not yet substantiated by empirical evidence (An et al. 2020, Roy et al. 2017).

Microorganisms also colonize flowers through interactions with honey bees, which act as vectors for microbial transfer (Shi et al. 2025). When honey bees visit flowers to collect nectar and pollen, microbes from the honey bees or hive environments can adhere to floral surfaces and nectar (Hietaranta et al. 2022). Honey bees visitation transfers microbes from the insect to the flower, shaping the floral microbiome (Lignon et al. 2024). The presence of honey bees significantly alters the community composition of both bacteria and fungi on inflorescences, highlighting their role in structuring floral microbial ecosystems (Hietaranta et al. 2022). This dynamic interplay underscores the ecological importance of honey bees in mediating plant-microbe-pollinator interactions (Shi et al. 2025).

Epiphytic microorganisms can reach flowers from leaves, or from a shared external source, via wind, water, rain splash, or insects. Bacterial communities on petals and leaves often overlap, but floral microorganisms tend to be less diverse and unevenly distributed (Junker et al. 2014, Massoni et al. 2020, Wei and Ashman 2018). This supports the idea that microorganisms move from leaves (or a common source) to flowers. While microbial transfer from flowers back to leaves is possible, it is likely rarer due to flowers' shorter lifespans.

Although leaves and flowers often host similar microbial species, it remains unclear whether the strains differ between these tissues. Future studies could use single-cell tracking or comparative genomics to trace microbial origins and adaptations to floral environments (Vannette 2020).

A specialized group of microorganisms thrives in floral environments, often reaching high abundances on flower tissues but rarely on leaves or other plant parts. Though these bacteria and fungi also appear in honey bee crops and stored pollen, they are typically scarce outside of flowers (Brysch-Herzberg 2004, Pozo et al. 2012). Their limited distribution beyond nectar strongly suggests ecological specialization. Additionally, they exhibit traits that may be adaptations to floral life, including rapid growth, efficient nutrient assimilation (Dhami et al. 2016), tolerance to osmotic stress (Herrera et al. 2010), and the ability to metabolize floral-specific compounds (Lachance et al. 2001, Pozo and Jacquemyn 2019). However, further comparative and experimental studies are needed to confirm which traits truly represent floral adaptations (Pozo et al. 2012).

Flowers are not sterile, even at early developmental stages. Microorganisms are nearly always present on some floral tissues, though their abundance and composition vary widely. Detection methods differ in their biases, but studies consistently identify three key patterns in floral microbiome origins (Vannette 2020, Ilyasov et al. 2024).

Firstly, it has been determined that bacteria and fungi manifest during the initial phases of floral development, in some cases even preceding the opening of buds (Shade et al. 2013, von Arx et al. 2019). Newly opened petals and nectar-containing apple blossoms often harbor culturable microorganisms, though detection rates can be low (8–35% at anthesis) (Pusey et al. 2009). Filamentous fungi and bacteria have also been found in grass ovaries (Hinton and Bacon 1985) and herbaceous plant pollen (Hodgson et al. 2014) during early floral development (Vannette 2020).

Second, microbial abundance in flowers often increases over time. Strong evidence comes from studies of nectar and pistil surfaces. For example, in the nocturnal plants *Datura wrightii* and *Agave palmeri,* bacterial and fungal colony-forming units (CFUs) in nectar were low before flowers opened but rose exponentially afterward (von Arx et al. 2019). Similarly, in *Mimulus aurantiacus*, yeast detection increased from 20% in one-day-old flowers to 60–80% in older flowers (Peay et al. 2011). Bacteria also became more frequent and abundant over time in *Epilobium canum* nectar (Morris et al. 2020) and on apple flower stigmas (Pusey et al. 2009). While most studies focus on nectar, data on pollen and petal microbiomes remain scarce. To confirm whether this trend applies broadly, future research should use quantitative methods like qPCR or microscopy (Vannette 2020, Ilyasov et al. 2024).

Third, pollinators shape the nectar microbiome. Although microorganisms can occur in unvisited flowers, insects are key vectors for microbial transmission. As early as 1884, Boutroux observed more fermentative yeasts in honey bee-visited flowers than in untouched ones. Recent studies confirm that ascomycetous yeasts thrive in pollinator-visited nectar but are absent when honey bees and other large pollinators are excluded (Belisle et al. 2012, Herrera et al. 2008, 2010). Some pollinators even disperse specific microorganisms - hummingbirds and large insects boost bacterial abundance in *Mimulus aurantiacus* and *Epilobium canum* (Vannette and Fukami 2017, Morris et al. 2020), while Nitidulid beetles spread large-spored yeasts (Lachance et al. 2001), and ants carry diverse bacteria and yeasts (de Vega and Herrera 2012, Samuni-Blank et al. 2014). Smaller insects, like thrips, may also play an overlooked role, as they harbor bacteria (*Rosenbergiella*, *Pantoea*) commonly found in flowers (von Arx et al. 2019) and pollen (Manirajan et al. 2016).

Insect-associated microorganisms commonly colonize flowers. These bacteria, fungi, and viruses - often isolated from insect digestive tracts (Corby-Harris et al. 2014), mouthparts (Belisle et al. 2012, Pozo et al. 2012), or nest environments (Brysch-Herzberg 2004, McFrederick et al. 2012, 2017) - can be beneficial, neutral, or pathogenic to pollinators and other floral visitors. Although they rarely reach high abundances on flowers (Lachance et al. 2001), they persist long enough on floral surfaces to transfer to new hosts. While pollinators can acquire pathogens from flowers, the role of floral transmission compared to other routes remains unclear (Vannette 2020).

Pollinators shape microbial communities across floral tissues. Though most research focuses on nectar-inhabiting microorganisms, floral visitors also influence microbial composition on petals, stigmas, pollen, and other structures. Bumble bees, for instance, deposit bacteria primarily on petals and stamens (Russell et al. 2019). Bee feces, rich in microorganisms, often contaminate inner and outer corollas, bracts, and nearby leaves, with deposition patterns depending on flower morphology and bee species (Figueroa et al. 2019). Insects also alter the pollen microbiome’s species composition (Manirajan et al. 2016, Vannette 2020, Ilyasov et al. 2024).

Tracking microbial life cycles remains challenging. Short rRNA gene regions used in sequencing often fail to distinguish between closely related species or strains, masking ecologically distinct taxa (Dhami et al. 2018). Additionally, detecting environmental microorganisms is complex, making presence/absence determinations difficult. Microbial lineages likely vary from animal- to plant-associated, both ecologically and evolutionarily. For example, *Lactobacillus* (McFrederick et al. 2012), *Acinetobacter*, and *Starmerella* yeasts (Lachance et al. 2001, Rosa et al. 2003) include species specialized for animals or flowers, yet the frequency of host shifts remains poorly understood (Vannette 2020).

Pollinator-mediated shaping of nectar and honey microbial communities

Nectar serves as a unique habitat for microorganisms, fostering interactions between fungi, bacteria, and the nectar's chemical environment. Studies on nectar microbiomes have primarily examined bacteria and fungi, the dominant components of these communities (Vannette 2020, Herrera et al. 2009, Fridman et al. 2012). The composition of these microbial communities varies significantly depending on pollinator type, suggesting that pollinators not only transfer pollen but also disperse microorganisms, shaping distinct nectar microbiomes (Belisle et al. 2012, Morris et al. 2020, Vannette 2020). Interactions between these microorganisms further influence species diversity, highlighting the complexity of these microecosystems (Vannette and Fukami 2017).

Microbial abundance in nectar increases over the flower's lifespan, reaching densities of up to 10^5 yeast cells and 10^7 bacterial cells per microliter (Herrera et al. 2009, Fridman et al. 2012). In temperate regions, nectar microbiomes typically exhibit low diversity, often dominated by a single yeast or bacterial species (Belisle et al. 2012, Pozo et al. 2011). This limited diversity likely results from dispersal constraints, competition, and harsh conditions like high osmotic pressure and low nitrogen availability (Peay et al. 2011, Vannette and Fukami 2014). In contrast, subtropical and tropical regions may support greater microbial diversity due to extended flower availability, higher plant diversity, and shorter flower lifespans that reduce competitive exclusion (Mittelbach et al. 2015, Canto et al. 2017).

Floral nectar hosts specialized microbial communities dominated by osmotolerant and low-nitrogen-adapted species. The most common are ascomycete yeasts, including *Metschnikowia* (e.g., *M. reukaufii* and *M. gruessii*), *Wickerhamiella*, *Starmerella*, and *Kodamaea*, as well as bacteria like *Acinetobacter* and *Rosenbergiella*. These microorganisms thrive under nectar's high osmotic pressure and nutrient scarcity, outcompeting less-adapted species (Lachance et al. 2018, Santos et al. 2018, Vannette 2020, Martin et al. 2022).

Pollinator activity shapes nectar microbial composition: flowers visited by insects favor ascomycetous yeasts, while isolated flowers show higher basidiomycetous yeast abundance (Lachance et al. 2001, Herrera et al. 2008, 2010, Belisle et al. 2012, Hietaranta et al. 2022). Filamentous fungi, by contrast, are rare in nectar (Taniwaki et al. 2015). Although non-specialized microorganisms from soil, water, or plant surfaces occasionally enter nectar, they typically persist at low levels due to poor stress tolerance (de Vega and Herrera 2012, Martin et al. 2022, Ilyasov et al. 2024).

Microorganisms in floral nectar compete for resources, often excluding each other through niche preemption or modification (Fukami 2015). Bees ingest these nectar-dwelling bacteria, which then colonize their gut and influence the microbial diversity of their colonies - sometimes beneficially, sometimes harmfully (Anderson et al. 2013). Many of these microorganisms produce antibiotics, suppressing pathogens in nectar, stored food, or honey bee gut (McCormack et al. 1994, Parret and De Mot, 2002, Pozo et al. 2020). For instance, bacteria like *Lactobacillus kunkeei* - found in nectar and honey - can inhibit honey bee pathogens such as *Paenibacillus larvae* and *Nosema ceranae* (Arredondo et al. 2018, Nowak et al. 2021).

The honey bee gut microbiome also metabolizes nectar and pollen, producing lactic, acetic, and citric acids, which support energy metabolism, and suppress pathogens (Ricigliano and Anderson 2020). When honey bees eat pollen-deficient diets, their microbiome diversity declines, reducing organic acid production and weakening immunity. However, supplementing their diet with lactic acid can restore some resistance to infections (Ricigliano and Anderson 2020).

Species of *Lactobacillus*, the dominant genus in honey bee gut microbiota (Romanovich et al. 2020), drive carbohydrate fermentation, producing lactic acid that energizes honey bees and suppresses pathogenic *Enterobacteriaceae* by acidifying the gut environment (Ricigliano and Anderson 2020). Deficiencies in these organic acids are linked to impaired foraging behavior, including reduced activity and social interactions in hives (Ricigliano and Anderson 2020).

Although floral nectar is often dominated by single microbial species (Peay et al. 2011, Belisle et al. 2012, Vannette and Fukami 2014, Tucker and Fukami 2014), diverse microorganisms frequently co-occur (de Vega et al. 2021). For example, *Metschnikowia* yeasts and *Acinetobacter* bacteria exhibit positive associations, likely due to niche partitioning: *Metschnikowia* ferments glucose, while *Acinetobacter* metabolizes fructose (Álvarez-Pérez and Herrera 2013). Such interactions suggest microbial communities may have additive or synergistic effects on nectar chemistry and pollinator health. Indeed, yeast-bacteria consortia can enhance nectar aroma, boosting visits by honey bees and hoverflies (Golda et al. 2021), though their impact on bumble bee colony growth remains no greater than that of single species (Pozo et al. 2021).

The honey bee gut microbiome is largely derived from microorganisms in plant nectar, primarily bacteria and yeasts. Studies show that honey's microbial composition varies by geographic location, floral source, and storage conditions (Brudzynski 2021). Common bacterial genera include *Lactobacillus*, *Bifidobacterium*, *Gluconobacter*, and *Asaia*, which can function as beneficial symbionts or potential pathogens depending on their abundance and environmental context (Brudzynski 2021). For instance, *Lactobacillus* and *Bifidobacterium* exhibit probiotic properties and help protect honey bees from pathogens (Vásquez et al. 2012, Ilyasov et al. 2024).

Lactobacillus spp., a well-studied group of lactic acid bacteria in honey, play a key role in fermentation and preservation. They produce antimicrobial compounds such as hydrogen peroxide, bacteriocins, and organic acids like lactic acid. By lowering pH, lactic acid creates an inhospitable environment for pathogens, while hydrogen peroxide broadly inhibits bacterial growth. Certain *Lactobacillus* strains also secrete bacteriocins - peptide-based antimicrobials - such as nisin, which targets pathogens like *Listeria* (Brudzynski 2021).

Bifidobacteria (*Bifidobacterium spp.*), beneficial microorganisms found in honey, exhibit probiotic properties and produce antimicrobial compounds such as acetic acid, lactic acid, and bacteriocins. These substances inhibit pathogens by lowering environmental pH and directly targeting harmful bacteria like *Escherichia coli* and *Salmonella* (Brudzynski 2021).

Acetic acid bacteria (*Gluconobacter* and *Asaia*), also present in honey, contribute to its antimicrobial activity by producing organic acids that suppress pathogen growth. Their antibacterial effects are particularly strong against Gram-negative bacteria (Crotti et al. 2010).

Certain *Bacillus* species in honey generate antimicrobial peptides like bacitracin, which effectively target Gram-positive bacteria, including *Staphylococcus* and *Streptococcus* (Brudzynski 2021).

Yeasts such as *Metschnikowia reukaufii* may not always produce antimicrobials, but some species secrete ethanol and volatile organic compounds (VOCs) that inhibit microbial growth. Additionally, certain yeasts generate acetic and lactic acids, further enhancing honey's protective effects (Good et al. 2014). Although fungi like *Penicillium* are typically linked to honey spoilage, some species produce antibiotics such as penicillin, which combat Gram-positive bacteria (Brudzynski 2021).

Nectar microbiome dynamics and their functional consequences for pollination

Microorganisms in nectar significantly alter its chemical composition, thereby shaping plant-pollinator interactions. Through metabolic activity, they consume sugars - reducing overall sugar concentration - and convert sucrose into glucose and fructose (de Vega et al. 2009, Herrera et al. 2008, Canto et al. 2008, Vannette and Fukami 2017). Additionally, they modify amino acid levels and other nectar components, with effects varying by microbial species (Lenaerts et al. 2017, Rering et al. 2017).

Specialized bacteria such as *Neokomagataea*, *Rosenbergiella nectarea*, and *Acinetobacter spp.* exhibit metabolic effects similar to the yeast *Metschnikowia reukaufii*, reducing sucrose while increasing glucose and fructose (Lenaerts et al. 2017, Rering et al. 2017, Álvarez-Pérez et al. 2021, Kim et al. 2014). *Acinetobacter* species (e.g., *A. nectaris*, *A. boissieri*) preferentially consume fructose and nitrogenous yeast byproducts like ammonia, often co-occurring with yeasts (Álvarez-Pérez and Herrera 2013). While *R. nectarea* and *Acinetobacter* decrease amino acid concentrations, *Neokomagataea* increases them (Martin et al. 2022). These shifts in sugar and amino acid profiles may directly affect pollinator nutrition (Álvarez-Pérez et al. 2021).

It has been demonstrated that generalist bacteria, including *Lactococcus garvieae*, *Apilactobacillus kunkeei* (Zheng et al. 2020), *Erwinia tasmaniensis*, and *Asaia spp.*, also have an influence on the chemistry of nectar (Zheng et al. 2020). *E. tasmaniensis* does not alter sugar or amino acid levels but lowers nectar pH (Martin et al. 2022). In contrast, acetic acid bacteria (*Asaia platycodi*, *A. astilbes*) reduce sucrose and amino acids while increasing monosaccharides and acidity via acetic acid production (Lenaerts et al. 2017). The lactic acid bacterium *L. garvieae* leaves sugar levels unchanged but raises amino acid concentration and decreases pH through lactic acid secretion (Lenaerts et al. 2017).

Fungi play a key role in shaping nectar chemistry. For example, the black yeast *Aureobasidium pullulans* decreases sucrose concentration and metabolizes fructose, while the yeast *Sporobolomyces roseus* increases amino acid content (Sobhy et al. 2018). Similarly, *Hanseniaspora uvarum* alters the emission of volatile organic compounds (VOCs) (Sobhy et al. 2018). All three of these fungi also lower nectar pH (Sobhy et al. 2018, Ilyasov et al. 2024). Another common nectar yeast, *Metschnikowia*, reduces sucrose and glucose levels while increasing fructose proportions (Herrera et al. 2008, Canto et al. 2015, Pozo et al. 2020). It also produces VOCs (Sobhy et al. 2018) and lowers nectar pH (Vannette et al. 2013, Tucker and Fukami 2014). Additionally, *Metschnikowia reukaufii* depletes amino acids in nectar (Dhami et al. 2016).

It has been demonstrated that specialized nectar microorganisms modify nectar's nutritional properties by consuming sugars, thereby shifting their ratios and acidifying the nectar (Vannette et al. 2013, Tucker and Fukami 2014, Lenaerts et al. 2017, Pozo et al. 2020). They can also metabolize, modify, or synthesize amino acids and secondary metabolites, altering nectar's taste and aroma (Herrera et al. 2013, Schaeffer et al. 2017).

These microorganisms also release VOCs that influence nectar attractiveness. Some bacteria and fungi on flowers produce VOCs that blend with floral scents or break down plant volatiles (Farré-Armengol et al. 2016), ultimately affecting pollinator behavior (Schaeffer et al. 2019). Certain microorganisms - and even plants - produce compounds that repel insects, such as toluenediisocyanate. For instance, *Asaia astilbes* and *Neokomagataea sp.* emit 2,5-dimethylfuran, a potential deterrent (Schaeffer et al. 2019).

Nectar-inhabiting microorganisms, particularly yeasts and bacteria, can alter nectar chemistry and influence pollinator nutrition and foraging behavior. While some microorganisms reduce sugar concentrations, potentially creating competition between microorganisms and pollinators (Herrera et al. 2008), bumble bees often prefer yeast-colonized nectar (Schaeffer and Irwin 2014, Herrera et al. 2013, Yang et al. 2019). This preference may arise from changes in scent and taste, as the yeast *Metschnikowia reukaufii* produces attractive fruity and floral esters (Golonka et al. 2014).

Pollinators rely on visual, olfactory, and gustatory cues to find food, so microbial changes in nectar directly affect their choices. Both bumble bees and honey bees detect and respond to volatile organic compounds (VOCs) emitted by nectar microorganisms. For example, naive bumble bees (*Bombus impatiens* and *Bombus terrestris*) use *M. reukaufii* VOCs to locate nectar (Herrera et al. 2013, Schaeffer et al. 2017) and consume more yeast-infected nectar than sterile nectar (Herrera et al. 2013, Schaeffer et al. 2017). In contrast, their responses to bacteria are often neutral or negative (Good et al. 2014, Junker et al. 2014). Interestingly, while *B. impatiens* is attracted to odors from the bacterium *A. astilbes*, it still consumes more nectar infected with *M. reukaufii* (Schaeffer et al. 2017).

Bees are highly sensitive to changes in sugar composition and concentration. For example, low sugar levels reduce foraging activity in honey bees (Oldroyd et al. 1991, Seeley et al. 2000, Brunner et al. 2014, Stabler et al. 2015, Grund-Mueller et al. 2020). Bumble bees, in particular, prefer sucrose (Mommaerts et al. 2013, Gegear and Thomson, 2004), and immune-challenged workers consume 7.5% more sugars (Dolezal and Toth 2018). Nutrient scarcity can also weaken honey bee immune responses (Brunner et al. 2014, Stabler et al. 2015, Grund-Mueller et al. 2020).

Microorganisms in nectar can change its chemistry, affecting honey bee feeding behavior. Honey bees avoid nectar contaminated with *Asaia astilbes*, *Erwinia tasmaniensis*, and *Lactobacillus kunkeei* but show no aversion to *Metschnikowia reukaufii* (Good et al. 2014). Some bacteria, like *Asaia astilbes*, lower nectar pH while increasing glucose and fructose levels (Good et al. 2014). These chemical changes - rather than the microorganisms themselves - primarily drive honey bee preferences (Brudzynski 2021).

Microorganisms in nectar can increase hydrogen peroxide levels, potentially benefiting honey bee health (reducing pathogenic microorganisms and shaping their normal microbiome) (Vannette et al. 2013, Rothman et al. 2020). Some microorganisms can inhibit pathogens like *Crithidia bombi* in bumble bees (Richardson et al. 2015, Palmer-Young et al. 2019, Folly et al. 2020).

Changes in nectar composition influence adult honey bees, queen egg-laying, and brood health (Steffan et al. 2019). In honey bees and bumble bees, nutrition affects ovary development and egg production (Fine et al. 2018, Lin and Winston 1998). While nectar colonized by *M. reukaufii* does not alter worker bumble bee egg production (Schaeffer et al. 2017), nectar containing bacteria like *P. coronafaciens*, *A. nectaris*, and *R. nectarea* boosts oviposition and brood quantity in bumble bees (Pozo et al. 2021). Overall, microbial effects on bumble bee colony development vary from neutral to positive (Martin et al. 2022).

Specific yeasts and bacteria in nectar can shape bumble bee (*B. terrestris*) development (Pozo et al. 2020, Pozo et al. 2021). Two of five studied yeast species increased worker numbers, likely by enriching nectar micronutrients (Pozo et al. 2020). Each yeast species also produced distinct fructooligosaccharides - compounds with prebiotic properties (Peshev and Van den Ende 2014).

Nectar composition influences the bacterial community structure in honey bee gut. High sugar concentrations and larger nectar volumes increase flower visitation rates (Mallinger and Prasifka 2017). Honey bees fed sucrose-rich nectar develop more diverse midgut communities, whereas those consuming glucose- or fructose-rich nectar show greater hindgut diversity (Wang et al. 2020). Since honey bee gut microbiome affects host health (Hammer et al. 2021, Lee et al. 2015, Zheng et al. 2019, Martin et al. 2022).

Microorganisms also alter the nutritional value of pollen in nectar. For example, *Metschnikowia reukaufii* clusters around pollen grains, consuming their nutrients (Herrera 2017, Pozo and Jacquemyn 2019) and causing pollen rupture (Eisikowitch et al. 1990). Similarly, *Acinetobacter spp.* trigger pollen germination and rupture in *Eschscholzia californica* (Christensen et al. 2021). Some microorganisms degrade pollen quality - the pathogen *Microbotryum violaceum* replaces pollen with spores, disrupting plant reproduction (Alexander and Antonovics 1988). Non-pathogenic fungi and bacteria colonize pollen surfaces, reducing viability, as seen in *Asclepias syriaca* (Eisikowitch et al. 1990), and limiting nutrient availability for pollinators (Roulston and Cane 2000). However, some honey bee-associated bacteria aid digestion by producing pectinases that break down pollen (Engel et al. 2012, Vuong and McFrederick 2019).

Floral microorganisms also modify nectar, pollen, and floral traits that attract pollinators. Pathogens like *Microbotryum violaceum* lower nectar volume and sugar content (Biere and Honders 2006), while *Fusarium verticillioides* extends flowering in *Moussonia deppeana*, prolonging nectar availability (Lara and Ornelas, 2003).

Microorganisms can significantly alter nectar chemistry and properties, as demonstrated in laboratory studies (Vannette et al. 2013, Lenaerts et al. 2017, Vannette and Fukami, 2018). For example, flowers inoculated with *Neokomagataea anthophila* and *Gluconobacter sp.* produced less nectar, likely due to accelerated senescence (Vannette and Fukami, 2018). However, differences between laboratory and field results suggest that host plants may regulate microbial effects on nectar chemistry (Vannette et al. 2013).

Yeast and bacteria form complex microbial communities in nectar through aggregation, biofilm formation, nutrient competition, antagonism, signaling, and horizontal gene transfer (Álvarez-Pérez et al. 2013, Tucker and Fukami 2014, Álvarez-Pérez et al. 2019). Their co-occurrence is often negatively correlated, pointing to competitive interactions like antibiosis (Álvarez-Pérez et al. 2019). While these mechanisms explain some microbial patterns, they do not fully account for global variations in community composition (de Vega et al. 2021, Ilyasov et al. 2024).

Nectar chemistry - including sugars, amino acids, proteins, and alkaloids - plays a significant role in shaping these communities (Nicolson and Thornburg 2007). High osmotic pressure restricts colonization to osmotolerant species (Álvarez-Pérez et al. 2012, Lenaerts et al. 2014, Morris et al. 2020), favoring specific yeasts and bacteria (Adler 2000, Adler et al. 2020, Carter and Thornburg 2004). Yet, nectar chemistry alone does not fully explain microbial diversity (de Vega et al. 2021).

The sugar ratio in nectar, influenced by both plants and microorganisms, can affect pollinator attraction (Colda et al. 2021). Nectar composition often aligns with pollination strategies (Baker and Baker 1983, 1990), but even plants visited by the same pollinators show substantial chemical variation (Barnes et al. 1995, Brown et al. 2010). While sugars contribute to microbial differences, they are not the sole factor (Johnson 2000, Nicolson and Thornburg 2007). Plant-derived antimicrobial compounds may be more decisive in structuring these communities

(Buwa and Van Staden 2006, Aremu and Van Staden 2013, Amoo et al. 2014).

Floral volatile organic compounds (VOCs) can influence microbial growth, but their effects vary. For example, (E)-β-caryophyllene in *Arabidopsis thaliana* suppresses the pathogenic bacterium *Pseudomonas syringae* (Huang et al. 2012), while phenylacetonitrile and linalool have species-specific effects on bacteria (Hua et al. 2014, Junker et al. 2014, Burdon et al. 2018).

Plant secondary metabolites, such as flavonoids and alkaloids, may help structure floral microbial communities by deterring pathogens (Adler 2000, Rivest and Forrest 2019). In *Calluna vulgaris* (heather), the nectar compound callunene inhibits the bumble bee parasite *Crithidia bombi* at natural concentrations, suggesting that other metabolites with similar antimicrobial roles may exist (Koch et al. 2019). However, not all secondary metabolites necessarily evolve for microbial defense, as experimental evidence sometimes contradicts this hypothesis (Fridman et al. 2012, Pozo et al. 2012, Vannette and Fukami 2017).

Floral traits like high nectar osmolarity, antimicrobial-like proteins, elevated oxygen levels, and reactive oxygen species further restrict microbial growth (Herrera et al. 2010, Schmitt et al. 2018), making nectar inhospitable to certain pathogens (Carter et al. 1999, Schmitt et al. 2018). Their precise role in shaping microbial communities remains an important area for future research.

Plants employ induced defense mechanisms to regulate floral microbial communities. For example, pepper flowers respond to *Xanthomonas campestris* infection by producing antimicrobial enzymes faster than leaves (O'Garro and Charlemange 1994). Similarly, apple trees rely on pathogen-defense genes to resist *Erwinia amylovora* (Khan et al. 2012). While plants appear to actively manage floral microbiomes, it is unclear whether these responses target only pathogens or more general microbial regulation (Vannette 2020).

Nectar's antimicrobial compounds shape microbial communities by restricting survival and growth. Certain plants produce substances that specifically inhibit bacteria or yeasts (Ncube et al. 2015), though the full extent of these effects requires further study (de Vega et al. 2021).

Geographic factors influence nectar microbial communities, but plant-pollinator interactions have stronger effects. Nectar microbiomes show greater similarity among plants visited by the same pollinator group across different regions than among co-located plants with different pollinators (de Vega et al. 2021). Yeast communities demonstrate phylogenetic patterns tied to geography, reflecting historical dispersal (Lachance et al. 2005, de Vega et al. 2014), while some insect-associated yeasts show restricted distributions matching their host insects' ranges (de Vega et al. 2021).

Conclusion

Plants, pollinators, and microorganisms form a complex web of interactions, with microorganisms playing a crucial role in shaping these relationships in surprising ways. This review focuses on how nectar-feeding yeasts and bacteria influence the chemistry and physical properties of nectar, affecting pollinator behavior and plant reproduction.

Microorganisms can modify nectar's chemical composition and physical characteristics, making it more or less attractive to pollinators. For example, *Metschnikowia* yeast strains produce fruity esters that attract bumble bees, while bacteria such as *Asaia astilbes* sour nectar and repulse honey bees. These microorganisms demonstrate their ability to guide pollinator foraging decisions.

These interactions are bidirectional. Pollinators transfer microorganisms from one flower to another, but the microorganisms that they carry affect their health and nutrition. Bee gut bacteria, such as *Lactobacillus* and *Bifidobacterium*, help with digestion, boost immunity, and combat pathogens, creating a cycle in which pollinators influence the microbial composition of nectar, which then affects their own well-being.

This interaction reveals microorganisms as crucial players in plant-pollinator relationships, amplifying or moderating benefits for both parties. Geography and ecology add complexity to this system. Flowers in tropical regions, which bloom year-round, have richer microbial communities compared to those in temperate regions. The type of pollinator also matters - hummingbird-pollinated flowers carry different microorganisms than those visited by bees, demonstrating how pollinator behaviors shape the microbial profile of nectar.

Microorganisms play an important role in pollination, but they do more than just guide the process. They can alter nectar in ways that can either benefit or harm plants by attracting or draining nutrients, respectively. Some plants have developed defenses, like callunene in heather nectar, to fight off microorganisms and maintain their success. Pollinators also benefit from warmer flowers, thanks to yeast-produced heat, and protection against bumble bee pathogens, such as *Crithidia bombi.*

Despite these interactions, there are still many gaps in our understanding of how microorganisms, plants, and pollinators interact. Future research should combine tools such as gene sequencing, chemical analysis, and behavioral tests to better understand the roles of microorganisms in various ecosystems. Additionally, we know little about the effects of pesticides and habitat loss on these intricate relationships.

In short, microorganisms play an active role in shaping plant-pollinator interactions by adjusting nectar composition, supporting pollinator health, and helping them adapt to environmental changes. As the decline of pollinators threatens ecosystems and agricultural production, understanding the role of microorganisms could lead to innovative solutions such as bee probiotics and microbiome-enhanced pollination. By recognizing these tiny actors, we can appreciate the complexity of nature's interconnected systems and the need for broader efforts to protect them.

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