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Microbes and pollinator behavior in the floral marketplace

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Pollinator foraging decisions shape microbial dispersal, and microbes change floral phenotypes in ways perceivable by pollinators. Yet, the role microbes play in the cognitive ecology of pollination is relatively unexplored. Reviewing recent literature on floral microbial ecology and pollinator behavior, we advocate for further integration between these two fields. Insights into pollinator learning, memory, and decision-making can help explain their responses to microbially-altered floral phenotypes. Specifically, considering how pollinators forage for multiple nutrients, cope with uncertainty, structure foraging bouts, and move through their environment could inform predictions about microbial dispersal within plant communities. We highlight how behavior connects microbial changes in floral phenotype to downstream effects on both microbial dispersal and plant fitness.

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Introduction

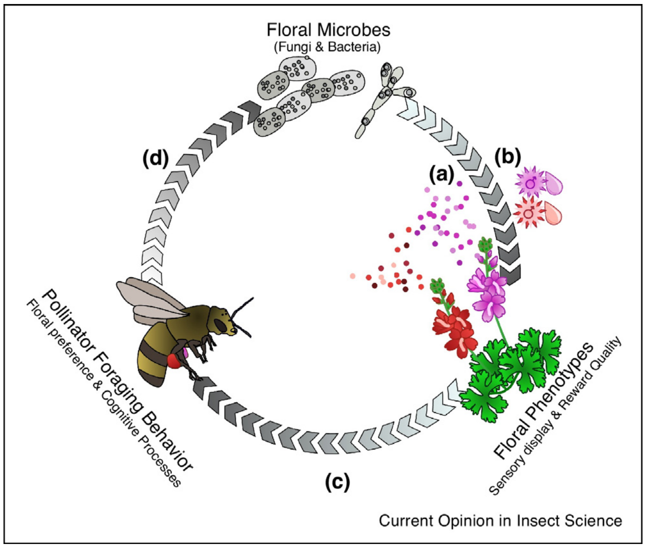
Pollinator cognition plays a key role in the outcome of plant–pollinator interactions [1]. Over a century of research has shown that how pollinators process, learn, and remember information about floral displays [2] is affected by the properties of the rewards (usually nectar and/or pollen) they collect (e.g. [3]). Further, some floral visitors can sense very fine differences in floral traits such as scent or color and learn to associate them with floral rewards (e.g. [4]). In turn, pollinator foraging decisions can scale up to impact plant reproduction by altering the frequency or probability of pollen transfer [5]. Although insights from this long-studied dyad help explain patterns of floral evolution and aspects of pollinator cognition, these interactions involve many more organisms than simply plants and the animals they rely on for reproduction [6••].

For example, flowers have an ecologically important microbiome: bacteria and fungi colonize nectar, pollen and other floral structures [6••,7,8]. These microbes can alter components of floral signals and rewards (Figure 1a, b), raising the question of how microbially-driven changes in floral phenotypes shape pollinator decision-making (Figure 1c). Any shifts in pollinator foraging behavior could have important consequences (Figure 1d) for flower-inhabiting microbes that are primarily pollinator-dispersed (though not all flower-inhabiting microbes are dispersed by pollinators [6••]) as well as, potentially, plant reproduction (Figure 2) [9,10]. Here we share insights from research on pollinator cognition (perception, learning, memory, and decision-making [11]) that could help predict (1) how pollinators respond to microbe-induced shifts in floral signals and rewards (Figure 1c), and (2) how microbial dispersal and colonization within a plant community may be shaped by pollinator behavior (Figure 1d). Although microbial presence can be relevant to interactions with a wide range of other pollinator taxa (including flies, moths, and bats [12]) we focus largely on those whose cognition has received the most attention, namely generalist bees (*Bombus*, *Apis*) and hummingbirds. We argue that a synthesis across the disparate fields of microbial and cognitive ecology has the potential to explain aspects of both microbial community assembly and pollinator foraging dynamics.

Microbes affect floral traits pollinators use to make foraging decisions

Microbes can alter nearly every aspect of nectar chemistry relevant to pollinators (Figure 1a). In addition to changing nectar sugar composition, microbes can also impact nectar secondary metabolites and amino acids [13] which pollinators assess [14,15••]. Any change to nectar's perceived quality can shape how well pollinators learn and remember floral information [16]; likewise, consumption of chemicals produced or modified by nectar microbes (e.g. secondary metabolites, ethanol) could have their own modulating effects on cognition [17].

Figure 1



Conceptual diagram illustrating the critical role that pollinator cognition plays in shaping plant–pollinator–microbe interactions. Microbes can change floral phenotypes in many ways including (**a**) display and (**b**) reward quality. These changes drive important shifts in (**c**) pollinator decision-making, which could impact (**d**) dispersal of microbes and possibly plant fitness.

Pollen harbors its own unique microbial community which has been the subject of recent study for its potential downstream effects on bee fitness [8,18,19]. Although the macronutrients sought by pollinators are mostly found within the pollen wall (intine), pollen is surrounded by a chemically diverse substance, pollenkitt [20]. Pollenkitt is partially volatile and may be a suitable substrate for microbial growth but may also contain secondary metabolites and fatty acids that protect pollen from some microbes [21]. Foraging bumblebees may assess pollenkitt chemistry, and can discriminate between flowers based on pollen alone [22]. However, the extent to which pollen microbes alter pollen surface chemistry remains an open question.

Beyond inhabiting pollen and nectar, microbes can also be found on nearly every other floral structure [6••,7,23], where they can alter floral signaling [24••]. Pollinators respond to many aspects of floral displays, including visual, olfactory, gustatory, and tactile stimuli [25,26]. Microbes potentially influence multiple signaling modalities [23], yet most work has focused on the scent of floral rewards [27–29].

Microbes shape pollinator behavior and possibly their own dispersal

Most work involving pollinator responses to floral microbes involves preference assays, which have been crucial to our understanding of pollinator–microbe–plant interactions [15••,27]. Beyond measuring preference, expanding the questions microbial ecologists ask about pollinator behavior could create new opportunities to predict how pollinators respond to microbially-altered floral phenotypes [24••]. For example, recent work shows that even subtle aspects of pollinator flower handling behaviors can scale up to shape microbial dispersal [10]. Likewise, pollinators are capable of distinguishing the complex relationships between floral stimuli and resources relevant to microbial ecologists [15••]: amidst a suite of potentially useful floral information, bees for example can learn to rely upon the single component of floral scent that most accurately predicts nectar quality [30]. Here we highlight four specific areas of possible further productive integration between behavioral and microbial perspectives.

Reward complexity

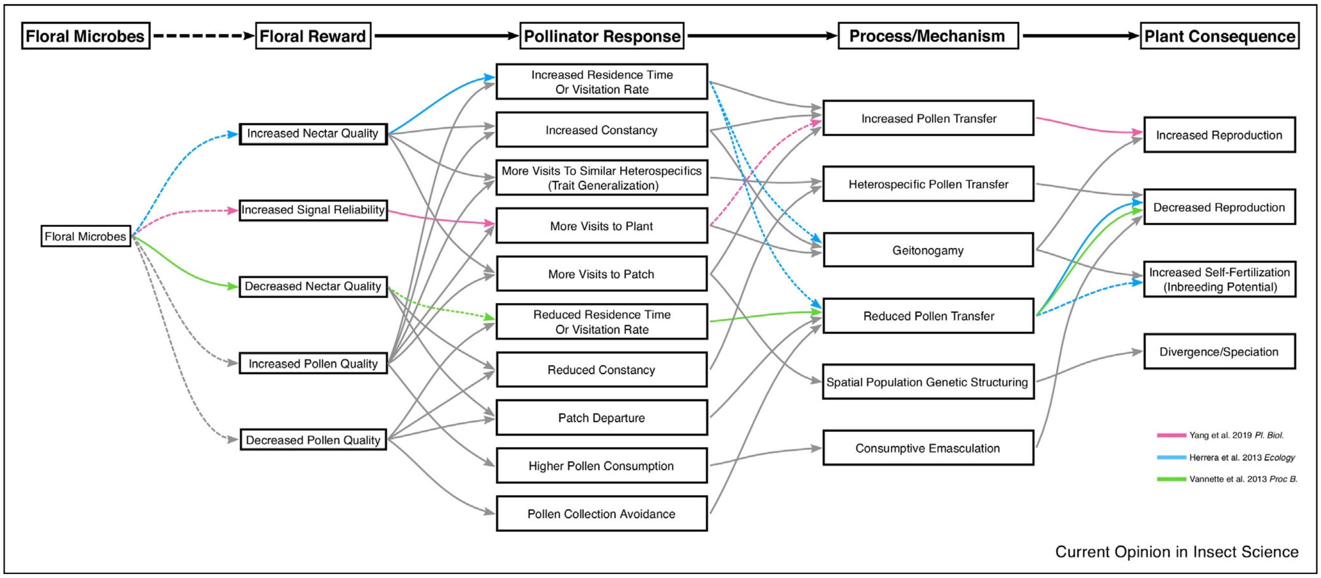
Most research on pollinator foraging behavior (in microbial and non-microbial contexts) measures responses to a single aspect of reward composition (e.g. sugar content *or* secondary metabolite concentration). However, floral rewards are chemically complex, and pollinator nutritional needs are multidimensional [31]. Although pollinator responses to reward complexity are not monolithic, it is increasingly recognized that pollinators trade-off multiple axes of reward variation when making foraging decisions. For example, bees' response to nectar alkaloids depends on sugar content [32], and likewise, their response to pollenkitt alkaloids and fatty acids may depend on the presence and concentration of nectar [33,34]. These insights highlight the utility of considering a flower's entire reward phenotype when trying to predict how pollinators might respond to microbial changes in a single resource (e.g. nectar). For example, microbial shifts in nectar chemistry should also impact bees' pollen foraging [35], with possible downstream impacts on plant fitness (Figure 2). From the microbial dispersal perspective, bees predictably forage on plants with particular ratios of protein:lipids in their pollen [31] which suggests that nutritionally similar plants might share communities of pollinator-dispersed microbes. Testing this prediction would require researchers to consider and characterize more than one aspect of reward composition.

Signals and uncertainty

Pollinators forage amidst environmental and floral variability that can make detection of and discrimination among flowers a challenge. Microbial third parties are often studied for their ability to alter a given component of a floral display (e.g. scent) with concomitant changes in pollinator preference. More broadly, microbial alteration of the floral display has the potential to enhance or impair foragers' ability to distinguish it from background stimuli or from other co-flowering plant species.

One approach used to study how pollinators make decisions about flowers under conditions of uncertainty is

Figure 2



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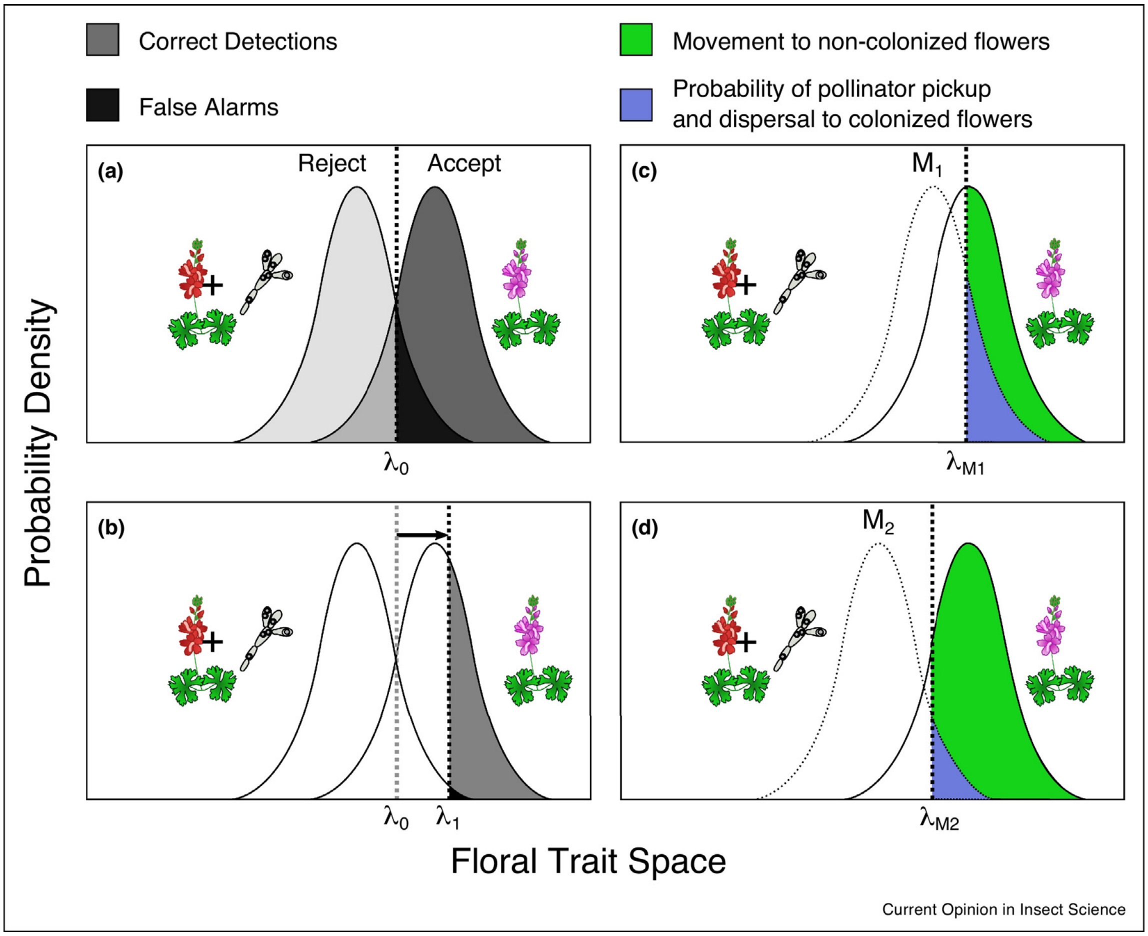
Floral microbes alter floral traits, which may in turn affect plant reproduction and population structure via changes in pollinator behavior. Here, we visualize pathways by which microbially-altered floral reward quality could impact plants. Listed below each component of the process (bold text, top) are non-exhaustive examples. To illustrate the complexity of this endeavor, links between some components (solid gray arrows) are well-described in pollination ecology literature; however, how they function in the context of floral microbes (dashed gray arrows) is largely unexplored, particularly with regard to pollen rewards. Colored pathways represent examples where this process has been investigated. Solid arrows represent published results, while dashed arrows represent linkages inferred from the data. Blue pathway: In Herrera *et al*. [52], nectar yeasts promoted higher bumble bee visitation to *Helleborus foetidus* (Ranunculaceae); however, this did not translate into increased pollen transfer. Instead, pollen transfer and fruit production were reduced, presumably because of high self-fertilization. Pink pathway: By contrast, Yang *et al*. [29] found increased fruit production in *Clematis akebioides* (Ranunculaceae), the result of increased visitation by bumble bees, presumably in response to an increase in sugar and amino acid content in the nectar. Green pathway: Vannette *et al*. [53] found that nectar bacteria, on the other hand, reduced pH and sugar content in *Mimulus aurantiacus* (Phrymaceae), which deterred hummingbird pollinators and reduced seed set.

Signal Detection Theory (SDT, Figure 3a , [36•]). This framework could be used to ask pollinators whether colonization by scent-producing microbes makes different flowers as a whole seem more or less similar (Figure 3b); it also might be used to explain why, despite evidence of strong preferences in relation to floral traits altered by microbes [15••], pollinators will inevitably make certain kinds of errors (e.g. 'incorrectly' visiting a flower with poor rewards or bypassing high quality floral resources). Signal Detection Theory could also be used to take a 'microbe's eye view' on how pollinators' tolerance for different error types might influence spread among co-flowering plants (Figure 3c,d).

Further, pollinators use multimodal floral signals to help cope with uncertainty when making decisions about which flowers to visit [37]. Some of this work shows that when environmental noise obscures floral stimuli in a given modality (e.g. wind affecting scent), foraging bees shift to rely on information in an unaffected modality (e.g. relying on color over scent when wind increases) [38]. Microbes might increase olfactory noise in a number of ways: making different flower types smell more similar than they would otherwise, masking floral scents that otherwise usefully indicate resource quality, or increasing variation in floral headspace within a species making it harder to learn that a given floral scent predicts reward. If microbial influence on floral phenotypes is largely restricted to the olfactory modality, we might expect bees challenged by too noisy a decision context when using scent alone to increase their reliance on stimuli in other modalities, such as vision. More generally, the literature on pollinators' use of multimodal floral stimuli suggests that, as with many behavioral experiments, there is a difference between what an animal *can* do (e.g. when responding to olfactory stimuli in a behavioral assay) and what it *actually* does when confronted with more sensorially complex floral displays. Thus, care should be taken extrapolating the findings of unimodal experiments (e.g. those which only assay pollinator behavior in relation to microbial or floral stimuli in a single sensory modality) to real-world, or even free-flying, foraging scenarios. Could knowledge about how pollinators use multimodal floral signals have implications for microbial dispersal? Research on discrimination learning in bumblebees suggests that one effect of the mere presence of microbial scent cues, even if they do not differ across floral options, could be an enhancement of certainty about floral color [37]. This could limit microbial

Figure 3



Microbial changes to floral displays present a problem that can be modeled in a Signal Detection Theory (SDT) framework. (**a**) Two flower types (either co-occurring species or conspecifics colonized vs. uncolonized by microbes) share partially overlapping distributions of sensory characteristics (e.g. hue, headspace) but vary in reward quality. Pollinators use a threshold decision rule to either land on (accept) or bypass (reject) flowers that fall to one side of the threshold (λ_0). If microbe-colonized flowers are of lower quality, four decision outcomes are possible, with relative probabilities represented by shading: correct rejections (light gray), missed detections (gray), correct detections (dark gray), and false alarms (black). (**b**) SDT offers a tool to ask pollinators how similar they find floral displays: when bees are uncertain in discriminating flowers and false alarms are costly, they show conservative shifts in preference away from aversive flowers (λ_0 shifts to λ_1). The magnitude of this shift gives an estimate of uncertainty about floral identity: for example, bees show stronger shifts when less certain about the identity of flower types [37]. The optimal location of a decision threshold can be predicted by a number of parameters including the relative payoffs associated with each flower type, the frequency of each type, and signal variation [54]. Using this paradigm, scientists could assess the similarity of microbe-colonized versus uncolonized plants' floral displays, or estimate how aversive microbe-colonized rewards are. **(c)**/**(d)**: SDT could also be used to predict the degree of change to a floral display that would benefit microbial dispersal under different circumstances. Microbes that change the sensory display of flowers and decrease nectar quality [53] may face a tradeoff between being picked up by a pollinator and being dispersed to suitable, non-colonized flowers. In SDT terms, a false alarm (a visit to a colonized flower, blue region) is required to pick up microbes, but subsequently risks bringing them to an already-colonized flower where they face competition. Alternatively, a correct detection (visit to a non-colonized flower, green region) disperses microbes to suitable (and competitor-free) habitat ([55•] offers a relevant case study). If a given microbe does not change the floral display very much (**c**; M_1) they have a high likelihood of being picked up, but also a high probability of being dispersed to a flower that is already colonized. Alternatively, if a microbe makes a floral display easily discriminable (**d**; M_2) their odds of being picked up by pollinators are lower, but the probability of reaching a non-colonized flower increases.

exchange across visually similar co-flowering plant species that differ in reward value.

Constancy

Floral constancy is the phenomenon whereby pollinators visit a single species or morph of a flower repeatedly, bypassing co-flowering options [39,40]. Rather than being all-or-nothing, a pollinator's constancy reflects the task at hand: both properties of floral rewards and displays can increase or decrease constancy. For example, bumblebees become more constant when floral options differ in an increasing number of display elements and handling requirements [41]. Correspondingly, microbial shifts in scent that alter the similarity of floral options should have predictable effects on constancy (independent of any effects on pollinator preference). A key insight from research into the cognitive basis of constancy is that a pollinator may avoid visiting a flower not because it is repelled by a microbial scent present on some (but not all) individuals within a community, but simply because the flower possesses a scent that is *different*.

Individual-level floral specialization associated with constancy characterizes many plant–pollinator networks [42], and the details of these behavioral patterns could impact microbial dispersal. For example, theoretical models of pollinator pathogens suggest that individual-level specialization can increase microbial pathogen prevalence in multi-species plant–pollinator–microbe systems [43••]. In the context of beneficial or commensal microbes, one testable prediction from this model is that the prevalence of a focal microbe should be highest when individual pollinator preferences last longer than half the lifetime of microbes on pollinators. This is because pollinators and the plants they temporarily specialize on might act as variable sources and sinks for microbial persistence. Intriguingly, because pollinators' floral constancy is sensitive to floral traits, constancy offers a mechanism by which microbes could influence their own dispersal destination: if microbial alterations to a floral trait increase constancy, microbes would be moved more frequently between flowers of a given type. Alternatively, microbes could alter floral traits in a way that disrupts floral constancy to maximize their own prevalence across different members of a plant community.

Spatial cognition

Members of key taxa studied for their role in microbial dispersal (bees and hummingbirds) do not move randomly through space [44]. Instead, they learn foraging routines and employ specific and often idiosyncratic movement rules that could both be influenced by microbial presence and help explain patterns of microbial community structure. For example, bees fly farther after experiencing low-quality rewards [45]; microbial changes in reward quality should induce similar movements. From a dispersal perspective, bees respond to the spatial structure of a flower patch in ways that could bias microbial dispersal away from plants on the edge [46]. Similarly, traplining, defined as repeated, ordered visitation to a given sequence of plants or flowers [47] could give rise to strong spatial structuring of the floral microbial community. For example, a study of microbial community structure in *Mimulus aurantiacus* found that spatial location was a stronger predictor of nectar yeast *Metschnikowia reukaufii* colonization than light availability, nectar volume, or floral density [48]. The pattern was attributed to the spatial foraging patterns of hummingbird pollinators. At much broader spatial scales (e.g. continental), proximity is a significant but much weaker predictor of microbial community than other aspects of the biotic and abiotic environment, perhaps as a result of limitations to long distance dispersal [49]. We argue that integrating insights from behavioral ecology about animals' decision making about 'where' and 'how far' to forage will help generate hypothesis regarding the scales at which microbes are dispersal-limited. Spatial memory and site fidelity of birds and bees [50] show that beyond our emphasis on the perceptual similarity of floral displays, simply inhabiting the same space could also be a strong determinant of shared microbial communities (e.g. plants that are intermingled are more likely to be sequentially visited [51]), even in the face of phenological separation.

Conclusion

The cognitive and microbial ecology of pollination represent two somewhat disparate literatures. Yet, they both revolve around the mechanisms and outcomes of pollinator choice in the floral marketplace. After all, the decisions pollinators make while foraging have the potential to shape microbial communities, and vice versa. This interplay has downstream effects on plant fitness and even larger, critical community-level processes, such as dispersal. We encourage behavioral biologists with expertise in the study of plant–pollinator interactions to consider increasing the ecological realism of their experiments by including a microbial component. Likewise, we have highlighted several areas where microbial ecologists might build on the rich pollinator behavior literature to inspire questions about the causes and consequences of microbial signaling in relation to dispersal. An integrated effort has the potential to better predict the microbial patterns we see in the floral marketplace.

Declaration of interest

The authors declare that they have no known competing financial interests.

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Honeybees may learn to discriminate between apple flowers colonized versus uncolonized by the floral pathogen *Erwinia amylovora*, a specialist on pomaceous host plants. Although the authors could not find any effect of the pathogen on pollen or nectar quality, slight differences in floral scent were enough to guide floral choice. The authors discuss the dispersal consequences of a microbe making flowers mildly unattractive: it may alter pollinator behavior such that the microbe becomes more likely to reach uncolonized host flowers, which could be a competitive advantage.