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Bee nutrition and floral resource restoration

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Bee-population declines are linked to nutritional shortages caused by land-use intensification, which reduces diversity and abundance of host-plant species. Bees require nectar and pollen floral resources that provide necessary carbohydrates, proteins, lipids, and micronutrients for survival, reproduction, and resilience to stress. However, nectar and pollen nutritional quality varies widely among host-plant species, which in turn influences how bees forage to obtain their nutritionally appropriate diets. Unfortunately, we know little about the nutritional requirements of different bee species. Research must be conducted on bee species nutritional needs and host-plant species resource quality to develop diverse and nutritionally balanced plant communities. Restoring appropriate suites of plant species to landscapes can support diverse bee species populations and their associated pollination ecosystem services.

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Introduction

A key factor driving pollinator declines is anthropogenic land-use intensification, which, among interacting factors such as pesticide use and introduced pests and pathogens, dramatically reduces the diversity and abundance of flowering plant species [1–5,6••,7••]. Bees (Hymenoptera: Apoidea: Anthophila), as a monophyletic group of ~20 000 species [8], depend entirely on nutrition derived from floral resources (especially nectar and pollen) obtained from diverse plant species [9]. Bees therefore experience nutritional stress when limited in their choices of host-plant species or when only suboptimal floral resources are available, both of which could result in reduced population sizes and pollination efficiency [1–5,6••,7••]. We propose a rational approach for restoring and conserving pollinator habitat that focuses on bee nutrition by firstly, determining the specific nutritional requirements of different bee species and how nutrition influences foraging behavior and host-plant species choice, and secondly, determining the nutritional quality of pollen and nectar of host-plant species. Utilizing this information, we can then thirdly, generate targeted plant communities that are nutritionally optimized for pollinator resource restoration and conservation. Here, we review recent literature and knowledge gaps on how floral resource nutrition and diversity influences bee health and foraging behavior. We discuss how basic research can be applied to develop rationally designed conservation protocols that support bee populations.

Bee nutrition

Adults and larvae of nearly all bee species depend on nutrients obtained from floral resources for development, reproduction, and health [9,10••]. Adult foragers are challenged with seeking out appropriate nutrients from the environment for developing larvae and/or nurse bees and queens confined to a nest [9]. At the simplest level, bee nutrition is partitioned between nectar and pollen: nectar provides bees' main source of carbohydrates, whereas pollen provides proteins, lipids, and other micronutrients [11–13]. To obtain optimal nutrition, insects can balance their nutrient intake from complementary food sources, which is considered one of the most important factors shaping foraging behavior and insect fitness [14••].

Bee species likely have different quantitative and qualitative nutritional requirements, which are suggested by their differences in life history, brood size, social structure, and different distributions among plant species. Whereas most bees are solitary and oligolectic (a single reproductive female lays eggs and provisions brood; specializes on one plant family or genus), the majority of literature studying the nutritional needs of bees have focused on two species of long-tongued bees: honey bees and bumble bees, both of which are generalists (foraging on a wide range of plant species in different families) and social (living in colonies with cooperative brood care and overlap of generations) [8,10••,11,15]. The nutritional requirements of honey bees (colony, adults, and larvae) has been comprehensively reviewed [10••], and even though this level of detail does not exist for other bee species, we can assume that other species have similar macronutrient demands; the proportions of macronutrients required may be species-specific (as exemplified in other closely related insect species that share the same host-plants [14••,16]).

We can infer the general dietary requirements of bees from existing research. It is clear that both adults and larvae will starve without a constant carbohydrate, mainly nectar, source [10••]. Relatively immobile larvae do not require the amounts of carbohydrate needed by foraging bees and their limited carbohydrate demands can be met by a blend of pollen, which contains digestible carbohydrates, and nectar [17–19]. Protein concentration of pollen is positively correlated with larval development and adult reproduction (ovarian development and egg laying) in honey bees, bumble bees, and the sweat bee *Lasioglossum zephyrum* [20–26,27••]. Lipids are crucial for a variety of physiological processes in bees (e.g. egg production, wax production, secondary energy source) and contribute to larval and adult health, ontogeny, and diapause/overwintering [10••,27••,28–30]. Linoleic acid (omega-6), an essential fatty acid for most insect species, in collected pollen has been associated with higher worker production in honey bee colonies [31]. A second essential fatty acid for insects, linolenic acid (omega-3), is also obtained from pollen, but its specific importance for bees is still not described [28]. Sterols obtained exclusively from pollen are the precursors for molting hormones, making pollen essential for larval development [10••,27••]. Recent research indicates that both honey bee and bumble bee foragers regulate their intake of carbohydrates and proteins to high ratios [32,33], and bumble bees can simultaneously regulate their intake of carbohydrates, proteins, *and* lipids (Vaudo *et al.*, unpublished). These studies reveal bees' specific nutritional requirements, and potentially highlight how adults prioritize their foraging efforts between nectar and pollen for their nutritional components.

Information is lacking for the specific nutritional requirements of the vast majority of solitary oligolectic bee species, though bee taxa appear to have different requirements in nectar sugar composition (see section 'Nectar' discussion below). Even less is known of bees' specific pollen nutritional requirements. For at least a few species of solitary bees, pollen quantity of brood provisions is linearly correlated to body size [34]. Additionally, some specialist bees do not survive well on non-host pollen [35], suggesting that either host-plant pollen is nutritionally optimal for specialists, or they cannot metabolize protective chemicals of non-host pollen. Because nectar and pollen quality varies considerably between host-plant species [11,12] and the bee community exhibits different host-plant visitation patterns over time [36–38], we can assume that different bee species have specific nutritional demands that may influence their host-plant foraging patterns [16].

Floral resource nutritional diversity and bee foraging behavior

Nectar

Nectar is the major carbohydrate source for most bee species [10••,39,40]. Bee larvae require carbohydrates for normal development often in the form of brood food (pollen and nectar mixtures), but the greatest quantity of carbohydrate-rich nectar is required for adult foraging [10••]. Nectar is an important floral reward and reinforcing stimulus for bee foragers, and profitable nectar sources can be learned and associated with floral characteristics such as scent and color [41–43]. Although nectar is a dynamic floral resource, varying by abiotic conditions and plant age [12,25,44–48], there are three relatively constant characteristics that influence bee host-plant choice for nectar: sugar composition, nectar volume, and nectar concentration [18,39]. Other characteristics of nectar composition undoubtedly play a significant role in nectar choice, such as amino acids, lipids, minerals, and secondary plant compounds [46,49–59]; however, research on these characteristics, perhaps with exception of amino acids (recently reviewed in Nepi [60]), has been limited and not systematic across bee species [59–63].

The three main sugars present in nectar are glucose and fructose (monosaccharide), and sucrose (disaccharide) [12,64,65]. Flowers of a given taxa vary in the relative amounts of these sugars and plant families show a characteristic pattern of sugar composition [12,48,64,65]. Early research found that long-tongued bees prefer high sucrose nectars and short-tongued bees prefer nectars with a higher percentage of monosaccharides [65]. Although the interpretation of these patterns has been questioned on many levels [12,66–68], it is likely that sugar composition of plant taxa is an important factor in determining pollinator host-plant choice [48,62,64, 65,69–75].

Nectar concentration also determines patterns of pollinator host-plant visitation [12,76–79], limiting which pollinators can mechanically obtain the nectar, either by adhesion and capillary action or by suction. The rationale is that pollinators with long feeding apparatuses (long-tongue bees, moth/butterfly proboscis, long-tongue fly proboscis) will be limited to more dilute nectars. Although overall viscosity is affected by temperature (and sugar concentration) [80], patterns of preference are evident (reviewed by Willmer [81]) and therefore likely play a role in the evolution of plant-pollinator communities. For example, honey bees (a long-tongued bee species) prefer a concentration of 30–50% whereas short-tongued bees utilize higher concentration nectars of 45–60% [82].

It has been proposed that nectar volume, a third characteristic of floral nectar, is the result of an evolutionary tradeoff [83] between high volumes that are energetically costly (potentially influencing vegetative growth and flower production) [84,85••] and volumes that are too low to attract pollinators. Ideally, nectar volume of a given plant species should be high enough to attract pollinators, but low enough to ensure efficient visitation to other conspecific flowers. Nectar volume, therefore, should be strongly associated with the primary pollinators of plant taxa [86,87]. In a classic study of Costa Rican plants and their pollinators, flowers producing high volumes of nectar, which also had large floral mass, were visited by larger bees in contrast to smaller flowers with lower nectar volumes, which were visited by small bees and wasps [44].

Pollen

Bees obtain the majority of their protein, including free and protein bound essential amino acids, from pollen, but protein concentration varies considerably between plant species, ranging from ~2 to 60% [88,89]. Although preference for high protein pollen has not been clearly demonstrated for honey bees [90,91], significant decreases in pollen protein in the colony result in higher pollen foraging rates [91]. It has been suggested that honey bees may prefer pollen higher in essential amino acids [92], or obtain a balance of amino acids by collecting a diverse pollen diet [89]. Increasing evidence exists that bumble bees do prefer and will increase foraging rates to pollen sources higher in protein or essential amino acid concentration [25,93,94,95••,96••]. Indeed, when foraging in the same habitat among the same host-plant species, bumble bees collect pollen higher in protein concentration than honey bees, which may be linked to different foraging strategies; bumble bees may preferentially forage for pollen quality, where honey bees may forage for quantity to meet the vast demands of the colony [97]. This tradeoff between quantity and quality likely exists in other bee species.

Pollen serves as bees' main lipid source (including essential fatty acids and sterols), and lipid concentrations from different plant species can range considerably, from 1 to 20% [11]. Furthermore, the lipid-rich oily exterior of entomophilous pollen, the pollenkitt, is an important discriminative stimulus, phagostimulus, and digestible component for pollen recognition and bee nutrition [98–102]. Bees, therefore, may be cued by pollenkitt chemistry to recognize host-plant pollen quality, but research is sparse on how pollen lipid content and the pollenkitt influence bee foraging choice in the field.

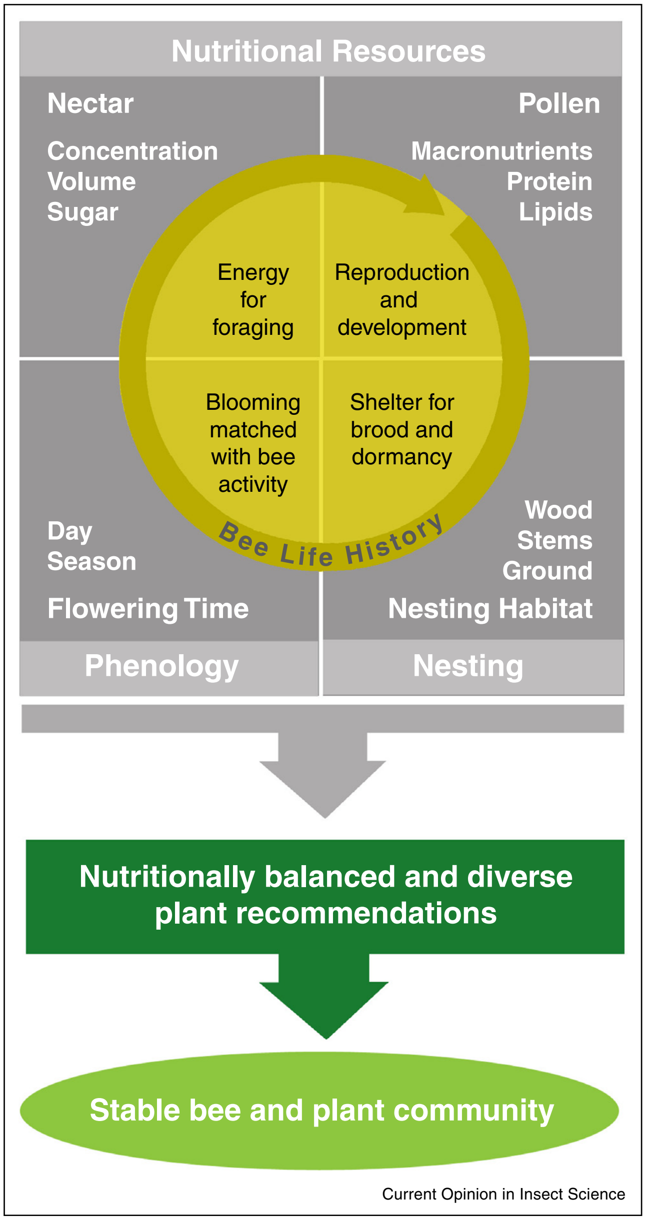
Because protein and lipid concentrations between pollen species are variable and uncoupled [11,13] (Vaudo *et al.*, unpublished), foragers may selectively collect pollen among plant species to regulate their intake of these nutrients, or, alternatively, collect from a large array of host-plant species to passively achieve a nutritional balance (this may apply to generalist and oligolectic foragers alike). Research in other arthropod species, including beetles and spiders, indicates that they sense and regulate their intake of protein and lipids when choosing among food sources [103–106]. Bumble bees, for instance, appear to collect pollen diets from the field that are both high in essential amino acid and sterol content [96••]. Our recent research has demonstrated that ratio of protein:lipid concentration of pollen best predicted host-plant species preference of bumble bees; and when given multiple synthetic food sources, bumble bees indeed regulated their protein and lipid intake (Vaudo et al., unpublished). These results suggest that bees potentially analyze pollen quality in multiple nutritional dimensions. Furthermore, because bees may not be able to taste protein directly [18], pollenkitt lipid and amino acid chemistry could convey information on pollen quality to bees.

Beyond proteins and lipids, pollen (and often nectar) is rich in micronutrients (e.g. vitamins and minerals) and phytochemicals (e.g. carotenoids, flavonoids, alkaloids and phenolics) that have antioxidant properties and antimicrobial activity [11,107–110]. High concentrations of secondary plant chemicals, however, as plant defenses, could be toxic to bees [54,111,112••]. Some specialist bee species do not survive well on exclusive non-host pollen, potentially because they cannot metabolize these chemicals [35]. It has been suggested that oligoleges of the genus *Colletes* specialize on pollen of the plant subfamily Asteroideae, while generalists of *Colletes* do not, possibly due to differences in their ability to cope with secondary plant chemicals of Asteroideae pollen [113]. A similar trend has been observed between larvae of closely related generalist *Osmia* species, having differing physiological abilities to survive on the same pollen diets due to pollen protective chemicals [114]. Therefore, bees could selectively collect or avoid host-plant pollen based on its phytochemical composition.

The importance of plant diversity for bee health

Large scale land-use that reduces floral abundance and species richness will negatively affect bee species populations through nutritional shortage in both quantity and quality of resources [1–5,6••,7••,115••]. For example, the recorded population declines of bumble bee and other bee species in Europe are associated with landscape-level reduction of host-plant availability [1–5,6••,7••,115••,116]. Although farmland of bee-pollinated crops may provide a large quantity of floral resources, these habitats may be insufficient at maintaining healthy bees because they may only present single-source pollen or nectar. Also, when the crop is not blooming, the landscape may have few flowering plants, affecting all bee species whose foraging periods do not discretely overlap with crop bloom. Without diverse foraging options and diets during critical periods of reproduction and development, bees may suffer negative health consequences. Additional intensification, such as agrochemical use, can further

Figure 1



Conceptual schematic presenting a holistic framework relating basic research and landscape application for bee conservation and habitat restoration. The essential research objectives are: (1) seasonal and daily phenology of bee and plant species, (2) bee nutritional requirements and the nutritional quality of nectar and pollen from commercially available host-plant species, and (3) bee species nesting requirements. These research areas provide the environmental criterion necessary for supporting bees' annual life cycle: (1) timing of blooming that matches with bee active foraging periods, (2) nectar characteristics necessary for bee energetic needs, especially during foraging, (3) pollen characteristics necessary for bee reproduction and development, and (4) nesting habitat for bees to rear brood and spend periods of time of inactivity and dormancy. We can then rationally design conservation plant communities by selecting host-plant species (and natural habitat) that meet these criteria. These plant communities constitute a diversity of host-plant species optimized for bee nutrition. The outcome of a comprehensive conservation effort is that we provide a diverse group of bee species appropriate nutrition and habitat that will stabilize their populations. Healthy and diverse bee populations will then be more effective pollinators of wild host-plant and crop species.

exacerbate stress, negatively affecting bee foraging behavior [4,7••,117,118] and fitness [7••,119–121].

Bees should be given a range of diverse floral resources from which they can self-select their diet to meet their component nutrient requirements, which will sustain healthy populations that can endure disease and stress. For example, in bumble bees, the reproductive benefits of polyfloral pollen diets surpassed those of monofloral diets, even when lower in protein concentration [24]. Polyfloral pollen diets can provide a balance of essential amino acids and fatty acids, whose concentrations differ between species [89]. Exposure to single pollen sources, such as *Lupinus* crops, that contain plant defensive chemicals can be detrimental to bumble bee colony fitness [111]. Therefore, generalist bees may visit a variety of host-plant species to obtain pollen to dampen or nullify the harmful effects of pollen secondary metabolites [112••]. Appropriate nutrition is necessary for bee immunity (DeGrandi-Hoffman and Chen, this issue); diverse pollen diets can enhance bees' immunocompetence and resistance to pathogens [122,123••] and pesticides [124].

Applying bee nutrition to floral resource habitat restoration

To alleviate the negative effects of reduced floral resource availability and interacting stressors of agricultural intensification on bee population health and crop pollination services, selective foraging habitats should be restored in sufficient quantity surrounding areas of land-change [7••,125••,126]. Thus, there is increasing demand and incentive based programs for farmers for application of agri-environmental schemes, including floral resource provisioning to support bee populations [7••,115••,127,128]. The development and design of these schemes have focused primarily on plant species that attract bee abundance and diversity. Because the bee community will visit different plant species throughout the day, season, and between years [36–38,129–131], floral diversity is the best way to attract and support multiple pollinator species over time. Furthermore, farmland in proximity to natural habitat and/or supplemented with floral resources will attract a wider species richness and functional-group diversity of bees that can result in higher fruit yield [132–138,139••,140], and economic benefit [139••].

However, plant species diversity alone is not sufficient to ensure pollinator conservation and thus the aim should be to provide nutritionally optimized floral resources. Figure 1 provides a conceptual schematic relating research and application of criteria needed to support bee populations throughout their life cycle. While other factors (nesting habitat [141], structure of the pollinator community [131]) are important for developing pollinator plantings, for this review, we focus on the bee nutrition and the role it plays selecting appropriate plants that support a nutritionally balanced and diverse community. Foremost, plants should be chosen that present floral rewards in phenological succession throughout the day and season [129–131] spanning the active periods of bee species [139••]. Then, firstly, determine the nutritional value of the nectar and pollen of the agricultural crop, and commercially available native and, where advisable, non-invasive exotic host-plant species (exotic plants species should only be chosen that will not compete with endemic plant species and will promote plant-pollinator community stability [142]). These studies include analyzing nectar composition, concentration, and volume, and pollen protein, lipid, and micronutrient quality. Secondly, determine the nutritional needs of different bee species occupying the landscape, including those important for crop pollination. These studies can be conducted in field, semi-field, or laboratory settings correlating resource quality to nectar and pollen visitation data [94,129], or feeding assays using synthetic or supplemented diets [14••].

Integrating this information will allow us to select plant-species that better meet bees' nutritional needs. Rich nectar sources diverse in their quality and quantity will provide the differing carbohydrate needs of bees and other pollinators. Further, plant species that are attractive, but whose pollen are complementary (to each other and the agricultural crop) in their protein, lipid, and micronutrient quality will allow bees to self-select their diet to balance their intake of these nutrients to maximize their reproductive output and larval development/survival. Additionally, plant communities can be designed to match the changing nutritional needs of bees throughout the growing season. For example, with a strong understanding of pollen and nectar nutritional quality, we should be able to provide pollen sources early in the season to boost worker population growth for honey bee and bumble bee colonies [143,144], and late season nectar flow for honey bee overwintering and bumble bee gyne survival [115••,145] (SH Woodard, abstract 0406, Entomology 2014, Austin, TX). Finally, once pollen and nectar nutritional quality is better characterized, devised plantings should support wide generalists that collect diverse resources for quantity, or selectively for nutritional value. Because generalists visit the majority of host-plant species in local plant-pollinator communities [131], achieving diversity in our plant communities will also likely maximize attractiveness to solitary or specialist species that have limited foraging distances, shorter active periods, and narrower host-plant preferences.

Developing rationally designed floral provisioning schemes that optimize pollinator nutrition requires information about the nutritional requirements of pollinators, how these shape their foraging preferences, and the nutritional profiles of a range of the floral resources of native and agricultural plant species. Integrating this information will allow development of targeted, and simplified, plant communities, which can be used for conservation of a diverse range of bee species in a diversity of landscapes. These healthy and abundant bee populations will then sustain agricultural production in the face of increasing demands for food in a changing environment.

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