

Wild bee nutritional ecology: predicting pollinator population dynamics, movement, and services from floral resources

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Pollination services are inherently shaped by floral resource availability, through the mediation of pollinator population dynamics and the influence on energetically costly processes, such as foraging. Here, we review recent insights that have improved our mechanistic understanding of how floral resources shape bee populations and pollination services. Our scope includes advances in our understanding of how individual bees and their populations are shaped by nutrient availability; investigations into how contemporary floral resource landscapes influence foraging; and new insights into how these relationships are indirectly impacted by biotic and abiotic factors across communities and landscapes. Throughout our review, we take a mechanistic, multi-scalar approach that highlights the complexity of interactions between floral resources and bees, across space and time.

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Introduction

Food resources play an important role in regulating animal activity and population dynamics [1]. In the case of pollinators, who rely heavily or entirely on food obtained from flowering plants, floral resource availability mediates the suite of population dynamic [2] and energetic [3] processes that collectively shape the spatial distribution, abundance, and quality of pollination ecosystem services (Figure 1). Bees (Hymenoptera: Apoidea: Anthophila) pollinate the majority of global crop species [4], including many food crops that provide necessary nutrients for humans [5]. Thus, enormous attention has been placed

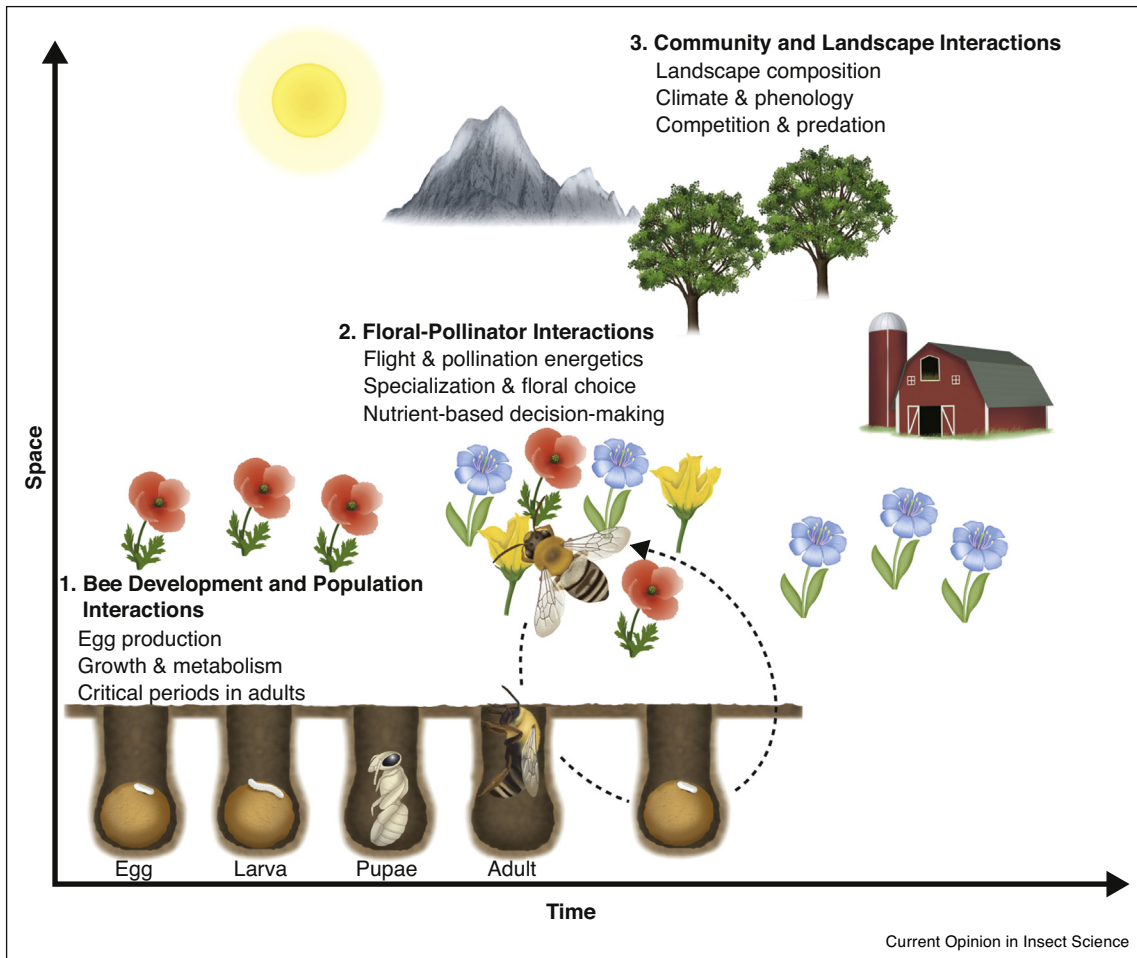
recently on the need to manage floral food resources for wild bees [6,7,8] and use habitat characteristics to predict bee-mediated pollination services at large spatial scales [9]. Mechanistic studies linking bee nutrition with broader bee population and energetic processes across both temporal and spatial scales are necessary for generating a more predictive framework for anticipating and managing pollinator populations and services.

Bee development and population interactions

The overwhelming majority of bees forage for two primary food resources, pollen and nectar, which they obtain from flowering plants. Perhaps the most direct mechanistic link between floral resources and bee abundance is the connection between pollen availability and the production of offspring by female bees. Laboratory-based studies in species such as the honey bee *Apis mellifera* [10] and the solitary species *Osmia californica* [11**] indicate that nutrients provided from pollen (including protein, lipids, and micronutrients) are necessarily ingested by adult female bees for egg production. These studies in managed bee species under controlled or confined conditions underscore the importance of pollen for reproduction, but likely underestimate the quantities of pollen needed for egg production in wild bees, who must forage more intensively under natural conditions (but see Ref. [12]). Beyond initial nutritive investments in egg production, nutrients from pollen are also continuously required by larvae for metabolic processes and assimilation into developing tissues, and nutrient limitations during early development may have persistent negative effects on adult bee physiology and performance [13,14*].

Carbohydrates (obtained primarily from nectar) are also required for growth and metabolic processes that underlie population dynamics in bees, and may be particularly important under certain ecological circumstances or life history stages. For example, bumble bee queens metabolize sequestered glycogen during an overwintering period [15,16] and exhibit higher mortality when they lack access to sufficient carbohydrates during the pre-overwintering nutrient sequestration period [16,17]. Carbohydrate availability is also likely important during periods of intensive flight, such as when females forage for long periods to collect nest provisions (e.g., 5–6 hours per day in *Megachile rotunda*; [18]), or when males engage in vigorous mate-seeking flights, as seen in some species [19].

Figure 1



Floral food resources shape bee populations and pollination services across spatial and temporal scales.

Floral resource availability impacts bees across a range of temporal (X-axis) and spatial (Y-axis) scales, from direct effects of nutrition on developmental and population-level interactions (1) to impacts on floral-pollinator interactions (2), and the direct and indirect impacts of context-dependent factors at the community and landscape scale (3). Artwork by A. Sanderson.

A strong emphasis has been placed recently on exploring impacts of pollen and nectar availability on wild bee populations, across spatial and temporal scales. Population genetic studies have repeatedly indicated that natural habitat cover (*e.g.*, woodlands, gardens) is positively associated with increased nesting densities for social, ground-nesting bumble bee species ([20,21]), but it has not been clear whether nesting or floral resources (or both) drive these relationships. Other studies have indicated a more direct relationship between floral availability within a 1 km radius and nesting densities [22], suggesting that either more queens choose to nest in high floral resource areas, or more nests persist in these areas. Carvell and co-workers [23**] recently provided support for both of these phenomena by tracking both lineage (*i.e.*, colony genotype) survival and queen dispersal for *Bombus terrestris*,

B. lapidarius, and *B. pascuorum* in the context of the UK's agri-environment scheme. Their results indicate that lineages are more likely to survive in areas with higher quality local food resources, and queens may not disperse far from flower-rich areas. Experimental research conducted with captive colonies maintained at landscape-scales has identified additional mechanistic connections between food resources and bee populations, including between increased pollen resource availability and increased bumble bee colony growth and reproduction [24–26]; increased land intensification and increased nutritional deficits in social bees [27**,28,29]; and increased food resource availability and increased population sizes in subsequent life cycles of specialist solitary bees [30*,31–34]. Complementary progress has also been made in regard to quantifying food resources [35] and

needs [36] for bees at larger spatial scales, together with methodological developments related to assessing and comparing the nutritional quality of food for bees [37].

Ongoing work in this area is needed to provide more direct evidence for positive relationships between floral resources and population stability across land use types, and to examine these patterns for a broader group of wild-living bee species (but see work on *O. lignaria* in Ref. [38]). Important frontiers in this research area include identifying how specific macronutrients and micronutrients impact bee behavior and development across landscapes, and how nutrient landscape surfaces ultimately influence plant–pollinator interactions.

Floral-pollinator interactions: pollinator movement, floral availability, and specialization

The nutritional needs of bees can also be considered with respect to their energetic demands for flight and the various movements that underlie pollination, which are fueled almost exclusively by nectar (see Ref. [39] for a recent review on this topic). In foraging ecology, animals experience dynamic informational contexts, potentially leading to different motivational states and movement outcomes (reviewed in Ref. [40]). For food collection in bees, this broadly involves responding to an individual or colony-level cue indicating resource need and availability (*e.g.*, chemical cues in bumble bee, reviewed in [41]), flying in either a random or organized fashion in search of foraging patches across the broader landscape (*e.g.*, [42]), and then engaging in patch- or site-selection as well as fine-scale movement activities, such as floral species selection, which facilitate the final step of resource collection (*e.g.*, [43]).

Although flight energetics have been studied more intensively, the fine-scale movement activities related to bee foraging are also likely impacted by food resource availability. For example, buzz pollination (or sonication) is a plastic behavior [44,45] performed by some bees, which involves rapid contraction of the thoracic muscles [46]. Recent work has identified that buzz pollination is influenced by environmental factors such as pesticide exposure (which leads to a reduced propensity to buzz [47]) and ambient humidity conditions (which can impact frequency and duration [48]); its performance is also likely impacted by diet-related factors, such as energetic limitations from nectar unavailability, although this has not been examined. Bumble bees [49] and other bees [50] also expend nectar-derived energy to warm themselves in preparation for flight, which might be inhibited under nectar-limited conditions. In addition to these physiological effects of food availability, nectar limitation can also change pollination-related decision-making in bees in ways that impact the quality of their pollination services, for example when bees take ‘shortcuts’ to access nectar

resources, such as nectar robbing [51]. Research on nectar, energy, and pollination is particularly timely given recent work demonstrating that nectar resources and pollination services are negatively influenced by increasing drought conditions [52–54].

For generalist species, the distribution of floral resources can play a critical role in influencing foraging distance, and presumably energetic costs of flight. For example, studies of semi-wild bumble bees indicate that foraging durations are longer in landscapes with more sparse floral resources [55]. Additionally, molecular studies of wild bumble bees have indicated that they may forage optimally at landscape scales by foraging shorter distances for high quality patches [56], and exhibit a sophisticated ability to forage longer distances within landscapes with less heterogeneously distributed (*i.e.*, less patchy) resources [20]. Recent work further indicates that wild bumble bees shift foraging patterns as landscape-level resources decline, becoming more selective and willing to forage further for high quality floral patches [57].

Floral resource distributions and their impacts on foraging and brood provisioning are likely even more critical for specialist bee species, where specialization is defined as the act of provisioning offspring with a phylogenetically narrow group of pollen species (*e.g.*, a single species, genus, or species set from a single plant family) [58]. Floral specialization is an ancient strategy in some bee lineages [59,60] that today is exhibited by many of the world’s >20,000 extant bee species [61]. Recent studies indicate that specialist solitary bees lengthen their foraging distances when floral resources are located more distantly from nest sites, but this extended foraging reduces brood cell provisioning, with negative impacts on total brood cell count [33]. What is not known is how specialist bees respond to floral diversity within their phylogenetically narrow group of focal pollen species (*e.g.*, generic diversity) or within the potentially broader group of plants used for nectar resources. Narrow pollen diet breadth, as seen in specialist species, has long been hypothesized as a potential driver or correlate of bee decline, and studies examining pollen composition across species have often indicated that bee species with more narrow pollen diets are more rare (bumble bees, [62]; solitary bees, [63]); concurrent declines in bee species and their focal plant food resources are further evidence of the link between food resource decline and bee decline [64,116*]. Recent analysis in an *Osmia* species also demonstrated considerable inter-individual variation in the ability to digest non-host pollen [65], underscoring the need to consider specialization as a plastic or variable phenomenon, rather than a static, species-specific trait.

The ability of bees to assess the nutrient content of foods and make decisions based on nutritional quality is another rapidly developing area of research. There is increasing

evidence that bees make short-term foraging decisions based on direct food resource quality assessments, for example based on sweet versus bitter taste [66], to optimize the content [67–70] or ratios [71*,72,73] of particular nutrient classes, or to account for nutritional inadequacies in any one pollen type [74*,75]. However, these direct food quality assessments do not necessarily result in beneficial feeding decisions, for example when there are potentially conflicting signals from non-nutritive substances that influence feeding or foraging-related behaviors, such as pesticides [76] and plant secondary compounds [77**,78]. An emerging trend is that generalist species appear to obtain fitness-related benefits from including pollen from multiple plants species in their diet [13,79], although some plant species appear to independently provide adequate levels of individual nutrient classes [75,80,81]. In contrast, other studies indicate that bees may specialize on a particular food resource even when its nutritional quality appears to be suboptimal [82,83].

Among all bees, but especially generalist species, individuals may exhibit floral preferences and constancy (or, fidelity) along shorter, ecological timescales. Floral constancy describes a tendency for foragers to revisit the same species or taxa, and is believed to be driven by the existence of search images and/or reductions in handling or resource extraction time (reviewed in Ref. [84]). Floral constancy and pollen collection patterns can change over space and time, due to changes in factors such as phenological period [85], offspring provisioning responsibilities (*e.g.*, female bees only), and landscape composition [86]. In social species, individual differences in short-term specialization can be organized into a division of labor (for bumble bees see [87*]; for honey bees see Ref. [88]), in which case colony-level nutritional state may be a function of social structure complexity and individual-level behavioral variation, among other factors [89*].

Community and landscape interactions: abiotic and biotic factors impacting floral visitation

Studies in landscape and community ecology provide broader insights into how floral resource availability, and the abilities of bees to access these food resources, are shaped by a variety of biotic and abiotic factors. Landscapes are spatially explicit mixes of ecosystems and land-use types that encompass the short-term movement processes of a focal organism; they are often characterized by composition (*i.e.*, proportion of habitat types) and configuration (*i.e.*, spatial arrangement of habitat types) [90]. In two recent meta-analyses investigating landscape effects on bee diversity within agricultural systems across the globe, Kennedy and co-workers [91**] found that bee abundance and richness were higher in agricultural landscapes with greater semi-natural habitat composition, and similarly Lichtenberg and colleagues

[92] found greater richness in farms embedded in more complex landscapes. Interestingly, Kennedy and co-workers [91**] also determined that landscape configuration (patch shape, inter-patch connectivity, and habitat aggregation) had weak effects on bee diversity and abundance, relative to landscape composition. These results indicate that resource configuration is less important than availability, and suggest that bee vagility may make floral resources accessible regardless of configuration. Although informative, landscape-level reviews tend to focus on community metrics, and future work would benefit from incorporation of information related to bee foraging, nesting, and movement patterns to better understand habitat composition configuration impacts across species.

Among abiotic factors, precipitation has repeatedly, albeit indirectly, been identified as a key driver of bee access to food resources. This has been demonstrated in regard to plant flowering, for example in the cases of natural or experimentally-induced variation in spring snow melt and its relationship with earlier flowering time in alpine ecosystems [93,94], or in the regulation of mass-flowering events for tropical tree species [95]. Temperature also influences floral resource access through its effects on flowering phenology and the production of floral rewards on diurnal timescales (*e.g.*, [96]). Temperature additionally influences when bees will forage [97], illustrated by the greater energetic demands on bees in higher temperature environments [98]; it can also influence when parasites are active [99]. At landscape and community scales, temperature and precipitation, among other abiotic factors (*e.g.*, CO₂ concentration) can mediate floral resource availability and diversity and thus may correspondingly alter plant–pollinator interactions across the community (reviewed in Ref. [100]). Whereas recent pollination network analyses suggest that substantial behavioral rewiring can occur across space and time [101], and may facilitate bee community persistence despite changes in plant beta diversity, these studies have largely focused on visitation patterns as opposed to nutrient acquisition. Further research exploring the nutritional implications of turnover in network interactions could provide greater insight into the costs of these rewiring events and how they may impact longer-term persistence of bee populations in dynamic landscapes.

Floral resource availability can also be indirectly and directly influenced by conspecific foragers, other bee species, predators/parasites, and microorganisms, who may compete for food resources or otherwise influence the ability or motivation of bees to access resources. For example, conspecifics or closely related species with similar traits (*e.g.*, tongue lengths) are more likely to compete for the same food resources (reviewed in Ref. [62]), whereas non-conspecifics may also compete directly for food resources, or may indirectly influence bee movement patterns [102]. Foraging is also influenced by the

presence of parasites and natural enemies of bees, such as birds, robber flies, and crab spiders, among many others (reviewed in Ref. [2]). These species interactions may further impact ecological function, as recent studies indicate that increased parasite load can reduce pollination success [103]. Microorganisms can also influence pollinator attraction to floral resources; for example, the presence of certain yeasts in nectar can increase the attractiveness of nectar to pollinators [104], in part by altering secondary compound composition [105].

Conclusions and future directions

An improved understanding of species-specific impacts of floral resource availability on bee population dynamics and movement is vital for predicting and managing bee-mediated pollination services. The following are among many of the promising research directions for improving the mechanistic understanding of how floral food resources shape the availability and quality of bee-mediated pollination services:

Refined understanding of bee nutritional health

Historically, studies on the nutritional quality of food resources for bees have focused heavily on crude macronutrient content (*e.g.*, total protein), but recent studies have expanded their scope to examine more fine-scale nutritive components, such as individual amino acids [70] and minerals [106], and even non-nutritive components of diet that contribute to health [107]. Future directions in this area include examining complex combinatorial relationships between individual nutrient classes, and more thoroughly addressing connections between nutrient levels and health-related phenotypes in bees.

Synergistic interactions between nutrition and other factors involved in bee decline

There is increasing evidence that bee nutritional states interact synergistically with environmental factors (such as landscape composition, pesticide exposure, and pathogens) to impact pollination services. These synergistic interactions are being widely studied in the context of bee decline [108], but not yet in the context of pollination service delivery (but see Refs. [109,110]). Synergistic effects on learning and memory may be a particularly compelling direction for this work, given that foraging involves cognitively demanding tasks [111], and both nutritional stress (*e.g.*, linoleic acid limitation in honey bees; [112]) and other causal factors involved in bee declines (*e.g.*, *Crithidia*-parasitization in bumble bees, [113]; cholinergic pesticide exposure in honey bees, [114]) have demonstrated negative impacts on bee cognition.

Effects of continued floral resource loss with ongoing global change

Loss of floral resources is cited as the primary driver of native bee decline [108,115] and examination of pollen use from museum specimens of declining species indicate

that declines in host plants may be linked to species-level decline [116]. These studies and other examinations of bee decline across taxonomic groups (*e.g.*, [117]) additionally indicate that large-bodied species are particularly at risk, possibility due to greater pollen requirements than smaller species. These relationships suggest that nutrition and plant–pollinator relationships may be particularly important in the context of global change. Global change forces may additionally alter food quality; specifically, recent experimental as well as museum-based research has indicated that pollen protein concentration may decline as CO₂ concentrations increase [118]. Understanding the mechanisms behind global change-induced alterations to floral availability and pollen and nectar quality may be one of the most urgent areas of focus in bee ecology, with critical implications for foraging, population dynamics, and community-level research.

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