

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

S Hollis Woodard<sup>1</sup> and Shalene Jha<sup>2</sup>



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.

## Addresses

<sup>1</sup> Department of Entomology, University of California, Riverside, Riverside, CA 92521, USA

<sup>2</sup> Department of Integrative Biology, University of Texas at Austin, Austin, TX 78782, USA

Corresponding author: Woodard, S Hollis ([hollis.woodard@ucr.edu](mailto:hollis.woodard@ucr.edu))

Current Opinion in Insect Science 2017, 21:83–90

This review comes from a themed issue on **Behavioural ecology**

Edited by **Shalene Jha** and **Hollis Woodard**

<http://dx.doi.org/10.1016/j.cois.2017.05.011>

2214-5745/© 2017 Elsevier Inc. All rights reserved.

## 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

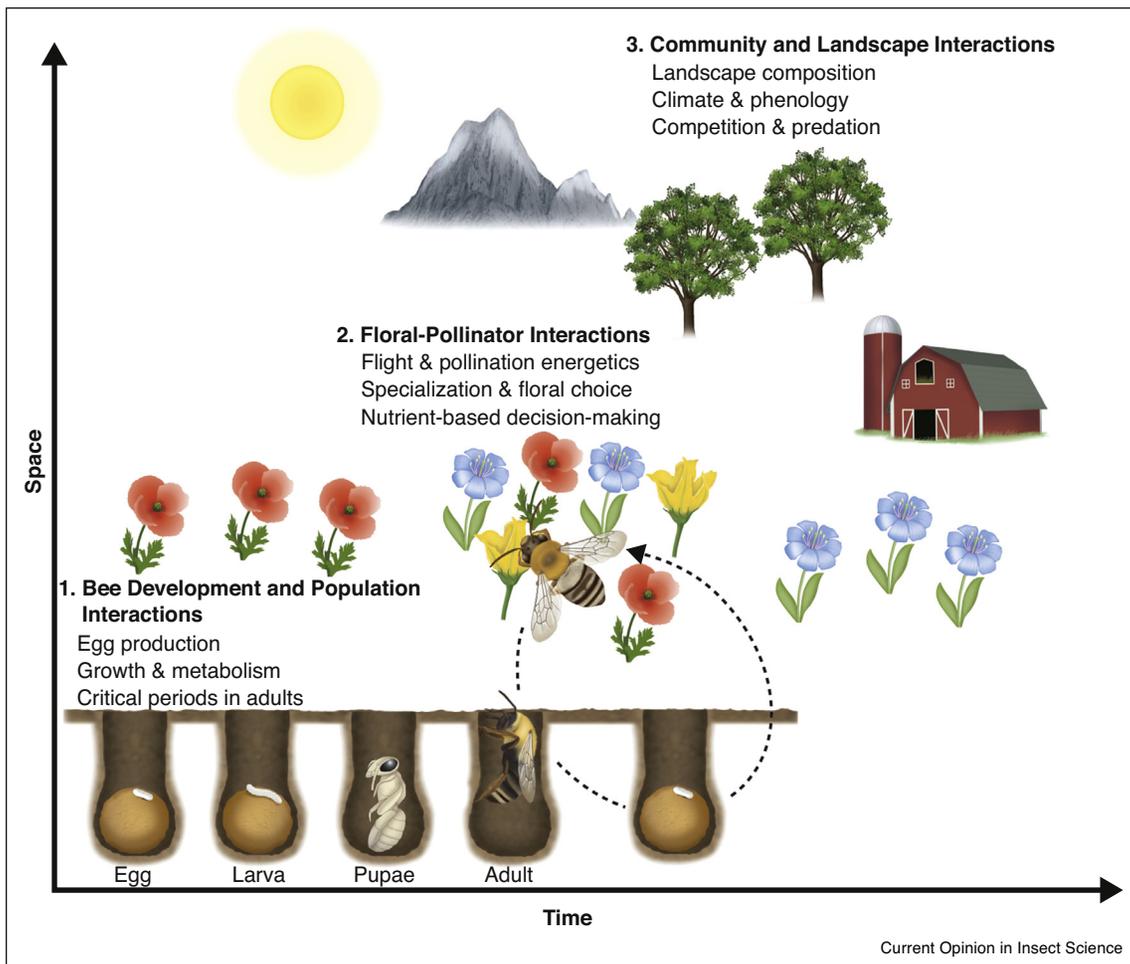
recently on the need to manage floral food resources for wild bees [6,7,8] and use habitat characteristics to predict bee-mediated pollination services at large spatial scales [9]. Mechanistic studies linking bee nutrition with broader bee population and energetic processes across both temporal and spatial 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.*, CO<sub>2</sub> 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 CO<sub>2</sub> 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.

## Acknowledgements

We thank members of the Woodard and Jha labs for instructive feedback on the manuscript, A. Sanderson for her artwork, and the National Science Foundation and Army Research Office for funding (to S. Jha).

## References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
  - of outstanding interest
1. Raubenheimer D, Simpson SJ, Mayntz D: **Nutrition, ecology and nutritional ecology: toward an integrated framework.** *Funct. Ecol.* 2009, **23**:4-16.
  2. Roulston TH, Goodell K: **The role of resources and risks in regulating wild bee populations.** *Annu. Rev. Entomol.* 2011, **56**:293-312.
  3. Heinrich B: **Energetics of pollination.** *Annu. Rev. Ecol. Syst.* 1975, **6**:139-170.
  4. Klein A-M, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T: **Importance of pollinators in changing landscapes for world crops.** *Proc. R. Soc. Lond. B* 2007, **274**:303-313.
  5. Eilers EJ, Kremen C, Smith Greenleaf S, Garber AK, Klein A-M: **Contribution of pollinator-mediated crops to nutrients in the human food supply.** *PLoS One* 2011, **6**:e21363-6.
  6. Vaudo AD, Tooker JF, Grozinger CM: **Bee nutrition and floral resource restoration.** *Curr. Opin. Insect Sci.* 2015, **10**:133-141.
  7. Williams NM, Ward KL, Pope N, Isaacs R, Wilson J, May EA, Ellis J, Daniels J, Pence A, Ullmann K, Peters J: **Native wildflower plantings support wild bee abundance and diversity in agricultural landscapes across the United States.** *Ecol. Appl.* 2015, **25**:2119-2131.
  8. Dicks LV, Baude M, Roberts SPM, Phillips J, Green M, Carvell C: **How much flower-rich habitat is enough for wild pollinators? Answering a key policy question with incomplete knowledge.** *Ecol. Entomol.* 2015, **40**:22-35.
  9. Koh I, Lonsdorf EV, Williams NM, Brittain C, Isaacs R, Gibbs J, Ricketts TH: **Modeling the status, trends, and impacts of wild bee abundance in the United States.** *Proc. Natl. Acad. Sci. U. S. A.* 2015, **113**:140-145.

Used a modeling approach to assess spatial patterns of bee-supporting habitat in the US and how this relates to areas of agricultural importance.

10. Frias BED, Barbosa CD, Lourenço AP: **Pollen nutrition in honey bees (*Apis mellifera*): impact on adult health.** *Apidologie* 2016, **47**:15-25.
11. Cane JH: **Adult pollen diet essential for egg maturation by a solitary *Osmia* bee.** *J. Insect Physiol.* 2016, **95**:105-109.  
Conducted a detailed experimental analysis demonstrating the importance of pollen consumption for ovary development and egg production in a solitary bee species.
12. Cane JH, Dobson HEM, Boyer B: **Timing and size of daily pollen meals eaten by adult females of a solitary bee (*Nomia melanderi*) (Apiformes: Halictidae).** *Apidologie* 2016, **48**:17-30.
13. Bukovinsky T, Rikken I, Evers S, Wackers FL, Biesmeijer JC, Prins HH, Kleijn D: **Effects of pollen species composition on the foraging behaviour and offspring performance of the mason bee *Osmia bicornis* (L.).** *Basic Appl. Entomol.* 2016, **18**:21-30.
14. Wang Y, Campbell JB, Kaftanoglu O, Page RE, Amdam GV, Harrison JF: **Larval starvation improves metabolic response to adult starvation in honey bees (*Apis mellifera* L.).** *J. Exp. Biol.* 2016, **219**:960-968.  
Demonstrated that nutritional stress during the larval stage can influence metabolic processes in adult honey bees, potentially in positive (or, protective) ways.
15. Amsalem E, Galbraith DA, Cnaani J, Teal PEA, Grozinger CM: **Conservation and modification of genetic and physiological toolkits underpinning diapause in bumble bee queens.** *Mol. Ecol.* 2015, **24**:5596-5615.
16. Duennes MA, Der J, Jha S, Woodard SH: in preparation.
17. Woodard SH, Duennes MA, Watrous K, Jha S: in preparation.
18. Maeta Y, Adachi K: **Nesting behaviors of the alfalfa leaf-cutting bee, *Megachile (Eutricharaea) rotundata* (Fabricius) (Hymenoptera, Megachilidae).** *Chugoku Kontyu* 2005, **18**:5-21.
19. Stone GN: **Female foraging responses to sexual harassment in the solitary bee *Anthophora plumipes*.** *Anim. Behav.* 1995, **50**:405-412.
20. Jha S, Kremen C: **Resource diversity and landscape-level homogeneity drive native bee foraging.** *Proc. Natl. Acad. Sci. U. S. A.* 2013, **110**:555-558.
21. Goulson D, Lepais O, O'Connor S, Osborne JL, Sanderson RA, Cussans J, Goffe L, Darvill B: **Effects of land use at a landscape scale on bumblebee nest density and survival.** *J. Appl. Ecol.* 2010, **47**:1207-1215.
22. Knight ME, Osborne JL, Sanderson RA, Hale RJ, Martin AP, Goulson D: **Bumblebee nest density and the scale of available forage in arable landscapes.** *Insect Conserv. Divers.* 2009, **2**:116-124.
23. Carvell C, Bourke AFG, Dreier S, Freeman SN, Hulmes S, Jordan WC, Redhead JW, Sumner S, Wang J, Heard MS: **Bumblebee family lineage survival is enhanced in high-quality landscapes.** *Nature* 2017, **543**:547-549.  
Examined the survival of bumble bee lineages in a region through time, and demonstrated greater persistence in areas with more abundant floral resources.
24. Kämper W, Werner PK, Hilpert A, Westphal C, Blüthgen N, Eitz T, Leonhardt SD: **How landscape, pollen intake and pollen quality affect colony growth in *Bombus terrestris*.** *Landsc. Ecol.* 2016, **31**:2245-2258.
25. Crone EE, Williams NM: **Bumble bee colony dynamics: quantifying the importance of land use and floral resources for colony growth and queen production.** *Ecol. Lett.* 2016, **19**:460-468.
26. Williams NM, Regetz J, Kremen C: **Landscape-scale resources promote colony growth but not reproductive performance of bumble bees.** *Ecology* 2012, **93**:1049-1058.
27. Alaux C, Allier F, Decourtye A, Odoux JF, Tamic T, Chabirand M, Delestra E, Decugis F, Le Conte Y, Henry M: **A "landscape physiology" approach for assessing bee health highlights the benefits of floral landscape enrichment and semi-natural habitats.** *Sci. Rep.* 2017, **7**:40568.
- Found evidence that fat body mass and vitellogenin levels are positively associated with the presence of flowering catch crops and natural land cover surrounding honey bee hives.
28. Dolezal AG, Carrillo-Tripp J, Miller WA, Bonning BC, Toth AL: **Intensively cultivated landscape and varroa mite infestation are associated with reduced honey bee nutritional state.** *PLoS One* 2016, **11**:e0153531.
29. Smith GW, Debinski DM, Scavo NA, Lange CJ, Delaney JT, Moran RA, Miller JR, Engle DM, Toth AL: **Bee abundance and nutritional status in relation to grassland management practices in an agricultural landscape.** *Environ. Entomol.* 2016, **45**:338-347.
30. Franzén M, Nilsson SG: **High population variability and source-sink dynamics in a solitary bee species.** *Ecology* 2013, **94**:1400-1408.  
Conducted a nine-year study of population dynamics in a declining solitary bee (*Andrena* sp.) that identified significant fluctuations in population size through time.
31. Franzén M, Nilsson SG: **Both population size and patch quality affect local extinctions and colonizations.** *Proc. R. Soc. Lond. B* 2010, **277**:79-85.
32. Crone EE, Polansky L, Lesica P: **Empirical models of pollen limitation, resource acquisition, and mast seeding by a bee-pollinated wildflower.** *Am. Nat.* 2005, **166**:396-408.
33. Zurbuchen A, Cheesman S, Klaiber J, Müller A, Hein S, Dorn S: **Long foraging distances impose high costs on offspring production in solitary bees.** *J. Anim. Ecol.* 2010, **79**:674-681.
34. Zurbuchen A, Landert L, Klaiber J, Müller A, Hein S, Dorn S: **Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances.** *Biol. Conserv.* 2010, **143**:669-676.
35. Hicks DM, Ouvrard P, Baldock KCR, Baude M, Goddard MA, Kunin WE, Mitschunas N, Memmott J, Morse H, Nikolitsi M, Osgathorpe LM: **Food for pollinators: quantifying the nectar and pollen resources of urban flower meadows.** *PLoS One* 2016, **11**:e0158117.
36. Cane JH, Tepedino VJ: **Gauging the effect of honey bee pollen collection on native bee communities.** *Conserv. Lett.* 2016, **10**:205-210.
37. Vanderplanck M, Leroy B, Wathelet B, Wattiez R, Michez D: **Standardized protocol to evaluate pollen polypeptides as bee food source.** *Apidologie* 2014, **45**:192-204.
38. Palladini JD, Maron JL: **Reproduction and survival of a solitary bee along native and exotic floral resource gradients.** *Oecologia* 2014, **176**:789-798.
39. McCallum KP, McDougall FO, Seymour RS: **A review of the energetics of pollination biology.** *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* 2013, **183**:867-876.
40. Bartumeus F, Campos D, Ryu WS, Lloret-Cabot R, Méndez V, Catalan J: **Foraging success under uncertainty: search tradeoffs and optimal space use.** *Ecol. Lett.* 2016, **19**:1299-1313.
41. Ayasse M, Jarau S: **Chemical ecology of bumble bees.** *Annu. Rev. Entomol.* 2014, **59**:299-319.
42. Lihoreau M, Raine NE, Reynolds AM, Stelzer RJ, Lim KS, Smith AD, Osborne JL, Chittka L: **Radar tracking and motion-sensitive cameras on flowers reveal the development of pollinator multi-destination routes over large spatial scales.** *PLoS Biol.* 2012, **10**:e1001392.
43. Ogilvie JE, Thomson JD: **Site fidelity by bees drives pollination facilitation in sequentially blooming plant species.** *Ecology* 2016, **97**:1442-1451.
44. Morgan T, Whitehorn P, Lye GC, Vallejo-Marín M: **Floral sonication is an innate behaviour in bumblebees that can be fine-tuned with experience in manipulating flowers.** *J. Insect Behav.* 2016, **29**:233-241.
45. Russell AL, Leonard AS, Gillette HD, Papaj DR: **Concealed floral rewards and the role of experience in floral sonication by bees.** *Anim. Behav.* 2016, **120**:83-91.

46. King MJ, Buchmann SL, Spangler H: **Activity of asynchronous flight muscle from two bee families during sonication (buzzing)**. *J. Exp. Biol.* 1996, **199**:2317-2321.
47. Switzer CM, Combes SA: **The neonicotinoid pesticide, imidacloprid, affects *Bombus impatiens* (bumblebee) sonication behavior when consumed at doses below the LD50**. *Ecotoxicology* 2016, **25**:1150-1159.
48. Switzer CM, Combes SA: **Bumblebee sonication behavior changes with plant species and environmental conditions**. *Apidologie* 2016, **48**:223-233.
49. Heinrich B: **Thermoregulation in bumblebees**. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* 1975, **96**:155-166.
50. Stone GN, Willmer PG: **Warm-up rates and body temperatures in bees—the importance of body size, thermal regime and phylogeny**. *J. Exp. Biol.* 1989, **147**:303-328.
51. Rojas Nossa SV, Sánchez JM, Navarro L: **Nectar robbing: a common phenomenon mainly determined by accessibility constraints, nectar volume and density of energy rewards**. *Oikos* 2016, **125**:1044-1055.
52. Waser NM, Price MV: **Drought, pollen and nectar availability, and pollination success**. *Ecology* 2016, **97**:1400-1409.
53. Burkle LA, Runyon JB: **Drought and leaf herbivory influence floral volatiles and pollinator attraction**. *Glob. Change Biol.* 2016, **22**:1644-1654.
54. Thomson DM: **Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources**. *Ecol. Lett.* 2016, **19**:1247-1255.
55. Westphal C, Steffan-Dewenter I, Tschamtko T: **Foraging trip duration of bumblebees in relation to landscape-wide resource availability**. *Ecol. Entomol.* 2006, **31**:389-394.
56. Redhead JW, Dreier S, Bourke AFG, Heard MS, Jordan WC, Sumner S, Wang J, Carvell C: **Effects of habitat composition and landscape structure on worker foraging distances of five bumble bee species**. *Ecol. Appl.* 2016, **26**:726-739.
57. Pope N, Jha S: **Wild bees forage further and more selectively as landscape floral resources decline**. in revision.
58. Cane JH, Sipes SD: **Characterizing floral specialization by bees: analytical methods and a revised lexicon for oligolecty**. *Plant–Pollinator Interactions: From Specialization to Generalization*. 2006:99-122.
59. Wappler T, Labandeira CC, Engel MS, Zetter R, Grímsson F: **Specialized and generalized pollen-collection strategies in an ancient bee lineage**. *Curr. Biol.* 2015, **25**:3092-3098.
60. Ramírez SR, Gravendeel B, Singer RB, Marshall CR, Pierce NE: **Dating the origin of the Orchidaceae from a fossil orchid with its pollinator**. *Nature* 2007, **448**:1042-1045.
61. Michener CD: *The Bees of the World*. Johns Hopkins University Press; 2000.
62. Goulson D, Lye GC, Darvill B: **Diet breadth, coexistence and rarity in bumblebees**. *Biodivers. Conserv.* 2008, **17**:3269-3288.
63. Wood TJ, Holland JM, Goulson D: **Diet characterisation of solitary bees on farmland: dietary specialisation predicts rarity**. *Biodivers. Conserv.* 2016, **25**:2655-2671.
64. Kleijn D, Raemakers I: **A retrospective analysis of pollen host plant use by stable and declining bumble bee species**. *Ecology* 2008, **89**:1811-1823.
65. Haider M, Dorn S, Müller A: **Intra- and interpopulational variation in the ability of a solitary bee species to develop on non-host pollen: implications for host range expansion**. *Funct. Ecol.* 2013, **27**:255-256.
66. Muth F, Francis JS, Leonard AS: **Bees use the taste of pollen to determine which flowers to visit**. *Biol. Lett.* 2016, **12**:20160356.
67. Ruedenauer FA, Spaethe J, Leonhardt SD: **Hungry for quality—individual bumblebees forage flexibly to collect high-quality pollen**. *Behav. Ecol. Sociobiol.* 2016, **70**:1209-1217.
68. Ruedenauer FA, Spaethe J, Leonhardt SD: **How to know which food is good for you: bumblebees use taste to discriminate between different concentrations of food differing in nutrient content**. *J. Exp. Biol.* 2015, **218**:2233-2240.
69. Somme L, Vanderplanck M, Michez D, Lombaerde I, Moerman R, Wathelet B, Wattiez R, Lognay G, Jacquemart AL: **Pollen and nectar quality drive the major and minor floral choices of bumble bees**. *Apidologie* 2015, **46**:92-106.
70. Kriesell L, Hilpert A, Leonhardt SD: **Different but the same: bumblebee species collect pollen of different plant sources but similar amino acid profiles**. *Apidologie* 2017, **48**:102-116.
71. Vaudo AD, Patch HM, Mortensen DA, Tooker JF, Grozinger CM: **Macronutrient ratios in pollen shape bumble bee (*Bombus impatiens*) foraging strategies and floral preferences**. *Proc. Natl. Acad. Sci. U. S. A.* 2016, **113**:E4035-42.
- Demonstrated that bumble bee foragers may preferentially feed on pollen containing higher protein:lipid ratios.
72. Vaudo AD, Stabler D, Patch HM, Tooker JF, Grozinger CM, Wright GA: **Bumble bees regulate their intake of the essential protein and lipid pollen macronutrients**. *J. Exp. Biol.* 2016, **219**:3962-3970.
73. Stabler D, Paoli PP, Nicolson SW, Wright GA: **Nutrient balancing of the adult worker bumblebee (*Bombus terrestris*) depends on the dietary source of essential amino acids**. *J. Exp. Biol.* 2015, **218**:793-802.
74. Eckhardt M, Haider M, Dorn S, Müller A: **Pollen mixing in pollen generalist solitary bees: a possible strategy to complement or mitigate unfavourable pollen properties?** *J. Anim. Ecol.* 2014, **83**:588-597.
- Found that the solitary, generalist bee species *Osmia cornuta* can develop on sub-optimal (in fact, lethal) pollen if it is mixed with pollen from other plant species.
75. Moerman R, Vanderplanck M, Fournier D, Jacquemart A-L, Michez D: **Pollen nutrients better explain bumblebee colony development than pollen diversity**. *Insect Conserv. Divers.* 2017, **10**:171-179.
76. Kessler SC, Tiedeken EJ, Simcock KL, Derveau S, Mitchell J, Softley S, Stout JC, Wright GA: **Bees prefer foods containing neonicotinoid pesticides**. *Nature* 2015, **521**:74-76.
77. Wright GA, Baker DD, Palmer MJ, Stabler D, Mustard JA, Power EF, Borland AM, Stevenson PC: **Caffeine in floral nectar enhances a pollinator's memory of reward**. *Science* 2013, **339**:1202-1204.
- Found that the presence of caffeine in nectar can improve floral scent-based learning in foraging honey bees, which may promote fidelity of foragers to a food resource.
78. Søvik E, Even N, Radford CW, Barron AB: **Cocaine affects foraging behaviour and biogenic amine modulated behavioural reflexes in honey bees**. *PeerJ* 2014, **2**:e662.
79. Tasei J-N, Aupinel P: **Nutritive value of 15 single pollens and pollen mixes tested on larvae produced by bumblebee workers (*Bombus terrestris*, Hymenoptera: Apidae)**. *Apidologie* 2008, **39**:397-409.
80. Moerman R, Vanderplanck M, Roger N, Declèves S, Wathelet B, Rasmont P, Fournier D, Michez D: **Growth rate of bumblebee larvae is related to pollen amino acids**. *J. Econ. Entomol.* 2016, **109**:25-30.
81. Moerman R, Roger N, De Jonghe R, Michez D, Vanderplanck M: **Interspecific variation in bumblebee performance on pollen diet: new insights for mitigation strategies**. *PLoS One* 2016, **11**:e0168462.
82. Spear DM, Silverman S, Forrest JRK: **Asteraceae pollen provisions protect *Osmia* mason bees (Hymenoptera: Megachilidae) from brood parasitism**. *Am. Nat.* 2016, **187**:797-803.
83. Praz CJ, Müller A, Dorn S: **Specialized bees fail to develop on non-host pollen: do plants chemically protect their pollen**. *Ecology* 2008, **89**:795-804.

84. Goulson D: **Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution.** *Perspect. Plant Ecol. Evol. Syst.* 1999, **2**:185-209.
85. Burkle LA, Alarcón R: **The future of plant–pollinator diversity: understanding interaction networks across time, space, and global change.** *Am. J. Bot.* 2011, **98**:528-538.
86. Ritchie AD, Ruppel R, Jha S: **Generalist behavior describes pollen foraging for perceived oligolectic and polylectic bees.** *Environ. Entomol.* 2016, **45**:909-919.
87. Russell AL, Morrison SJ, Moschonas EH, Papj DR: **Patterns of pollen and nectar foraging specialization by bumblebees over multiple timescales using RFID.** *Sci. Rep.* 2017, **7**:42448.  
Used radio frequency identification to show that most bumble bee foragers exhibit daily specialization in floral resource collection (pollen vs nectar).
88. Page RE, Scheiner R, Erber J, Amdam GV: **The development and evolution of division of labor and foraging specialization in a social insect.** *Curr. Top. Dev. Biol.* 2006, **74**:253-286.
89. Lihoreau M, Buhl J, Charleston MA, Sword GA, Raubenheimer D, Simpson SJ: **Nutritional ecology beyond the individual: a conceptual framework for integrating nutrition and social interactions.** *Ecol. Lett.* 2015, **18**:273-286.  
Extended the The Nutritional Geometric modeling framework to social organisms.
90. Tschamtkke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, Bengtsson J, Clough Y, Crist TO, Dormann CF, Ewers RM: **Landscape moderation of biodiversity patterns and processes—eight hypotheses.** *Biol. Rev. Camb. Philos. Soc.* 2012, **87**:661-685.
91. Kennedy CM, Lonsdorf E, Neel MC, Williams NM, Ricketts TH, Winfree R, Bommarco R, Brittain C, Burley AL, Cariveau D, Carvalheiro LG: **A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems.** *Ecol. Lett.* 2013, **16**:584-599.  
Analyzed data from 23 crop systems to identify landscape characteristics that impact bee richness and abundance, and detected a positive influence of habitat quality on both.
92. Lichtenberg EM, Kennedy CM, Kremen C *et al.*: **A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes.** *Glob. Change Biol.* 2017, **00**:1-12 <http://dx.doi.org/10.1111/gcb.13714>.
93. Inouye DW: **Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers.** *Ecology* 2008, **89**:353-362.
94. Gezon ZJ, Inouye DW, Irwin RE: **Phenological change in a spring ephemeral: implications for pollination and plant reproduction.** *Glob. Change Biol.* 2016, **22**:1779-1793.
95. Lasky JR, Uriarte M, Muscarella R: **Synchrony, compensatory dynamics, and the functional trait basis of phenological diversity in a tropical dry forest tree community: effects of rainfall seasonality.** *Environ. Res. Lett.* 2016, **11**:115003-115016.
96. Jakobsen HB, Kristjansson K: **Influence of temperature and floret age on nectar secretion in *Trifolium repens* L.** *Ann. Bot.* 1994, **74**:327-334.
97. Polatto LP, Chaud-Netto J, Alves-Junior VV: **Influence of abiotic factors and floral resource availability on daily foraging activity of bees.** *J. Insect Behav.* 2014, **27**:593-612.
98. Willmer P, Stone G: **Temperature and water relations in desert bees.** *J. Therm. Biol.* 1997, **22**:453-465.
99. Forrest JRK, Chisholm SPM: **Direct benefits and indirect costs of warm temperatures for high-elevation populations of a solitary bee.** *Ecology* 2017, **98**:359-369.
100. Forrest JRK: **Plant–pollinator interactions and phenological change: what can we learn about climate impacts from experiments and observations?** *Oikos* 2015, **124**:4-13.
101. CaraDonna PJ, Petry WK, Brennan RM, Cunningham JL, Bronstein JL, Waser NM, Sanders NJ: **Interaction rewiring and the rapid turnover of plant–pollinator networks.** *Ecol. Lett.* 2017, **20**:385-394.
102. Brittain C, Williams N, Kremen C, Klein A-M: **Synergistic effects of non-*Apis* bees and honey bees for pollination services.** *Proc. R. Soc. Lond. B* 2013, **280**:20122767.
103. Gillespie SD, Adler LS: **Indirect effects on mutualisms: parasitism of bumble bees and pollination service to plants.** *Ecology* 2013, **94**:454-464.
104. Schaeffer RN, Mei YZ, Andicoechea J, Manson JS, Irwin RE: **Consequences of a nectar yeast for pollinator preference and performance.** *Funct. Ecol.* 2016, **31**:613-621.
105. Vannette RL, Fukami T: **Nectar microbes can reduce secondary metabolites in nectar and alter effects on nectar consumption by pollinators.** *Ecology* 2016, **7**:1410-1419.
106. Bonoan RE, Tai TM, Rodriguez MT, Feller L, Daddario SR, Czajka RA, O'Connor LD, Burruss G, Starks PT: **Seasonality of salt foraging in honey bees (*Apis mellifera*).** *Ecol. Entomol.* 2016, **42**:195-201.
107. Richardson LL, Adler LS, Leonard AS, Andicoechea J, Regan KH, Anthony WE, Manson JS, Irwin RE: **Secondary metabolites in floral nectar reduce parasite infections in bumblebees.** *Proc. R. Soc. Lond. B* 2015, **282**:20142471.
108. Goulson D, Nicholls E, Botías C, Rotheray EL: **Bee declines driven by combined stress from parasites, pesticides, and lack of flowers.** *Science* 2015, **347**:1255957.
109. Stanley DA, Raine NE: **Chronic exposure to a neonicotinoid pesticide alters the interactions between bumblebees and wild plants.** *Funct. Ecol.* 2016, **30**:1132-1139.
110. Stanley DA, Garratt MPD, Wickens JB, Wickens VJ, Potts SG, Raine NE: **Neonicotinoid pesticide exposure impairs crop pollination services provided by bumblebees.** *Nature* 2015, **528**:548-550.  
Demonstrated that lower visitation and reduced pollen collection are among the sublethal impacts of neonicotinoid pesticide exposure demonstrated by a bumble bee species (*B. terrestris*) in an agricultural system (apple).
111. Chittka L, Raine NE: **Recognition of flowers by pollinators.** *Curr. Opin. Plant Biol.* 2006, **9**:428-435.
112. Arien Y, Dag A, Zarchin S, Masci T, Shafir S: **Omega-3 deficiency impairs honey bee learning.** *Proc. Natl. Acad. Sci. U. S. A.* 2015, **112**:15761-15766.
113. Gegeer RJ, Otterstatter MC, Thomson JD: **Bumble-bee foragers infected by a gut parasite have an impaired ability to utilize floral information.** *Proc. R. Soc. Lond. B* 2006, **273**:1073-1078.
114. Palmer MJ, Moffat C, Saranzewa N, Harvey J, Wright GA, Connolly CN: **Cholinergic pesticides cause mushroom body neuronal inactivation in honeybees.** *Nat. Commun.* 2013, **4**:1634.
115. Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE: **Global pollinator declines: trends, impacts and drivers.** *Trends Ecol. Evol.* 2010, **25**:345-353.
116. Scheper J, Reemer M, van Kats R, Ozinga WA, van der Linden GTJ, Schaminée JHJ, Siepel H, Kleijn D: **Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands.** *Proc. Natl. Acad. Sci. U. S. A.* 2014, **111**:17552-17557.  
Found that loss of host plants is strongly associated with population decline in bee communities in the Netherlands.
117. Bartomeus I, Ascher JS, Gibbs J, Danforth BN, Wagner DL, Hedtke SM, Winfree R: **Historical changes in northeastern US bee pollinators related to shared ecological traits.** *Proc. Natl. Acad. Sci. U. S. A.* 2013, **110**:4656-4660.  
Identified traits (including small diet breadth) associated with population decline in bee communities in the northeastern US.
118. Ziska LH, Pettis JS, Edwards J, Hancock JE, Tomecek MB, Clark A, Dukes JS, Loladze I, Polley HW: **Rising atmospheric CO<sub>2</sub> is reducing the protein concentration of a floral pollen source essential for North American bees.** *Proc. R. Soc. Lond. B* 2016, **283**:20160414-20160417.