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Interactions between bee foraging and floral resource phenology shape bee populations and communities

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Flowers are ephemeral, yet bees rely on them for food throughout their lives. Floral resource phenology – which can be altered by changes in climate and land-use – is therefore key to bee fitness and community composition. Here, we discuss the interactions between floral resource phenology, bee foraging behaviour, and traits such as diet breadth, sociality, and body size. Recent research on bumble bees has examined behavioural responses to local floral turnover and effects of landscape-scale floral resource phenology on fitness, abundance, and foraging distances. Comparable studies are needed on non-social, pollen-specialist species. We also encourage greater use of information contained in museum collections on bee phenologies and floral hosts to test how phenology has shaped the evolution of bee–plant associations.

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Introduction

Bees are a species-rich and abundant group of flower-feeding insects that are important pollinators of crops and wild plants [1–3]. Bees are nutritionally dependent throughout their lives on floral resources, which they acquire while adults are active—a period when females of non-parasitic species gather floral resources for their offspring, and males and females of all species consume nectar (and sometimes pollen) for their own sustenance [3]. Bee abundance or reproductive output often correlates with floral abundance (*e.g.* [4–6]), supporting the idea that floral resources are key drivers of bee population dynamics [7]. However, bee populations and individuals have finite flight seasons, which must be timed to coincide with floral resource availability [7].

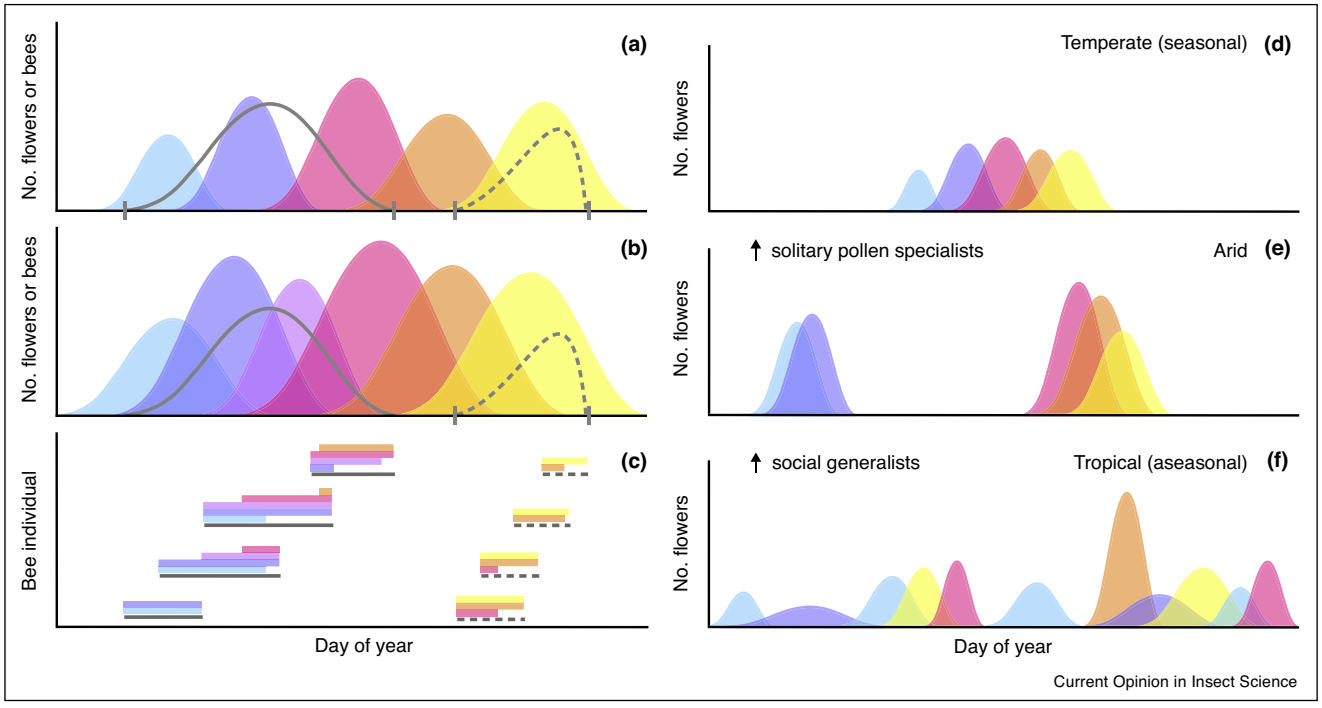
We define *floral resource phenology* as the temporal distribution of floral species available to a particular bee population (Figure 1a)—that is, within the bees' flight season and foraging range, and with accessible (and acceptable) rewards. Here, we argue that floral resource phenology plays a key and underappreciated role in shaping bee foraging ecology, community assembly, and evolution. First, we define important aspects of floral resource phenology for bees and describe the ubiquity of spatiotemporal floral resource variation. Second, we synthesize recent work on life-history traits and behaviours that influence how bees interact with changing floral resources. Third, we discuss the possible relationship between community floral resource phenology and bee community composition via the life-history and behavioural traits associated with foraging. Lastly, we point out that anthropogenic changes often alter floral resource phenologies in ways that affect bees. Throughout, we draw heavily on our experience in north-temperate ecosystems, while also noting ways in which other ecosystems can differ.

Floral resources in time and space

Bees have species-specific foraging phenologies and (except for cleptoparasitic species, which we do not consider here) central-place foraging behaviour [3]. These traits, combined with finite foraging ranges [8], define the temporal and spatial extent of floral resources with which bees can interact. Bee flight seasons (Figure 1a) vary from weeks to years [3] and often vary among sexes and castes within species. The floral resource phenology experienced by a bee population is characterized by its duration, total floral abundance, species richness, resource turnover (change in different species' relative floral abundances), and resource shortages and pulses (Figure 1a–c).

Within a landscape, floral resources are heterogeneous in time and space. Plant species and habitats flower at different times (*e.g.* [9–11]), leading to temporal turnover in the floral assemblage (*e.g.* [12•,13])—which itself may vary spatially. Thus, bee individuals and populations encounter changes in relative floral frequencies, and periods and areas of scarce resources. Seasonal and spatial variation in the composition of floral resources may pose challenges for bees that are behaviourally or physiologically tied to particular floral hosts (see Bee life-history traits and Behaviour, below). However, such variation may also be a vital source of nutritional diversity for species that are not pollen specialists (*e.g.* [14]). By

Figure 1



Conceptual illustration of the **(a–c)** floral resource phenology experienced by bee populations in a plant community, and **(d–f)** floral phenologies of different climate zones over a year. (a) Flower distribution through time of six plant species, represented by solid-coloured curves, the flowers of which have rewards accessible to the two illustrated bee species and are within their normal foraging range. The grey lines are the population flight seasons of two bee species (solid line is a long-season bee, dashed line is a short-season bee). The former species is likely to encounter more resource turnover and shortages than the latter. (b) The floral resource phenology experienced by the two bee species in (a) if they expand their foraging range. They would likely encounter more flowers and floral types. (c) The lifetime foraging durations of individual bees from the two bee populations, represented by the grey lines, and the floral species that each experiences, represented by the stacked coloured lines, given the floral resource phenological curves in (b). Individuals from the same population will experience different resource phenologies and thus have idiosyncratic behavioural responses to resource turnover and shortages. For example, the third bee of the solid line species may prefer the light blue flowers. When faced with declining numbers of light blue flowers, the bee may switch to the pink flowers, despite these being less abundant than other floral types, because they occur in the same area. Panels (d–f) show examples of community floral resource phenologies in different climate zones that each differ in their duration, position within the year, periodicity within a year, and principal climate variable that drives flowering. Across years, arid phenologies should be more variable because they are driven by variable precipitation. Characteristic regional resource phenologies likely contribute to shaping bee community composition by favouring particular bee life-history traits.

influencing opportunities for foraging, floral resource phenology can affect the vital rates of bee populations and may exert selection on life history-traits.

Bee life-history traits

Life-history traits govern the floral resource phenology experienced by bees and the sensitivity of their populations to temporal changes in floral resources. Bees with longer flight seasons encounter more resource turnover, flower species, and resource gaps than bees with shorter seasons (Figure 1a, compare grey lines; Table 1). Larger bees, which tend to have broader foraging ranges [8], have more opportunities to adjust to local floral resource changes than bees with smaller ranges (compare Figure 1a,b; Table 1); however, their resource requirements are correspondingly greater.

Flight-season length is associated with other traits pertinent to how bees experience floral resource change – floral specialization and sociality – forming a loose phenology syndrome. Floral specialization, or lecty, determines the breadth of resources that a bee exploits: oligolectic bees collect pollen from a narrow range of (usually related) plant genera, while polylectic bees have a broader diet [15]. Long-season bees tend to be social, with successive broods of workers foraging over long timespans, and are by necessity polylectic, because they must forage on a series of floral hosts to survive through the season [16]. At the other extreme, short-season bee species are typically solitary and are more likely to be oligolectic.

In addition, resource reserves, typically stored outside the body in social bees (in food pots) and internally (in fat

Table 1

Hypothesized general links between floral resource phenology and bee traits. Note that several bee traits are often correlated (*e.g.* social bees tend to have longer flight seasons and broader diets than solitary bees), so that many of the hypothesized associations are not independent of one another

Aspect of floral phenology	Bee trait	Hypothesized association	Supporting references
Resource shortages and turnover	Flight-season length	Longer flight periods → greater sensitivity to turnover and shortages, but also stronger selection for behavioural flexibility	[18••,23]
	Floral specialization (lecty)	Greater floral specialization → greater sensitivity to turnover, but also stronger selection for tight phenological cueing with host	[26,27]
	Sociality	More social → more sensitive to shortages and turnover	[18••]
	Quantity of resource reserves	Fewer resource reserves → greater sensitivity to shortages	Compare Refs. [9,17]
	Body size and foraging range	Larger size and foraging range → lower sensitivity	
Community season length and regularity	Sociality	Discrete, regular seasons → social and solitary bees Short, irregular seasons → solitary bees Long seasons/ aseasonal → social bees	[3,27,37,55]
	Floral specialization	Discrete, regular seasons → oligoleges and polyleges Short, irregular seasons → oligoleges Long seasons/ aseasonal → polyleges	[3,27,37]
Season timing	Overwintering life-stage	Bees associated with early-season plants → adults Bees associated with late-season plants → larvae/pre-pupae	[3]

bodies) in solitary bees, can allow bees to withstand periods of resource scarcity in the landscape (Table 1). Thus, social bees with large honey stores can persist through long resource droughts (*e.g.* [17]). However, in social, long-season bumble bees (*Bombus* spp.), which do not maintain large honey reserves, brood production is greater when resources are consistently available, and reduced by periods of resource shortage (*e.g.* [9,18••,19,20,21•,22]). Bumble bee species with long colony cycles are more negatively affected than short-season species by landscape simplification, perhaps because of resource shortages [23]. However, resource shortages at particular times were predicted to cause colony extinctions in honey bees (*Apis mellifera*), despite their ability to store food [24•]. Although research suggests fitness consequences of resource shortages for long-season bees, we need studies that comprehensively quantify floral resource phenology to pinpoint the mechanism.

We generally lack information on the fitness consequences of mistiming or resource gaps for solitary bees, though reproductive output in trap-nesting bees of arid shrubland is seemingly unaffected by variation in resource phenology [25]. Short-season, oligolectic bees likely experience severe fitness consequences of complete mismatch with floral hosts. However, this has rarely been documented (though see Ref. [26])—perhaps due to the difficulty of observing and measuring fitness of wild bees that fail to nest. Severe fitness consequences of mistiming may be the reason short-season specialist bees often show tight phenological cueing with their host

plants [27]. Conversely, we hypothesize that long-season bees are under strong selection to have flexible behavioural responses to variable resources (Table 1). We need long-term monitoring of social and solitary bee populations along with their primary floral hosts to understand how floral resource phenology affects the population dynamics of bees with different life histories.

Behaviour

Bees often encounter resource turnover and shortages, and individuals' foraging experiences will be idiosyncratic because they encounter different resource phenologies depending on their flight season timing (Figure 1c) and location. When faced with resource changes, bees can respond by changing their floral usage or by foraging elsewhere, but the exact response may depend on individual traits and foraging histories. Bees can adjust their foraging distances according to resource availability, foraging at relatively short distances in resource-rich landscapes. For example, bumble bee workers typically forage over distances less than 100 m in flower-rich montane areas [28], but a few hundred metres to kilometres in resource-poor agricultural landscapes (*e.g.* [21•,29,30]). In human-modified landscapes, bumble bees forage further when local floral abundance (*e.g.* [21•,29,31]) or floral richness [32] is low. Additionally, social apid bees can communicate with nestmates about resources and thus deploy workers rapidly, in numbers appropriate to floral availability (*e.g.* [17,33]). At a population level, bee species seem to track the spatiotemporal availability of floral resources in human-modified landscapes [34,35•]. However, more research is needed to examine whether expanding foraging distances can reduce bee survival and provisioning if the time and energy costs outweigh the benefits of the new resources [24•,36].

Floral specialization is central to an individual bee's response to periods of floral turnover and shortages. Polylectic bees can shift or expand their floral usage with availability. The commonness of resource switching is indicated by the high frequency of 'rewiring', or bee species interacting with different plants across time and space, in plant–pollinator networks (*e.g.* [12•,37,38]). Furthermore, bees can have broader diets in areas and years in which resources are sparser [39], or when floral richness is higher [40,41]. However, we need to better understand the fitness consequences of switching floral types; for example, pollens may differ in nutritional quality (*e.g.* [42]). Oligoleges should have less flexibility when faced with shortages or declines in their hosts (Table 1). Indeed, sometimes they are unwilling to try new foods [43,44]. However, oligoleges will occasionally broaden their pollen diets if normal hosts are scarce [43], and if morphologically or biochemically similar flowers are available (*e.g.* [45]). In general, we lack understanding of what oligolectic bees do under duress—do they pause nesting [44], or do they search elsewhere for their host, given their finely-tuned host-localization behaviours (*e.g.* [46])? We need more comparative analyses of the pollen diets of oligolectic bee populations in different environmental contexts, along with experimental tests of behaviour in settings where floral hosts are scarce, to better predict responses of specialist bees to changes in floral availability.

Our understanding of behavioural responses to floral resource turnover comes primarily from work with bumble bees. Many individual bees have preferred or 'major' flowers that they visit most commonly [47] and may be slow to incorporate new plant species into their repertoire [48]. However, individual bumble bees can also be opportunistic. Individuals often have 'minor' flowers that they visit infrequently, perhaps to keep track of changing resources [47], and will switch floral types upon encountering low-reward and low-frequency flowers [49]. In the lab, bumble bees are quick to switch to high-quality pollen resources [50]. When faced with resource turnover in the field, alpine bumble bees mostly stayed in their foraging area and switched to a new, less-abundant food resource; that is, they remained site-constant rather than flower-constant [51••]. In regions where resource turnover is high, it is likely adaptive for polylectic bees to stay in areas they have previously found rewarding, because of the costs of searching elsewhere [51••]. We need more mechanistic research examining individual bee responses to floral resource change in the field, because these individual responses determine a population's local persistence.

Community ecology

Plant communities have varied floral resource phenologies, characterized by timing within a year, regularity, duration, total floral richness, and the principal climate variables that limit flowering (Figure 1d–f). For example, high-altitude and high-latitude areas have short, regular seasons driven by favourable temperatures (*e.g.* [52]) (Figure 1d); arid regions have irregular flowering pulses driven by precipitation (*e.g.* [27,53]) (Figure 1e); and aseasonal tropical areas have year-round (though spatially patchy) flowering (*e.g.* [54]) (Figure 1f). Given the role of floral resources in determining bee population growth rates and foraging decisions, floral phenology acts as an ecological filter, shaping the species (and life-history trait) composition of bee communities (Table 1). For example, areas with discrete, predictable flowering seasons longer than a couple of months, such as lowland temperate and subalpine areas, often support bee communities diverse in life-history traits related to floral resource use, that is, mixes of solitary and social bees, both specialist and generalist (*e.g.* [37]). Arid regions support many oligolectic solitary bees with short seasons that reliably coincide with irregular blooming [27] (Figure 1e). Aseasonal tropical regions often support a

high proportion of social bees such as *Apis* spp. or meliponine stingless bees [3], which require continuously available resources during their long foraging period but can recruit to patchy resources (Figure 1f). At higher elevations and latitudes, shorter flowering seasons create a challenge for social bees, which must squeeze two or more generations into a season (at least one generation of workers and a reproductive generation). Indeed, within the Halictidae, the occurrence of sociality is associated with warmer climates and longer growing seasons [55]. Nevertheless, one social lineage of apid bees – the bumble bees – has been extremely successful in habitats with short flowering seasons, apparently thanks to well-developed thermoregulatory abilities, which allow foraging and rapid larval development even at low temperatures [55].

Just as different plant families have characteristic flowering periods in temperate biomes [56], bee taxa also differ in seasonality. For example, most species of *Andrena* (outside the subgenus *Callandrena*; [57]) are vernal, as are most *Osmia*; several other taxa, such as the leaf-cutter bees (*Megachile* spp.), are typically active in late summer. Seasonality is strongly associated with overwintering life-stage (Table 1), which may explain its strong phylogenetic signal. Spring-active bees (including mated queens of social halictids and apids) typically over-winter as adults, while species active later in the season (including *Callandrena* and most *Megachile* spp.) typically overwinter as larvae (pre-pupae) [3]. These phylogenetically constrained activity periods mean that bee–plant associations can, to some extent, be predicted based on phenology. For example, *Callandrena* spp. are unusual among *Andrena* not only for their autumnal phenology but also in specializing on the late-flowering family Asteraceae [57]. Phylogenetic associations between particular sets of plants and pollinators, as noted in a study of 47 pollination networks [58], likely owe something to shared phenologies—although phenology was a trait the authors of that study were unable to examine. Most bee biologists are aware of the phylogenetic signal in bee and plant seasonality, but in our opinion it is underused both in predicting pollination network structure and in understanding evolutionary shifts in floral host use—likely because phenology is less readily measured than morphological traits. We urge researchers to take fuller advantage of the data contained in museum collections to rigorously document the phenologies and floral-host associations of bees (*e.g.* [59,60]). These databases can then be used to conduct much-needed evaluations of the evolutionary and ecological linkages between phenology and floral-host associations.

Floral resource phenology and global change

Floral resource phenology can be altered by climate change and habitat modification in ways that may affect bee populations and communities. Over four decades in subalpine Colorado, the flowering season has extended as summers have warmed, but this extension has been accompanied by a midseason floral decline [10,52]. Expanding floral shortages may harm long-season *Bombus* (as suggested by Ref. [10]), yet other species may benefit from the longer periods of resource availability. We need more research examining how climate-driven alterations in floral resource phenology affect bee foraging and vital rates. Much recent research has focused on the potential for pollinator and flower timing to differentially shift, leading to reduced overlap and reproductive declines in one or both partners [61]. However, a recent review concluded that pollinator and plant phenologies generally respond to similar environmental cues, and that there is so far little evidence for phenological mismatches between partners [61]. When examining the potential for phenological mismatch, we suggest that future research explicitly consider the bee life-history traits and behaviours described in the current review, because these traits may contribute to the resilience of bee populations to temporal decoupling from their floral resources.

The habitat alterations associated with agricultural and urban landscapes also change floral resource phenology. The phenologies of agricultural landscapes differ from that of most natural habitats in having short pulses of mass-flowering crops, such as oilseed rape, within otherwise low-abundance resource phenologies. Bee populations that overlap with such pulses may benefit if they have short flight seasons, or fail to benefit if their flight season extends beyond the pulse [18••]. Landscapes with mixtures of agricultural, urban, and natural areas have higher bee abundance than landscapes with fewer habitats, perhaps because the phenologies integrated across habitats prolong flower availability [11,35•,62,63]. Furthermore, floral resource phenologies characteristic of human-modified habitats may act as filters, such that bees with different functional traits are associated with agricultural and natural habitats [16]. Restoring habitat with plant mixes that provide continuous, season-long floral resources should support larger bee populations [21•] and higher species richness [64,65].

Conclusions

Floral resource phenology is central to the ecology and evolution of bee foraging, and to bee community composition—yet much remains unknown about the relationships between bees and floral phenology. We call, first, for more basic research on bee foraging ranges, flight seasons, and floral-host associations. Second, we need studies that examine bee behavioural and reproductive responses to fluctuations in resource availability through time (especially in bees outside *Apis* and *Bombus*). Finally, we encourage researchers to begin examining how bee foraging and floral phenology have co-

evolved, by examining data on floral host use and phenology in the context of phylogenetic relatedness. Given the alterations of floral resource phenology that accompany anthropogenic environmental change, a better understanding of bee responses to global changes will be necessary to anticipate their future population and community trajectories.

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