PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Review

**Cite this article:** Grüter C. 2026 Flower constancy in pollinators: a bouquet of agendas shapes interactions among mutualistic partners. *Proc. R. Soc. B* **293**: 20252103.
https://doi.org/10.1098/rspb.2025.2103

Received: 15 August 2025
Accepted: 8 December 2025

**Subject Category:**
Ecology

**Subject Areas:**
behaviour, ecology, ecosystem

**Keywords:**
pollination, cognition, facilitation, flower constancy, behavioural flexibility, plant–pollinator interactions

**Author for correspondence:**
Christoph Grüter
e-mail: c.grueter@bristol.ac.uk

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8213610.

THE ROYAL SOCIETY
PUBLISHING

# Flower constancy in pollinators: a bouquet of agendas shapes interactions among mutualistic partners

Christoph Grüter

School of Biological Sciences, University of Bristol, Bristol, UK

Plant–pollinator interactions have become a major research area because of their impact on key ecosystem services. One pollinator behaviour of particular importance is flower constancy, the tendency to temporarily focus on one flower species during a foraging trip, thereby promoting cross-pollination. The costs and benefits of flower constancy for plants and pollinators are varied, complex and far from understood. This review aims to synthesize studies spanning the last decades, from both plant and pollinator perspectives. Flower constancy is often viewed as an epiphenomenon of pollinator cognition, but there is increasing recognition that pollinators show remarkable behavioural flexibility in their flower choice, often in response to ecological and social factors. Plants usually benefit from flower constancy, which reduces pollen loss and interspecific pollen transfer. However, in some situations, pollinator inconstancy can be advantageous owing to increased visits from pollinators shared with co-flowering plants, a process called facilitation. The fitness consequences of pollinator behaviour for rare or invasive plants are intriguing yet little understood, with important implications for plant conservation. Rather than seeing flower constancy as a strategy imposed on pollinators by cognitive constraints, this review emphasises that plants and pollinators pursue varied agendas depending on their ecological context and lifestyle.

## 1. Introduction

Most flowering plants depend on animal pollinators for sexual reproduction [1]. The effectiveness of pollinators for this role depends on a range of morphological and behavioural traits. One behaviour of particular importance is flower constancy, the tendency of a pollinator to visit flowers of the same plant species during a foraging trip, sometimes for days [2–5], while bypassing rewarding alternative flowers [2,6–9]. While flower constancy has been observed and studied predominantly in bees (e.g. [2,4,7,10–12]), it has also been reported in butterflies [13–15], hoverflies [16], beetles [17] and birds [18] (see the electronic supplementary material, table S1 for a list of examples mentioned in this review). Flower constancy ensures that flowers receive pollen from the same species, facilitating cross-pollination. From a pollinator perspective, flower constancy is often viewed as a suboptimal strategy and the result of pollinators attempting to mitigate cognitive limitations [2,7–9]; and yet, a growing number of studies highlight that pollinators, such as honeybees (Apini) or bumblebees (Bombini), are flexible and differ in their flower choice behaviour, e.g. in response to ecological or social factors. This review brings together traditional views and recent insights into the causes and consequences of flower constancy from both pollinator and plant perspectives, with the aim of better understanding the varied interests that shape interactions among plants and their pollinators.

At first glance, flower constancy is a deceptively simple behaviour, a choice of a flower of one type over another type, and yet a closer look reveals a perplexing complexity that spans biological levels, from neurons to species communities, shapes plant–pollinator communities and raises a number of intertwined mechanistic and evolutionary questions. Here, flower constancy refers to the tendency to move between flowers of the same species when other rewarding flower types are available. Flower constancy is based on associative learning—e.g. between colour, odour or shape and floral rewards [8]—and is different from the innate dietary preferences found in specialist (monolectic and oligolectic) pollinators [5,19] (note that bees can be specialists when collecting pollen, but generalists when collecting nectar [20]. For more details about innate dietary preferences in bees, see [20]). This definition of flower constancy is descriptive and agnostic regarding the causes and adaptive value of flower constancy (similar to Takagi & Ohashi [19], but different from Waser's [7] classic definition, who considered flower constancy a non-optimal foraging strategy caused by cognitive limitations).

Researchers have used two main approaches to quantify flower constancy: first, by observing movements between natural or artificial flowers, sometimes with the aim to calculate a flower constancy index. Calculating indices can be feasible and useful in relatively simple and controlled settings (e.g. [7,21–25]), but they are challenging to apply and interpret in a more complex and natural setting with multiple species, uneven floral distributions, abundances or energetic costs associated with each (see [7,21,26,27] for discussion of different indices); and second, by analysing pollen load purity of foraging bees, which reflects the sum of its foraging choices during a foraging trip (e.g. [28,29]). While the study of natural flower movements provides information about flower choice, the diversity and frequency of available options, it is often not feasible in natural habitats because of habitat and interaction network complexity or inaccessibility (e.g. the forest canopy). Analysing pollen load purity can be a convenient shortcut, but findings can be misleading as pollen purity could be the result of local abundance and clustering of flowers. Pollinators could also be visiting different flower types while collecting pollen only from one [7,8]. Artificial flower set-ups solve many of these challenges (e.g. [10,19,23,30]), but they are feasible only for a small number of pollinators, predominantly large social bees, and artificial set-ups work best with sugar solution as a reward. Pollinators are likely to modify their strategies depending on whether they collect pollen or nectar, e.g. by being more specialized when collecting pollen [11,20].

## 2. The plant perspective

Animal-mediated pollination involves the transfer of pollen from the male parts of the flower, the anthers, to the female parts, the stigma, with the help of a pollinator. Darwin [6, p. 419] noted that flower constancy is of 'great significance to the plant, as it favours cross-fertilization of distinct individuals of the same species'. Flower constancy and inconstancy differentially shape competition between plant species by affecting both the quantity and quality of plant-pollinator interactions (figure 1; [15,31–35,38–44]).

### (a) Interspecific pollen transfer

Inconstant pollinators will frequently transfer pollen from one species to the stigmas of a different species. This interspecific pollen transfer (IPT) is ubiquitous [32,33,42,45–48] and can reduce plant fitness through a variety of mechanisms [33,41,48–51]. If a pollinator switches plant species, much of the original pollen is lost on the heterospecific flowers or it is groomed off in the process, which can reduce the seed set of conspecifics that receive less pollen as a result [33,35,39,41,52,53]. Pollen misplacement can also lower outcrossing rate, thereby reducing not only offspring quantity but also quality [53].

For the plant receiving heterospecific pollen, the deposition of this pollen can impair seed set [35,39,41], for example, through stigma clogging, which is the reduction of the receptive stigma surface area for conspecific pollen, stigma closure, which reduces the receptivity for conspecific pollen, or active inhibition of germination and hybridization (see [41] for a review). IPT could be especially costly for rare plants co-flowering with more common species as they are likely to receive relatively more heterospecific pollen [35,38,41,51,54,55], which could increase the risk of extinction of rare plants [41,56]. IPT from invasive to native plants has the potential to reduce the reproductive success of native plants ([41,48]; but see [45,46,57]). Flower constancy affects the strength of this effect; for example, the solitary bee *Rhodanthidium septemdentatum* switched more often from invasive to native plants and carried more pollen between species than the highly flower constant honey bee *Apis mellifera*, with negative impacts on seed production in one of three native plant species visited by the solitary bees [58]. This highlights how different types of pollinators can create different interaction pollen transfer networks (see also [59]). More flower constant pollinators reduce the risk of ITP and facilitate cross-pollination [60], but they may also increase repeat visits to flowers of the same plant, thereby increasing self-pollination (geitonogamy), which can impair plant fitness [61].

The costs of these interspecies pollen transactions have long been seen as a driver for greater divergence in floral traits, e.g. different habitat choice, flowering times or floral morphology (e.g. morphology, colour or scent; see §4) and self-pollination [15,33,38–42,49,62]. A striking example is the closely related plants *Phlox drummondii* and *Phlox cuspidata*, which share the butterfly *Battus philenor* as their primary pollinator. Butterflies show little constancy when the two plants appear in their ancestral colours, leading to pollen loss and hybridization [15]. Where the two species are sympatric, however, selection on an allele affecting flower pigment intensity causes flowers to have more distinctive colours, which increases flower constancy of their pollinator and promotes reproductive isolation in the plants [15]. This example highlights how flower constancy can drive evolutionary divergence in closely related sympatric lineages (see also [63,64]).

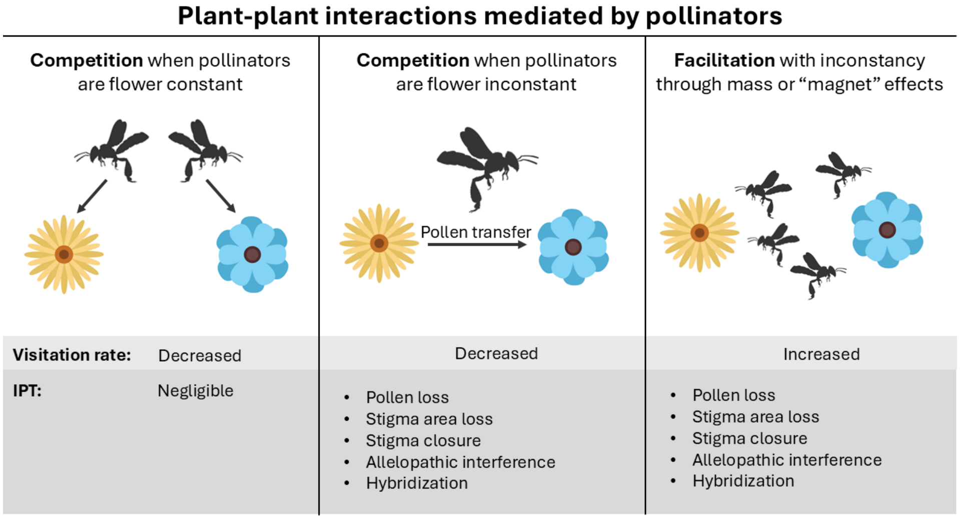


**Figure 1.** Pollinator behaviour affects interactions between plants. If plants from different species share the same pollinator, then this will probably affect the fitness of plants positively or negatively. While sharing pollinators with a second plant species will often have a negative impact on flowers, e.g. by reducing visitation rate or the cost of interspecific pollen transfer (IPT), there may be circumstances when the sharing of inconstant pollinators benefits plants through facilitation [31–37], which could lead to increased visitation rates, e.g. for rare plants. Plants visited by inconstant pollinators may still pay some costs owing to IPT, but these costs are outweighed by the benefits of increased visitation.

### (b) Facilitation

In recent years, research has increasingly emphasized that pollinator sharing does not necessarily have negative effects on plant fitness. Floral infidelity can be neutral or even beneficial for co-flowering plant species through facilitation (figure 1; [32,34,36,37,65,66]), i.e. an increase in visitation rate owing to the presence of co-flowering plants through 'magnet' or 'mass' effects. For example, non-rewarding orchids benefit from [67] or provide benefits to [68] co-flowering rewarding plants (see also [69,70]). In the latter case, the rewarding *Iris tuberosa* benefitted from *Andrena* bees attracted to the sexually deceptive orchid *Ophrys fusca* [68]. Furthermore, unattractive plants have been shown to benefit from the presence of a rewarding attractive, closely related species via increased pollinator visitation [71]. Importantly, when simulating heterospecific pollen deposition, Zhang & Agrawal [71] found no evidence of costs for either species. In high-altitude plant communities where pollinators are scarce, facilitation may be common [32]. More generally, when plant abundance is low and pollination services are limited, sharing inconstant pollinators with co-flowering plant species could increase visitation rates because of the attraction of pollinators to the area (or the survival of pollinators in an area) [32,35,37,72].

Another potential benefit of gene flow driven by pollinator inconstancy is increased genetic variation or an exchange of adaptive traits (adaptive introgression) between non-fully reproductively isolated plant species, which may have been an important evolutionary force in many plant clades [33]. In summary, the effects of floral inconstancy on plant fitness are varied, and a variation in the degree of flower constancy among pollinators, both at species and individual level, may benefit plant biodiversity (see also [73,74]).

## 3. The pollinator perspective

Pollinators are expected to maximize energy intake—either in terms of rate [75] or efficiency [76]—while making sure they also collect all required nutrients for a healthy diet [77,78]. In bees, the first requirement is primarily achieved by collecting nectar, and the second is achieved by collecting different types of pollen. Flower constancy appears to be at odds with both of these requirements: bypassing rewarding flowers risks reducing energy intake [79] because of time (increased foraging trip duration) and opportunity (missed rewards) costs [79], sub-optimal flower choice [7,80] and increased flight distances [81]. Accordingly, computer simulations of flower constant and inconstant bee colonies suggest that strict flower constancy is usually less successful in terms of net energy intake than foraging indiscriminately [79]. In addition, focusing on a particular plant species risks missing out on important nutrients (see §4b) [82].

So why should bees exhibit flower constancy? One traditional view is that cognitive limitations imposed by the processing, storage and retrieval of information favour flower constancy. Extracting a reward efficiently requires pollinators to learn a wealth of information about floral colours, odours, shapes, textures and motor skills, involving a range of cognitive tools [8]. Owing to limitations of these cognitive tools, pollinators switching between plants would be less efficient at extracting rewards [7–9,83,84]. An alternative view is that flower constancy is the economically most successful foraging strategy given the limited information a pollinator has about its environment [9,21].

## (a) Cognitive limitations

Darwin [6] and von Frisch [85] suggested that flower constancy is favoured because of the benefits of learning: a bee that has learnt how to extract nectar from, for example, linden (*Tilia*) blossoms is more efficient than a bee unfamiliar with this flower [2,14] (an idea sometimes misleadingly called 'Darwin's interference hypothesis' [86,87]). The flipside of this argument is that learning has costs and a pollinator switching to a new flower type would need time and energy to learn how to extract rewards efficiently [7,88–90]. However, research on the learning efficiency of bees and butterflies suggests that pollinators learn fast: cabbage white butterflies (*Pieris rapae*) need only a couple of flower visits to learn how to efficiently reach the nectar in two different flower types [13] and naïve *Bombus impatiens* bees collecting pollen from four plants reached a plateau in pollen collection efficiency within the first 20 visits [90]. On the other hand, *Bombus terrestris* collecting pollen from poppy flowers (*Papaver rhoeas*) improved their foraging efficiency over several foraging trips that included visiting more than a hundred flowers [89], showing that learning to exploit flowers sometimes does take time. Whether and how plant fitness is affected by pollinator learning is not well understood, but a recent study found that pollination success did not change as a result of learning how to handle flowers by *Bo. impatiens* foragers [90]. Overall, observations lead to the conclusion that bees and butterflies are quick learners, which challenges Darwin's idea that the benefits of knowing how to exploit a flower species are sufficient to favour bypassing rewarding alternatives.

Limitations in working- and long-term memory may also favour flower constancy because they cause time costs if pollinators are inconstant. Long-term memories, while robust and durable, may be costly or slow to retrieve [7,8,19]. Working memory, on the other hand, is prone to rapid decay and interference from competing information, such as new floral traits [8,13,91,92]. Inter-flower flights of inconstant bumblebees were found to be longer (approx. 1–3 s) than flights between flowers of the same species [22,93]. These delays in inconstant flights could be owing to a transient working memory that is stable for only a few seconds, or they could indicate that bees switching flower species need time to access long-term memory about the alternative type (if the second flower type is already familiar). These time delays in inter-floral flights and learning how to extract nectar are likely to accelerate flower visitation owing to flower constancy, while also facilitating information consolidation from working- to long-term memory [22]. Overall, however, time costs because of inconstancy appear to be low. Laverty [94], for instance, found that *Bombus fervidus* experienced no time costs when switching between two types of flower with simple morphologies and only an approximate 1 s delay when switching between flower types with more complex morphologies, similar to the small increases in handling time found by Raine & Chittka [22] and Goulson *et al.* [14]. One might argue that even small-time gains can add up to a substantial amount of time saved as, for instance, bees visit hundreds or even thousands of flowers per day. However, pollinators also accumulate time, opportunity and energy costs every time they fly past a rewarding flower. Computer simulations suggest that time costs of flower inconstancy need to be considerable (>30 s with each visit in the simulations) to make flower constancy more successful than inconstancy [79]. There are currently no empirical studies comparing the time costs of switching flower type—owing to learning and/or memory processes—to the costs of ignoring flowers of a different type. Such studies are most likely absent because they are exceedingly difficult to perform.

The 'search image' hypothesis proposes that flower constancy is the result of pollinators establishing a search image of a specific flower type in a complex visual environment [87]. Search images are useful when looking for cryptic targets, i.e. those that are difficult to find [95,96]. By contrast, flower constancy tends to be stronger when flowers become easier to detect or flower species become easier to differentiate (see §4a). Convincing evidence that 'search images' cause flower constancy is currently missing, but more research into visual background effects on flower constancy and attention priming [95,96] is needed to rule out that search 'search images' affect plant-pollinator interactions.

While research suggests that multiple, non-mutually exclusive cognitive processes may contribute to the strength of flower constancy in some pollinator species, the idea that cognitive constraints predispose pollinators to flower constancy is at odds with evidence that pollinators are: (i) able to process impressive amounts of information efficiently, and (ii) are varied and flexible in their behaviour, often in response to ecological circumstances and their social lifestyle (§4). This suggests that ecological and social interactions shape the cognitive tools and behavioural strategies pollinators have at their disposal, as will be discussed in §4.

## (b) Informational limitations

The costly information hypothesis [8,9] posits that flower constancy is the best strategy in an uncertain environment where acquiring information about better plant species would cost time and energy. Assessing the profitability of alternatives may require sampling a large number of flowers since different flowers of the same plant species offer variable rewards [97]. Flower constancy might then be the best option if the rewards currently experienced by a pollinator are above a threshold. Honeybees are indeed almost fully flower constant when the rewards they receive are above a reward threshold [23,98]. As the number of plant species in an environment increases, so do the sampling costs to obtain reliable information, thus favouring flower constancy [8,9]. While this hypothesis is intuitively appealing, computer simulations suggest that flower constancy becomes more costly as plant species diversity increases [79]. This is because the time, energy, and opportunity costs of bypassing flowers also increase when alternative options become relatively more numerous. Pollinators should be *less* flower-constant in a habitat with more flower species. The simulation findings highlight an important point often missed in discussions about flower constancy: even if pollinators visit the most profitable flower species, flower constancy may not be the best strategy, especially when alternative options become more abundant [79]. Empirical evidence for this is mixed, however: while Gervais *et al.* [99] and Martínez-Bauer *et al.* [100] found that increasing plant diversity was indeed associated with lower flower constancy in bumblebees, Austin *et al.* [101] found that bumblebees became more flower constant when there were more options available. The first two studies were performed under natural conditions, whereas Austin *et al.* [19] used artificial flower arrays and laboratory conditions. More research is needed to understand how increasing plant diversity affects flower constancy in different pollinators.

## 4. Behavioural flexibility and species variation

If the discussion so far has given the impression that strict flower constancy is the rule among pollinators, then this would be misleading. We know little about the degree of flower constancy for the vast majority of pollinators, but numerous studies and the widespread phenomenon of heterospecific pollen transfer (see §2) suggest that pragmatism and flexibility guide flower choice in the pollinator world. Indeed, we would expect an optimal pollinator with multiple options to divide its time between exploiting familiar flowers and sampling alternative ones [102,103]. The impression that bees are commonly flower constant may have resulted from the focus on the Western honeybee *Ap. mellifera*, a highly flower constant species [3,80,104], but even honeybees show flexibility in their floral choices in response to reward characteristics ([9]; electronic supplementary material, table S1). These two findings—variation between species and flexibility within species—suggest that there is ample scope for natural selection to drive flower choice strategies [9]. Below, I discuss three types of drivers that may be key to understanding behavioural flexibility: floral features, ecological factors and sociality.

### (a) Floral features

A key determinant of the strength of flower constancy is the value of the reward offered by flowers, which depends on the quality (e.g. sugar concentration) and quantity (amount or production rate) of the offered rewards [93,105–110]. Bumblebees preferentially foraged on more complex flowers only if they offered sucrose solution of higher concentration than simple flowers in experimental set-ups [107,108]. Bumblebees foraging naturally on different shrubs preferred the species with higher daily sucrose production per flower [111]. The small skipper butterfly was twice as likely to switch plant species after receiving a below-average reward quantity [14]. Even the highly flower-constant honeybee *Ap. mellifera* adjusted the degree of flower constancy within seconds following a flower visit, with bees becoming less flower constant when reward quality, quantity and number were reduced [23].

The response to rewards also interacts with other floral features, and flower constancy often increases as options become more dissimilar, either in a specific trait, such as flower colour and morphology, or when options differ in a greater number of traits, such as a combination of both visual and olfactory traits [7,19,30,50,84,93,104,106,112–114]. The link between flower constancy and pollinator perception is probably owing to pollinators being able to learn to differentiate more efficiently among flowers with divergent traits, which, in turn, can drive evolutionary divergence among similar plant morphs (see §2). Bees also increase flower constancy as flower size and floral display size (i.e. larger number of inflorescences per plant) increase [115,116]. Because flower and display size have been shown to correlate positively with reward size [117], flower and display sizes could be traits (among many others) used by pollinators as proxies of relative profitability of a flower species, and become less inclined to switch away from large flowers.

Reward value and extraction costs also depend on flower morphology, since the way flowers are built affects how fast pollinators can learn to extract rewards as well as the subsequent handling time costs and foraging rate (see also §3) [90,110,113,118,119]. For instance, visiting complex flowers is associated with handling times several times longer than those for simple flowers (up to 25 s versus a few seconds for simple flowers) [90,118,119]. One might, therefore, predict that pollinators prefer simple flowers. Evidence, however, is mixed: while *Bo. impatiens* preferred the simpler of two artificial flower types [107], naïve *Bo. terrestris* foraging on natural flowers preferred complex types [118]. Similarly, *Bo. fervidus* were only flower constant when visiting plants with complex morphologies [94]. What could explain these counterintuitive observations? First, bees might be discouraged to switch to an alternative type because of their experience that becoming an expert forager is costly. Second, morphological complexity might discourage or exclude some pollinators while providing rewards for the expert forager [120,121]. Visiting a complex flower type could, thus, be beneficial for pollinators experiencing intense competition, while plants might benefit if flower morphology filters out ineffective pollinators [121].

### (b) Ecological factors: spatial distribution of flowers

Recent studies have highlighted the importance of the spatial arrangement of flowers in influencing how pollinators balance floral fidelity versus behavioural flexibility [19,24]. Cape sugarbirds (*Promerops cafer*), a rare example of a flower constant bird, adjust the degree of flower constancy in relation to the relative abundance of flower species [18]. Abundance and degree of clustering of co-flowering plants determine the distances an individual needs to fly between flowers. As distances between conspecific flowers (and flowers in general) increase, both honeybees and bumblebees become less flower constant, and switching to the nearest flower type becomes more common [19,24,30,93,122–124]. Pollinators could gauge these distances based on travel costs [7] or based on floral visual angles [116]. Computer simulations similarly found that flower constancy reduces energy intake when flower density is low [79] as energy, time and opportunity costs of bypassing flowers increase when flower abundance is low. Thus, flower constancy is predicted to increase with flower abundance based on both energetics

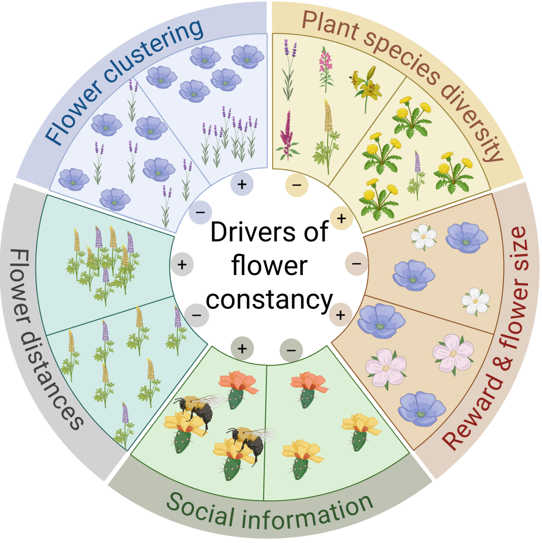


**Figure 2.** Factors affecting behavioural flexibility and the strength of flower constancy. Flower constancy depends on floral features like reward size [23], ecological factors like the arrangement of flowers in space (e.g. [19,24,125]), flower diversity [99,100] or social factors like social information [5,79,106]. + and − indicate whether a particular factor is expected to increase or decrease flower constancy (created with BioRender.com/2x874zj).

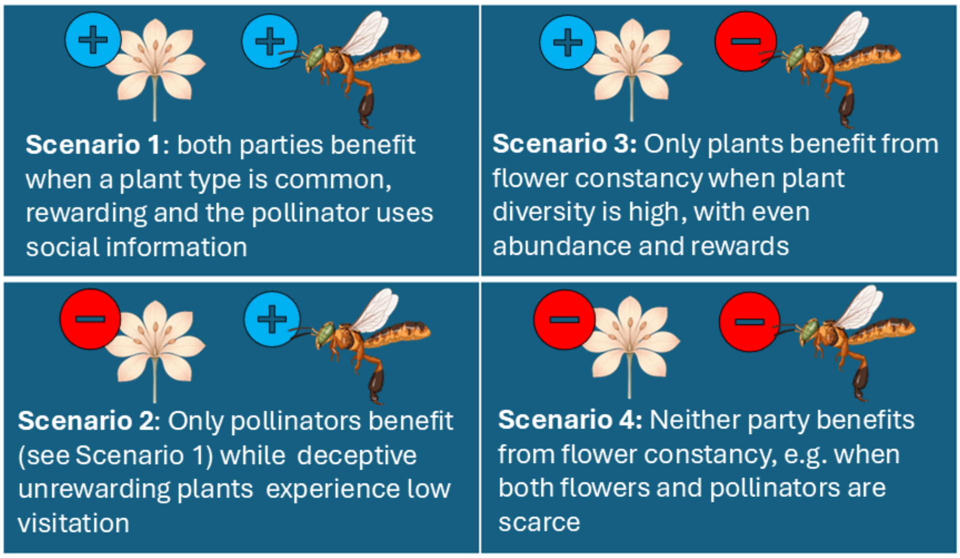
**Figure 3.** A bumblebee forager collecting pollen on meadowsweet (*Filipendula ulmaria*). Her pollen package has two colours, showing the bee has visited two types of flowers during the same foraging trip (*Rubus* before switching to meadowsweet, photo: C.G.).

and cognitive limitations (working memory instability) arguments [8,124]. Working memory instability could be the underlying mechanism that allows bees to adjust flower constancy adaptively in relation to food source abundance.

The effects of inter-floral distances also explain why flower constancy is often higher when food sources are arranged in clusters rather than when evenly mixed (figure 2; [19,125]). For plants, on the other hand, the more frequent switching in more evenly mixed situations could be costly owing to increased IPT.

## (c) Interspecies variation and the effects of sociality

Different observers have noticed that pollinator species can vary considerably in how flower constant they are [2,7,9,44,82,126]. Bateman [25] and Waser [7], observing bees moving between flowers, found that honeybees were more flower constant than bumblebees. Furthermore, honeybees returning to their hive have mostly pure pollen loads [3], whereas those of bumblebees are commonly mixed (figure 3; [127]). In controlled laboratory experiments, *Bo. impatiens* foragers were also quicker to switch from a deteriorating sugar solution to an alternative one than *Ap. mellifera* [128]. Even within bumblebees (*Bombus*), there appear to be considerable differences: in the South American *Bombus atratus* and *Bombus bellicosus*, 80% and 84% of pollen foragers visited just one plant during a foraging trip [11], whereas only 23% of pollen foragers showed flower constancy in the European *Bo. terrestris* ([129]; see also [29]). Whether these differences indeed reflect innate interspecific differences or differences in ecological or floral factors remains to be studied. Overall, however, evidence supports the view that pollinator groups vary in the degree of flower constancy.



**Scenario 1:** both parties benefit when a plant type is common, rewarding and the pollinator uses social information

**Scenario 3:** Only plants benefit from flower constancy when plant diversity is high, with even abundance and rewards

**Scenario 2:** Only pollinators benefit (see Scenario 1) while deceptive unrewarding plants experience low visitation

**Scenario 4:** Neither party benefits from flower constancy, e.g. when both flowers and pollinators are scarce

**Figure 4.** Interests of both plants and their pollinators when pollinators are *flower constant*. Four scenarios (1–4) are suggested that reflect different situations. The + and − indicate whether an individual may benefit or not in this particular scenario (created with Illustrae and BioRender.com).

One factor that has been linked to flower constancy is sociality and social lifestyle. Solitary pollinators, including bees, butterflies and flies, are often less flower constant than highly social bees [25,47,58,130]. In a comparative study of pollen loads of 56 bee species in a temperate bee community, Smith *et al.* [126] found that social bees were more flower constant than solitary bees. Three explanations for this sociality effect have been proposed: the resource-partitioning hypothesis [8,9,105], the communication hypothesis [5,8,79] and the diet breadth hypothesis [82,131].

The resource partitioning hypothesis argues that flower constancy in social bees is a form of task partitioning that helps foragers reduce competition with nestmates by specializing on different flower species [8,105,129]. However, if a subset of nestmates specialises in a subset of flowers, then they still compete within their group for flowers of one type, while now also paying the energy, time and opportunity costs of flower constancy.

Sociality could favour flower constancy in bees because many social bees communicate about food sources [5,79]. Because social bees share information selectively about high-quality food sources, nestmates using social information are likely to discover more profitable food sources [132–136]. For example, honeybees use the waggle dance, and some stingless bees lay pheromone trails to food sources [132,134,136–139]. Most social bees perform excitatory behaviours, such as jostling runs and trophallaxis (food sharing) inside the nest after finding particularly good food sources, which facilitate the learning of floral odours and stimulate the search for flowers with these odours [133–135,138,140,141]. This selective information sharing lowers the risk of focusing on flowers offering low-quality rewards and, therefore, reduces the benefits of sampling alternatives. Simulated bee colonies with communication and flower constancy indeed collected more energy than those without communication because selective information sharing allowed colonies to specialize on the most profitable flower species in their environment [79]. In environments with abundant food sources and large rewards, flower constancy in combination with communication was the best strategy overall when plant diversity was low [79]. As plant diversity increased, inconstancy became the best strategy (see §3b). Thus, while communication about profitable flower types reduces one risk of flower constancy, namely focusing on sub-optimal flower species, it does not affect the time and energy costs of flower constancy.

Finally, sociality could affect flower constancy through indirect effects on diet diversity. Pollinators require a range of nutrients for a healthy diet [77,78,142]. In bees, nectar is the main source of carbohydrates, while pollen provides most of the proteins, lipids and micronutrients [77,142]. As pollen from different plant species differs in their nutrient composition [77], collecting a small number of pollen types risks nutritional imbalances [143,144], with potentially negative fitness consequences [145–147]. In social bees, nectar and different types of pollen are often collected by different colony members as a form of division of labour [148–150]. A solitary bee, on the other hand, needs to collect both nectar and pollen by herself. Williams & Tepedino [131] found that the need to collect both nectar and pollen most likely explained why the solitary mason bee *Osmia lignaria* switched between plant species during foraging trips.

Because different colony members exploit different flower species in social species, flower constancy might not affect diet breadth or even increase it, especially with larger colony sizes [79,129,131]. Thus, flower constancy probably has different impacts on nutrition in social bees with large colony sizes compared to solitary pollinators. For example, pollen analysis confirms that colonies of highly flower-constant species exploit many plant species simultaneously [151–153]. However, only a small number of pollen types, usually less than five, is collected in significant quantities. Thus, social bees may still risk nutritional deficiencies owing to flower constancy, especially in environments with low plant diversity, but controlled empirical studies on the link between diet breadth, colony size and flower constancy are currently lacking. However, computer simulations have found that flower constant colonies with fewer than 50 foragers often exploit less than half as many plant species as inconstant colonies [82]. A larger colony size did increase the number of flower types visited even if colonies were flower constant, suggesting that larger colony sizes mitigate the risks of nutritional deficiencies owing to flower constancy. This could help explain why individual bumblebees, which live in smaller colonies than honeybees and stingless bees, are less flower constant than the latter two groups [82].

## 5. Summary: a bouquet of agendas

Plants and pollinators have different agendas, i.e. fitness interests, and these agendas are often viewed as contrasting, with plants favouring flower constancy and pollinators favouring behavioural flexibility. However, plant and pollinator interests are varied; for instance, common and rare plants may experience different outcomes when their pollinators are flower constant [154]. Likewise, social and solitary pollinators are likely to experience different costs and benefits owing to flower constancy. As a result, the interests of plants and pollinators may align in some situations, yet contrast in others (figure 4): for example, when a plant is abundant, flower visitation and flower constancy increase [18,155,156], which is likely to favour both plants and pollinators in terms of seed set for the former [156] and energy intake rate for the latter [79] (figure 4, scenario 1). Deceptive, unrewarding plants and rare plants co-flowering with abundant flower species, on the other hand, may experience reduced visitation rates due to flower constancy (figure 4, scenario 2). The negative impacts of low visitation rates could outweigh the benefits of reduced IPT owing to flower constancy under some circumstances (figure 4, scenario 2; figure 1). In plant species-rich habitats with a relatively even abundance and distribution, IPT owing to inconstancy is likely to be common, and flowers are likely to benefit from flower constancy. Flower constant pollinators, on the other hand, pay considerable opportunity costs in such biodiverse habitats as most of the flowers they encounter will not be their preferred type (figure 4, scenario 3; [8,79]). Finally, when plants and pollinators are scarce, flower constancy could reduce pollinator visits to plants and energy gain for pollinators owing to increased costs of skipping rewards, thus negatively impacting the fitness of both plants and pollinators (figure 4, scenario 4).

While some empirical and theoretical support for these scenarios exists, the interests of plants and pollinators remain far from understood. These knowledge gaps, especially when considering rare species, represent largely uncharted areas for conservation: some evidence suggests that rare plants experience higher costs because of IPT [38,41,55,56], whereas others found that rare plants may benefit from facilitation at the cost of more abundant plants [154]. Whether and when IPT costs outweigh the benefits of facilitation [32,35,37,66] remains poorly understood. Another important knowledge gap is the dietary requirements and foraging strategies, including flower constancy, of the vast majority of pollinators, such as small-bodied bees and those in the tropics [20,33,44].

Given that most bee species are solitary, while most flower-visiting bees are social [137,157,158], and thus likely to show pronounced flower constancy, this behaviour is an ecologically important trend rather than a taxonomically widespread rule. If pollinators are monolectic or oligolectic, i.e. have a specialized diet, they will play different roles and experience different pressures compared to pollinators with a more flexible diet. Research in both controlled environments and natural communities is needed to better understand how these different foraging habits impact pollen transfer networks, and how changes in species composition impact interactions among plants and their pollinators. Such an understanding is essential for linking mutualistic interactions to ecosystem functioning.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. A table with examples discussed in this manuscript can be found in the electronic supplementary material [159].

Declaration of AI use. I have not used AI-assisted technologies in creating this article.

Authors' contributions. C.G.: conceptualization, visualization, writing—original draft, writing—review and editing.

Conflict of interest declaration. I declare I have no competing interests.

Funding. No funding has been received for this article.

Acknowledgements. I thank two anonymous reviewers and editors for helpful comments on an earlier version of this manuscript and Kate Graydon for help with the figures.

## References

1. Ollerton J, Winfree R, Tarrant S. 2011 How many flowering plants are pollinated by animals? *Oikos* **120**, 321–326. (doi:10.1111/j.1600-0706.2010.18644.x)
2. Grant V. 1950 The flower constancy of bees. *Bot. Rev*. **16**, 379–398. (doi:10.1007/bf02869992)
3. Free JB. 1963 The flower constancy of honeybees. *J. Anim. Ecol.* **32**, 119. (doi:10.2307/2521)
4. White D, Cribb BW, Heard TA. 2001 Flower constancy of the stingless bee *Trigona carbonaria* Smith (Hymenoptera: Apidae: Meliponini). *Aust. J. Entomol*. **40**, 61–64. (doi:10.1046/j.1440-6055.2001.00201.x)
5. Heinrich B. 1976 The foraging specializations of individual bumblebees. *Ecol. Monogr*. **46**, 105–128. (doi:10.2307/1942246)
6. Darwin C. 1876 *Cross and self fertilization in the vegetable Kingdom*. London, UK: Murray.
7. Waser NM. 1986 Flower constancy: definition, cause, and measurement. *Am. Nat*. **127**, 593–603. (doi:10.1086/284507)
8. Chittka L, Thomson JD, Waser NM. 1999 Flower constancy, insect psychology, and plant evolution. *Naturwissenschaften* **86**, 361–377. (doi:10.1007/s001140050636)
9. Grüter C, Ratnieks FLW. 2011 Flower constancy in insect pollinators: adaptive foraging behaviour or cognitive limitation? *Commun. Integr. Biol.* **4**, 633–636. (doi:10.4161/cib.16972)
10. Judith Slaa E, Cevaal A, Sommeijer MJ. 1998 Floral constancy in *Trigona* stingless bees foraging on artificial flower patches: a comparative study. *J. Apic. Res.* **37**, 191–198. (doi:10.1080/00218839.1998.11100971)
11. Rossi N, Santos E, Salvarrey S, Arbulo N, Invernizzi C. 2015 Determination of flower constancy in *Bombus atratus* Franklin and *Bombus bellicosus* Smith (Hymenoptera: Apidae) through palynological analysis of nectar and corbicular pollen loads. *Neotrop. Entomol.* **44**, 546–552. (doi:10.1007/s13744-015-0322-5)
12. Gaiarsa MP, Rehan S, Barbour MA, McFrederick QS. 2022 Individual dietary specialization in a generalist bee varies across populations but has no effect on the richness of associated microbial communities. *Am. Nat.* **200**, 730–737. (doi:10.1086/721023)
13. Lewis AC. 1986 Memory constraints and flower choice in *Pieris rapae*. *Science* **232**, 863–865. (doi:10.1126/science.232.4752.863)

14. Goulson D, Stout JC, Hawson SA. 1997 Can flower constancy in nectaring butterflies be explained by Darwin's interference hypothesis? *Oecologia* **112**, 225–231. (doi:10.1007/s004420050304)
15. Hopkins R, Rausher MD. 2012 Pollinator-mediated selection on flower color allele drives reinforcement. *Science* **335**, 1090–1092. (doi:10.1126/science.1215198)
16. Goulson D, Wright NP. 1998 Flower constancy in the hoverflies *Episyrphus balteatus* (Degeer) and *Syrphus ribesii* (L.) (Syrphidae). *Behav. Ecol*. **9**, 213–219. (doi:10.1093/beheco/9.3.213)
17. Pellmyr O. 1985 Flower constancy in individuals of an anthophilous beetle, *Byturus ochraceus* (Scriba) (Coleoptera: Byturidae). *Coleopt. Bull.* **39**, 341–345.
18. Schmid B, Nottebrock H, Esler KJ, Pagel J, Böhning-Gaese K, Schurr FM, Mueller T, Schleuning M. 2016 A bird pollinator shows positive frequency dependence and constancy of species choice in natural plant communities. *Ecology* **97**, 3110–3118. (doi:10.1002/ecy.1565)
19. Takagi K, Ohashi K. 2025 Realized flower constancy in bumble bees: optimal foraging strategy balancing cognitive and travel costs and its possible consequences for floral diversity. *Funct. Ecol.* **39**, 863–875. (doi:10.1111/1365-2435.70008)
20. Cane JH, Sipes S. 2006 Characterizing floral specialization by bees: analytical methods and a revised lexicon for oligolecty. In *Plant-pollinator interactions: from specialization to generalization* (eds N Waser, J Ollerton), pp. 99–122. Chicago, IL: The University of Chicago Press.
21. Gegear RJ, Thomson JD. 2004 Does the flower constancy of bumble bees reflect foraging economics? *Ethology* **110**, 793–805. (doi:10.1111/j.1439-0310.2004.01010.x)
22. Raine NE, Chittka L. 2007 Flower constancy and memory dynamics in bumblebees (Hymenoptera: Apidae: *Bombus*). *Entomologia Generalis* **29**, 179–199. (doi:10.1127/entom.gen/29/2007/179)
23. Grüter C, Moore H, Firmin N, Helanterä H, Ratnieks FLW. 2011 Flower constancy in honey bee workers (*Apis mellifera*) depends on ecologically realistic rewards. *J. Exp. Biol*. **214**, 1397–1402. (doi:10.1242/jeb.050583)
24. Bruninga-Socolar B, Winfree R, Crone EE. 2022 The contribution of plant spatial arrangement to bumble bee flower constancy. *Oecologia* **198**, 471–481. (doi:10.1007/s00442-022-05114-x)
25. Bateman AJ. 1951 The taxonomic discrimination of bees. *Heredity* **5**, 271–278. (doi:10.1038/hdy.1951.24)
26. Chittka L, Spaethe J, Schmidt A, Hickelsberger A. 2001 Adaptation, constraint, and chance in the evolution of flower color and pollinator color vision. In *Cognitive ecology of pollination: animal behaviour and floral evolution* (eds J Thomson, L Chittka), pp. 106–126. Cambridge, UK: Cambridge University Press. (doi:10.1017/CBO9780511542268.007)
27. Papaj DR, Russell AL. 2024 The relationship between preference and switching in flower foraging by bees. *Behav. Ecol. Sociobiol.* **78**, 40. (doi:10.1007/s00265-024-03456-5)
28. Ramalho M, Giannini TC, Malagodi-Braga KS, Imperatriz-Fonseca VL. 1994 Pollen harvest by stingless bee foragers (Hymenoptera, Apidae, Meliponinae). *Grana* **33**, 239–244. (doi:10.1080/00173139409429005)
29. Somme L, Vanderplanck M, Michez D, Lombaerde I, Moerman R, Wathelet B, Wattiez R, Lognay G, Jacquemart AL. 2015 Pollen and nectar quality drive the major and minor floral choices of bumble bees. *Apidologie* **46**, 92–106. (doi:10.1007/s13592-014-0307-0)
30. Hill PSM, Hollis J, Wells H. 2001 Foraging decisions in nectarivores: unexpected interactions between flower constancy and energetic rewards. *Anim. Behav*. **62**, 729–737. (doi:10.1006/anbe.2001.1775)
31. Mitchell RJ, Flanagan RJ, Brown BJ, Waser NM, Karron JD. 2009 New frontiers in competition for pollination. *Ann. Bot*. **103**, 1403–1413. (doi:10.1093/aob/mcp062)
32. Tur C, Sáez A, Traveset A, Aizen MA. 2016 Evaluating the effects of pollinator-mediated interactions using pollen transfer networks: evidence of widespread facilitation in south Andean plant communities. *Ecol. Lett*. **19**, 576–586. (doi:10.1111/ele.12594)
33. Moreira-Hernández JI, Muchhala N. 2019 Importance of pollinator-mediated interspecific pollen transfer for angiosperm evolution. *Annu. Rev. Ecol. Evol. Syst.* **50**, 191–217. (doi:10.1146/annurev-ecolsys-110218-024804)
34. Sargent RD, Ackerly DD. 2008 Plant–pollinator interactions and the assembly of plant communities. *Trends Ecol. Evol.* **23**, 123–130. (doi:10.1016/j.tree.2007.11.003)
35. Rathcke B. 1983 Competition and facilitation among plants for pollination. In *Pollination biology* (ed. L Real), pp. 305–329. New York, NY: Academic Press. (doi:10.1016/B978-0-12-583980-8.50019-3)
36. Ashman TL, Alonso C, Parra-Tabla V, Arceo-Gómez G. 2020 Pollen on stigmas as proxies of pollinator competition and facilitation: complexities, caveats and future directions. *Ann. Bot*. **125**, 1003–1012. (doi:10.1093/aob/mcaa012)
37. Braun J, Lortie CJ. 2019 Finding the bees knees: a conceptual framework and systematic review of the mechanisms of pollinator-mediated facilitation. *Perspect. Plant Ecol. Evol. Syst*. **36**, 33–40. (doi:10.1016/j.ppees.2018.12.003)
38. Levin DA, Anderson WW. 1970 Competition for pollinators between simultaneously flowering species. *Am. Nat.* **104**, 455–467. (doi:10.1086/282680)
39. Waser NM. 1978 Interspecific pollen transfer and competition between co-occurring plant species. *Oecologia* **36**, 223–236. (doi:10.1007/bf00349811)
40. Geber MA, Moeller DA. 2006 Pollinator responses to plant communities and implications for reproductive character evolution. In *Ecology and evolution of flowers* (eds L Harder, SCH Barrett). Oxford, UK: Oxford University Press. (doi:10.1093/oso/9780198570851.003.0006)
41. Morales CL, Traveset A. 2008 Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. *Crit. Rev. Plant Sci*. **27**, 221–238. (doi:10.1080/07352680802205631)
42. Ashman TL, Arceo-Gómez G. 2013 Toward a predictive understanding of the fitness costs of heterospecific pollen receipt and its importance in co-flowering communities. *Am. J. Bot.* **100**, 1061–1070. (doi:10.3732/ajb.1200496)
43. Brosi BJ, Briggs HM. 2013 Single pollinator species losses reduce floral fidelity and plant reproductive function. *Proc. Natl Acad. Sci. USA* **110**, 13044–13048. (doi:10.1073/pnas.1307438110)
44. Bruninga-Socolar B, Socolar JB, Konzmann S, Lunau K. 2023 Pollinator-mediated plant coexistence requires high levels of pollinator specialization. *Ecol. Evol*. **13**, e10349. (doi:10.1002/ece3.10349)
45. Bartomeus I, Bosch J, Vilà M. 2008 High invasive pollen transfer, yet low deposition on native stigmas in a carpobrotus-invaded community. *Ann. Bot*. **102**, 417–424. (doi:10.1093/aob/mcn109)
46. Montgomery BR, Rathcke BJ. 2012 Effects of floral restrictiveness and stigma size on heterospecific pollen receipt in a prairie community. *Oecologia* **168**, 449–458. (doi:10.1007/s00442-011-2094-x)
47. Fang Q, Huang SQ. 2013 A directed network analysis of heterospecific pollen transfer in a biodiverse community. *Ecology* **94**, 1176–1185. (doi:10.1890/12-1634.1)
48. Parra-Tabla V, Alonso C, Ashman T, Raguso RA, Albor C, Sosenski P, Carmona D, Arceo-Gómez G. 2021 Pollen transfer networks reveal alien species as main heterospecific pollen donors with fitness consequences for natives. *J. Ecol.* **109**, 939–951. (doi:10.1111/1365-2745.13520)
49. Waser NM. 1978 Competition for hummingbird pollination and sequential flowering in two colorado wildflowers. *Ecology* **59**, 934–944. (doi:10.2307/1938545)
50. de Jager ML, Dreyer LL, Ellis AG. 2011 Do pollinators influence the assembly of flower colours within plant communities? *Oecologia* **166**, 543–553. (doi:10.1007/s00442-010-1879-7)

51. Runquist RB, Stanton ML. 2013 Asymmetric and frequency-dependent pollinator-mediated interactions may influence competitive displacement in two vernal pool plants. *Ecol. Lett.* **16**, 183–190. (doi:10.1111/ele.12026)
52. Campbell DR, Motten AF. 1985 The mechanism of competition for pollination between two forest herbs. *Ecology* **66**, 554–563. (doi:10.2307/1940404)
53. Bell JM, Karron JD, Mitchell RJ. 2005 Interspecific competition for pollination lowers seed production and outcrossing in *Mimulus ringens*. *Ecology* **86**, 762–771. (doi:10.1890/04-0694)
54. de Waal C, Anderson B, Ellis AG. 2015 Relative density and dispersion pattern of two southern African Asteraceae affect fecundity through heterospecific interference and mate availability, not pollinator visitation rate. *J. Ecol.* **103**, 513–525. (doi:10.1111/1365-2745.12358)
55. Arceo-Gómez G. 2021 Spatial variation in the intensity of interactions via heterospecific pollen transfer may contribute to local and global patterns of plant diversity. *Ann. Bot*. **128**, 383–394. (doi:10.1093/aob/mcab082)
56. Wolf DE, Takebayashi N, Rieseberg LH. 2001 Predicting the risk of extinction through hybridization. *Conserv. Biol*. **15**, 1039–1053. (doi:10.1046/j.1523-1739.2001.0150041039.x)
57. Charlebois JA, Sargent RD. 2017 No consistent pollinator-mediated impacts of alien plants on natives. *Ecol. Lett*. **20**, 1479–1490. (doi:10.1111/ele.12831)
58. Jakobsson A, Padrón B, Traveset A. 2008 Pollen transfer from invasive *Carpobrotus* spp. to natives – a study of pollinator behaviour and reproduction success. *Biol. Conserv*. **141**, 136–145. (doi:10.1016/j.biocon.2007.09.005)
59. Carneiro LT, Williams JN, Barker DA, Anderson JW, Martel C, Arceo-Gomez G. 2024 Patterns and drivers of pollen co-transport network structure vary across pollinator functional groups. *J. Ecol.* **112**, 2319–2332. (doi:10.1111/1365-2745.14397)
60. Knight TM, Ashman T -L., Bennett JM, Burns JH, Passonneau S, Steets JA. 2018 Reflections on, and visions for, the changing field of pollination ecology. *Ecol. Lett*. **21**, 1282–1295. (doi:10.1111/ele.13094)
61. Travis DJ, Kohn JR. 2023 Honeybees (*Apis mellifera*) decrease the fitness of plants they pollinate. *Proc. R. Soc. B* **290**, 20230967. (doi:10.1098/rspb.2023.0967)
62. Trunschke J, Lunau K, Pyke GH, Ren ZX, Wang H. 2021 Flower color evolution and the evidence of pollinator-mediated selection. *Front. Plant Sci* **12**, 617851. (doi:10.3389/fpls.2021.617851)
63. Oyama RK, Jones KN, Baum DA. 2010 Sympatric sister species of Californian antirrhinum and their transiently specialized pollinators. *Am. Midl. Nat.* **164**, 337–347. (doi:10.1674/0003-0031-164.2.337)
64. Wenzell KE, Neequaye M, Paajanen P, Hill L, Brett P, Byers KJRP. 2025 Within-species floral evolution reveals convergence in adaptive walks during incipient pollinator shift. *Nat. Commun.* **16**, 2721. (doi:10.1038/s41467-025-57639-3)
65. Feldman TS, Morris WF, Wilson WG. 2004 When can two plant species facilitate each other's pollination. *Oikos* **105**, 197–207. (doi:10.1111/j.0030-1299.2004.12845.x)
66. Carvalheiro LG, Souza RS, Gomes SG. 2025 What shapes pollinator-mediated facilitation? *Trends Ecol. Evol.* **40**, 831–833. (doi:10.1016/j.tree.2025.07.015)
67. Johnson SD, Peter CI, Nilsson LA, Ågren J. 2003 Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. *Ecology* **84**, 2919–2927. (doi:10.1890/02-0471)
68. Pellegrino G, Bellusci F, Palermo AM. 2016 Who helps whom? Pollination strategy of *Iris tuberosa* and its relationship with a sexually deceptive orchid. *J. Plant Res*. **129**, 1051–1059. (doi:10.1007/s10265-016-0853-9)
69. Thomson JD, Fung HF, Ogilvie JE. 2019 Effects of spatial patterning of co-flowering plant species on pollination quantity and purity. *Ann. Bot*. **123**, 303–310. (doi:10.1093/aob/mcy120)
70. Ye ZM, Dai WK, Jin XF, Gituru RW, Wang QF, Yang CF. 2014 Competition and facilitation among plants for pollination: can pollinator abundance shift the plant–plant interactions? *Plant Ecol*. **215**, 3–13. (doi:10.1007/s11258-013-0274-y)
71. Zhang X, Agrawal AA. 2025 Pollinator facilitation between florally contrasting congeners scales up to regional co-occurrence patterns. *J. Ecol*. **113**, 1780–1792. (doi:10.1111/1365-2745.70065)
72. Moeller DA. 2004 Facilitative interactions among plants via shared pollinators. *Ecology* **85**, 3289–3301. (doi:10.1890/03-0810)
73. Valdovinos FS, Moisset de Espanés P, Flores JD, Ramos-Jiliberto R. 2013 Adaptive foraging allows the maintenance of biodiversity of pollination networks. *Oikos* **122**, 907–917. (doi:10.1111/j.1600-0706.2012.20830.x)
74. Song Z, Feldman MW. 2014 Adaptive foraging behaviour of individual pollinators and the coexistence of co-flowering plants. *Proc. R. Soc. B* **281**, 20132437. (doi:10.1098/rspb.2013.2437)
75. Pattrick JG, Symington HA, Federle W, Glover BJ. 2023 Bumblebees negotiate a trade-off between nectar quality and floral biomechanics. *iScience* **26**, 108071. (doi:10.1016/j.isci.2023.108071)
76. Charlton NL, Houston AI. 2010 What currency do bumble bees maximize? *PLoS One* **5**, e12186. (doi:10.1371/journal.pone.0012186)
77. Brodschneider R, Crailsheim K. 2010 Nutrition and health in honey bees. *Apidologie* **41**, 278–294. (doi:10.1051/apido/2010012)
78. Vaudo AD *et al*. 2020 Pollen protein: lipid macronutrient ratios may guide broad patterns of bee species floral preferences. *Insects* **11**, 132. (doi:10.3390/insects11020132)
79. Hayes L, Grüter C. 2023 When should bees be flower constant? An agent-based model highlights the importance of social information and foraging conditions. *J. Anim. Ecol.* **92**, 580–593. (doi:10.1111/1365-2656.13861)
80. Wells H, Wells PH. 1983 Honey bee foraging ecology: optimal diet, minimal uncertainty or individual constancy? *J. Anim. Ecol.* **52**, 829. (doi:10.2307/4457)
81. Grüter C, Hayes L. 2022 Sociality is a key driver of foraging ranges in bees. *Curr. Biol*. **32**, 5390–5397.(doi:10.1016/j.cub.2022.10.064)
82. Grüter C, Segers F, Hayes L. 2024 Extensive loss of forage diversity in social bees owing to flower constancy in simulated environments. *Proc. R. Soc. B* **291**, 20241036. (doi:10.1098/rspb.2024.1036)
83. Chittka L, Thomson JD. 1997 Sensori-motor learning and its relevance for task specialization in bumble bees. *Behav. Ecol. Sociobiol*. **41**, 385–398. (doi:10.1007/s002650050400)
84. Gegear RJ, Laverty TM. 2005 Flower constancy in bumblebees: a test of the trait variability hypothesis. *Anim. Behav*. **69**, 939–949. (doi:10.1016/j.anbehav.2004.06.029)
85. von Frisch K. 1923 Über die 'Sprache' der Bienen. *Zoologisches Jahrbuch (Zoologie Und Physiologie)* **40**, 1–186.
86. Woodward GL, Laverty TM. 1992 Recall of flower handling skills by bumble bees: a test of Darwin's interference hypothesis. *Anim. Behav*. **44**, 1045–1051. (doi:10.1016/s0003-3472(05)80316-1)
87. Goulson D. 2000 Are insects flower constant because they use search images to find flowers? *Oikos* **88**, 547–552. (doi:10.1034/j.1600-0706.2000.880311.x)
88. Laverty TM. 1994 Bumble bee learning and flower morphology. *Anim. Behav*. **47**, 531–545. (doi:10.1006/anbe.1994.1077)
89. Raine NE, Chittka L. 2007 Pollen foraging: learning a complex motor skill by bumblebees (*Bombus terrestris*). *Naturwissenschaften* **94**, 459–464. (doi:10.1007/s00114-006-0184-0)
90. Mayberry MM, Naumer KC, Novinger AN, McCart DM, Wilkins RV, Muse H, Ashman TL, Russell AL. 2024 Learning to handle flowers increases pollen collection for bees but does not affect pollination success for plants. *Behav. Ecol.* **35**, arae083. (doi:10.1093/beheco/arae083)
91. Menzel R. 1999 Memory dynamics in the honeybee. *J. Comp. Physiol. A* **185**, 323–340. (doi:10.1007/s003590050392)

92. Menzel R. 2012 The honeybee as a model for understanding the basis of cognition. *Nat. Rev. Neurosci*. **13**, 758–768. (doi:10.1038/nrn3357)
93. Chittka L, Gumbert A, Kunze J. 1997 Foraging dynamics of bumble bees: correlates of movements within and between plant species. *Behav. Ecol*. **8**, 239–249. (doi:10.1093/beheco/8.3.239)
94. Laverty TM. 1994 Costs to foraging bumble bees of switching plant species. *Can. J. Zool*. **72**, 43–47. (doi:10.1139/z94-007)
95. Shettleworth SJ. 2010 *Cognition, evolution, and behavior*. Oxford, UK: Oxford University Press. (doi:10.1093/oso/9780195319842.001.0001)
96. Jackson RR, Cross FR. 2018 Search image. In *Encyclopedia of animal cognition and behavior* (eds J Vonk, T Shackelford), pp. 1–7. Cham, Switzerland: Springer International Publishing. (doi:10.1007/978-3-319-47829-6_1538-1)
97. Willmer P. 2011 *Pollination and floral ecology*. Princeton, NJ: Princeton University Press.
98. Greggers U, Menzel R. 1993 Memory dynamics and foraging strategies of honeybees. *Behav. Ecol. Sociobiol.* **32**, 17–29. (doi:10.1007/BF00172219)
99. Gervais A, Courtois È, Fournier V, Bélisle M. 2020 Landscape composition and local floral resources influence foraging behavior but not the size of *Bombus impatiens* Cresson (Hymenoptera: Apidae) workers. *PLoS ONE* **15**, e0234498. (doi:10.1371/journal.pone.0234498)
100. Martínez-Bauer AE, Chadwick FJ, Westmoreland AJ, Lander TA. 2021 Novel pollen analogue technique shows bumblebees display low floral constancy and prefer sites with high floral diversity. *Landsc. Ecol.* **36**, 3231–3247. (doi:10.1007/s10980-021-01304-9)
101. Austin MW, Horack P, Dunlap AS. 2019 Choice in a floral marketplace: the role of complexity in bumble bee decision-making. *Behav. Ecol*. **30**, 500–508. (doi:10.1093/beheco/ary190)
102. Charnov EL. 1976 Optimal foraging, the marginal value theorem. *Theor. Popul. Biol*. **9**, 129–136. (doi:10.1016/0040-5809(76)90040-x)
103. Heinrich B. 1979 Majoring' and 'minoring' by foraging bumblebees, *Bombus vagans*: an experimental analysis. *Ecology* **60**, 245–255. (doi:10.2307/1937652)
104. Hill PSM, Wells PH, Wells H. 1997 Spontaneous flower constancy and learning in honey bees as a function of colour. *Anim. Behav*. **54**, 615–627. (doi:10.1006/anbe.1996.0467)
105. Wells H, Rathore RRS. 1994 Foraging ecology of the Asian hive bee, *Apis cerane indica*, within artificial flower patches. *J. Apic. Res.* **33**, 219–230. (doi:10.1080/00218839.1994.11100875)
106. Slaa EJ, Tack AJM, Sommeijer MJ. 2003 The effect of intrinsic and extrinsic factors on flower constancy in stingless bees. *Apidologie* **34**, 457–468. (doi:10.1051/apido:2003046)
107. Muth F, Keasar T, Dornhaus A. 2015 Trading off short-term costs for long-term gains: how do bumblebees decide to learn morphologically complex flowers? *Anim. Behav*. **101**, 191–199. (doi:10.1016/j.anbehav.2014.12.024)
108. Krishna S, Keasar T. 2021 Generalization of foraging experience biases bees toward flowers with complex morphologies. *Front. Ecol. Evol.* **9**, 655086. (doi:10.3389/fevo.2021.655086)
109. Cnaani J, Thomson JD, Papaj DR. 2006 Flower choice and learning in foraging bumblebees: effects of variation in nectar volume and concentration. *Ethology* **112**, 278–285. (doi:10.1111/j.1439-0310.2006.01174.x)
110. Cakmak I *et al*. 2009 Different solutions by bees to a foraging problem. *Anim. Behav*. **77**, 1273–1280. (doi:10.1016/j.anbehav.2009.01.032)
111. Rathcke B. 1988 Interactions for pollination among co-flowering shrubs. *Ecology* **69**, 446–457. (doi:10.2307/1940443)
112. Ishii HS, Kadoya EZ. 2016 Legitimate visitors and nectar robbers on *Trifolium pratense* showed contrasting flower fidelity versus co-flowering plant species: could motor learning be a major determinant of flower constancy by bumble bees? *Behav. Ecol. Sociobiol.* **70**, 377–386. (doi:10.1007/s00265-016-2057-7)
113. Sanderson CE, Orozco BS, Hill PSM, Wells H. 2006 Honeybee (*Apis mellifera ligustica*) response to differences in handling time, rewards and flower colours. *Ethology* **112**, 937–946. (doi:10.1111/j.1439-0310.2006.01245.x)
114. Kulahci IG, Dornhaus A, Papaj DR. 2008 Multimodal signals enhance decision making in foraging bumble-bees. *Proc. R. Soc. B* **275**, 797–802. (doi:10.1098/rspb.2007.1176)
115. Ishii HS. 2006 Floral display size influences subsequent plant choice by bumble bees. *Funct. Ecol*. **20**, 233–238. (doi:10.1111/j.1365-2435.2006.01106.x)
116. Ishii HS, Masuda H. 2014 Effect of flower visual angle on flower constancy: a test of the search image hypothesis. *Behav. Ecol*. **25**, 933–944. (doi:10.1093/beheco/aru071)
117. Wright EK, Timberlake TP, Baude M, Vaughan IP, Memmott J. 2024 Quantifying the production of plant pollen at the farm scale. *New Phytol*. **242**, 2888–2899. (doi:10.1111/nph.19763)
118. Krishna S, Keasar T. 2019 Bumblebees forage on flowers of increasingly complex morphologies despite low success. *Anim. Behav.* **155**, 119–130. (doi:10.1016/j.anbehav.2019.06.028)
119. Ohashi K. 2002 Consequences of floral complexity for bumblebee-mediated geitonogamous self-pollination in *Salvia nipponica* Miq. (Labiatae). *Evolution* **56**, 2414–2423. (doi:10.1111/j.0014-3820.2002.tb00167.x)
120. Krishna S, Keasar T. 2018 Morphological complexity as a floral signal: from perception by insect pollinators to co-evolutionary implications. *Int. J. Mol. Sci*. **19**, 1681. (doi:10.3390/ijms19061681)
121. Heinrich B. 1979 *Bumblebee economics*. Cambridge, MA: Harvard University Press.
122. Marden JH, Waddington KD. 1981 Floral choices by honeybees in relation to the relative distances to flowers. *Physiol. Entomol*. **6**, 431–435. (doi:10.1111/j.1365-3032.1981.tb00658.x)
123. Kunin WE. 1993 Sex and the single mustard: population density and pollinator behavior effects on seed-set. *Ecology* **74**, 2145–2160. (doi:10.2307/1940859)
124. Ishii HS. 2005 Analysis of bumblebee visitation sequences within single bouts: implication of the overstrike effect on short-term memory. *Behav. Ecol. Sociobiol*. **57**, 599–610. (doi:10.1007/s00265-004-0889-z)
125. Katz EJ, Essenberg CJ. 2018 The effect of the dispersion of rewarding and rewardless flowers on visitation and constancy by bumblebees (*Bombus impatiens*). *J. Pollinat. Ecol*. **23**, 119–126. (doi:10.26786/1920-7603(2018)14)
126. Smith C, Weinman L, Gibbs J, Winfree R. 2019 Specialist foragers in forest bee communities are small, social or emerge early. *J. Anim. Ecol.* **88**, 1158–1167. (doi:10.1111/1365-2656.13003)
127. Leonhardt SD, Blüthgen N. 2012 The same, but different: pollen foraging in honeybee and bumblebee colonies. *Apidologie* **43**, 449–464. (doi:10.1007/s13592-011-0112-y)
128. Townsend-Mehler JM, Dyer FC, Maida K. 2011 Deciding when to explore and when to persist: a comparison of honeybees and bumblebees in their response to downshifts in reward. *Behav. Ecol. Sociobiol.* **65**, 305–312. (doi:10.1007/s00265-010-1047-4)
129. Yourstone J, Varadarajan V, Olsson O. 2023 Bumblebee flower constancy and pollen diversity over time. *Behav. Ecol*. **34**, 602–612. (doi:10.1093/beheco/arad028)
130. Alarcón R. 2010 Congruence between visitation and pollen-transport networks in a California plant–pollinator community. *Oikos* **119**, 35–44. (doi:10.1111/j.1600-0706.2009.17694.x)
131. Williams NM, Tepedino VJ. 2003 Consistent mixing of near and distant resources in foraging bouts by the solitary mason bee *Osmia lignaria*. *Behav. Ecol.* **14**, 141–149. (doi:10.1093/beheco/14.1.141)
132. von Frisch K. 1967 *The dance language and orientation of bees*. Cambridge, MA: Harvard University Press.

133. Farina WM, Grüter C, Arenas A. 2012 Olfactory information transfer during recruitment in honey bees. In *Honeybee neurobiology and behavior- a tribute to Randolf Menzel* (eds CG Galizia, D Eisenhardt, M Giurfa), pp. 89–101. Heidelberg, Germany: Springer. (doi:10.1007/978-94-007-2099-2_8)

134. Alves DA, George EA, Kaur R, Brockmann A, Hrncir M, Grüter C. 2023 Diverse communication strategies in bees as a window into adaptations to an unpredictable world. *Proc. Natl Acad. Sci. USA* **120**, e2219031120. (doi:10.1073/pnas.2219031120)

135. Hrncir M. 2009 Mobilizing the foraging force mechanical signals in stingless bee recruitment. In *Food exploitation by social insects: ecological, behavioral, and theoretical approaches* (eds S Jarau, M Hrncir), pp. 189–211. Boca Raton, FL: CRC Press. (doi:10.1201/9781420075618.ch11)

136. Jarau S. 2009 Chemical communication during food exploitation in stingless bees. In *Food exploitation by social insects: ecological, behavioral, and theoretical approaches* (eds S Jarau, M Hrncir), pp. 213–239. Boca Raton, FL: CRC University Press. (doi:10.1201/9781420075618.ch12)

137. Grüter C. 2020 *Stingless bees: their behaviour, ecology and evolution*. Cham, Switzerland: Springer International Publishing. See https://www.springer.com/gp/book/9783030600891.

138. Lindauer M, Kerr WE. 1960 Communication between the workers of stingless bees. *Bee World* **41**, 29–41. (doi:10.1080/0005772X.1960.11095309)

139. Nieh JC. 2004 Recruitment communication in stingless bees (Hymenoptera, Apidae, Meliponini). *Apidologie* **35**, 159–182. (doi:10.1051/apido:2004007)

140. Dornhaus A, Chittka L. 1999 Evolutionary origins of bee dances. *Nature* **401**, 38–38. (doi:10.1038/43372)

141. Hrncir M, Schmidt VM, Schorkopf DLP, Jarau S, Zucchi R, Barth FG. 2006 Vibrating the food receivers: a direct way of signal transmission in stingless bees (*Melipona seminigra*). *J. Comp. Physiol*. **192**, 879–887. (doi:10.1007/s00359-006-0123-8)

142. Vaudo AD, Tooker JF, Grozinger CM, Patch HM. 2015 Bee nutrition and floral resource restoration. *Curr. Opin. Insect Sci*. **10**, 133–141. (doi:10.1016/j.cois.2015.05.008)

143. Eckhardt M, Haider M, Dorn S, Müller A. 2014 Pollen mixing in pollen generalist solitary bees: a possible strategy to complement or mitigate unfavourable pollen properties? *J. Anim. Ecol*. **83**, 588–597. (doi:10.1111/1365-2656.12168)

144. Filipiak M, Kuszewska K, Asselman M, Denisow B, Stawiarz E, Woyciechowski M, Weiner J. 2017 Ecological stoichiometry of the honeybee: pollen diversity and adequate species composition are needed to mitigate limitations imposed on the growth and development of bees by pollen quality. *PLoS ONE* **12**, e0183236. (doi:10.1371/journal.pone.0183236)

145. Ruedenauer FA, Raubenheimer D, Kessner-Beierlein D, Grund-Mueller N, Noack L, Spaethe J, Leonhardt SD. 2020 Best be(e) on low fat: linking nutrient perception, regulation and fitness. *Ecol. Lett.* **23**, 545–554. (doi:10.1111/ele.13454)

146. Génissel A, Aupinel P, Bressac C, Tasei J -N., Chevrier C. 2002 Influence of pollen origin on performance of *Bombus terrestris* micro-colonies. *Entomol. Exp. Et Appl*. **104**, 329–336. (doi:10.1046/j.1570-7458.2002.01019.x)

147. Schmidt JO, Thoenes SC, Levin MD. 1987 Survival of honey bees, *Apis mellifera* (Hymenoptera: Apidae), fed various pollen sources. *Ann. Entomol. Soc. Am.* **80**, 176–183. (doi:10.1093/aesa/80.2.176)

148. Arenas A, Lajad R, Peng T, Grüter C, Farina W. 2021 Correlation between octopaminergic signalling and foraging task specialisation in honeybees. *Genes Brain Behav.* **20**, e12718. (doi:10.1111/gbb.12718)

149. Mateus S, Ferreira-Caliman MJ, Menezes C, Grüter C. 2019 Beyond temporal-polyethism: division of labor in the eusocial bee *Melipona marginata*. *Insectes Soc.* **66**, 317–328. (doi:10.1007/s00040-019-00691-2)

150. Balbuena MS, Farina WM. 2020 Chemosensory reception in the stingless bee *Tetragonisca angustula*. *J. Insect Physiol.* **125**, 104076. (doi:10.1016/j.jinsphys.2020.104076)

151. Ramalho M. 1990 Foraging by stingless bees of the genus, *Scaptotrigona* (Apidae, Meliponinae). *J. Apic. Res.* **29**, 61–67. (doi:10.1080/00218839.1990.11101198)

152. Brodschneider R *et al*. 2021 CSI pollen: diversity of honey bee collected pollen studied by citizen scientists. *Insects* **12**, 987. (doi:10.3390/insects12110987)

153. Jezeera AM, Mohan KM, Sreekumar S, Kelber A, Somanathan H. 2025 Influence of floral traits on visitation patterns in a miniature tropical stingless bee, *Tetragonula iridipennis*. *Sci. Nat.* **112**, 44. (doi:10.1007/s00114-025-01994-0)

154. Wei N, Kaczorowski RL, Arceo-Gómez G, O'Neill EM, Hayes RA, Ashman TL. 2021 Pollinators contribute to the maintenance of flowering plant diversity. *Nature* **597**, 688–692. (doi:10.1038/s41586-021-03890-9)

155. Bruninga-Socolar B, Crone EE, Winfree R. 2016 The role of floral density in determining bee foraging behavior: a natural experiment. *Nat. Areas J.* **36**, 392–399. (doi:10.3375/043.036.0406)

156. Dauber J *et al*. 2010 Effects of patch size and density on flower visitation and seed set of wild plants: a pan-European approach. *J. Ecol*. **98**, 188–196. (doi:10.1111/j.1365-2745.2009.01590.x)

157. Michener CD. 2007 *The bees of the world*, 2nd edn. Baltimore, MD: The Johns Hopkins University Press.

158. Hung KLJ, Kingston JM, Albrecht M, Holway DA, Kohn JR. 2018 The worldwide importance of honey bees as pollinators in natural habitats. *Proc. R. Soc. B* **285**, 20172140. (doi:10.1098/rspb.2017.2140)

159. Grüter C. 2025 Supplementary material from: Flower constancy in pollinators: a bouquet of agendas shapes interactions among mutualistic partners. Figshare. (doi:10.6084/m9.figshare.c.8213610)