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

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Abstract

Plant-pollinator interactions have become a major research area due to their impact on important ecosystem services that are driven by the outcomes of these mutualistic interactions. One pollinator behaviour of particular importance is flower constancy, *i.e.* the tendency of pollinators to temporarily specialise on one flower species during a foraging trip, thereby promoting cross-pollination. The costs and benefits of flower constancy for both plants and pollinators are varied, complex and far from understood. This review aims to synthesise and interpret 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 due to increased visits from pollinators shared with co-flowering plants. The fitness consequences of pollinator behaviour for rare or invasive plants is not well understood, which is blind spot 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.

Keywords: Pollination, cognition, facilitation, flower constancy, behavioural flexibility

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 [2,3], while bypassing rewarding alternative flowers [2,4–7]. While flower constancy has been observed and studied predominantly in bees (e.g. [2,5,8–11]), it has also been reported in butterflies [12–14], hover flies [15], beetles [16] and birds [17]. 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 the limitations of their nervous system [2,5–7]. And yet, a growing number of studies highlight that pollinators 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 to better understand the varied interests that shape interactions among plant 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 of pollinators 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 an floral rewards [6] – and is different from the innate dietary preferences found in specialist (oligolectic) pollinators [5,20; note that bees can be specialists when collecting pollen, but generalists when collecting nectar [18]). 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 [5] 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 (e.g. [2,5,20–23], see [5,20,24] for discussion of different indices). Second, by analysing pollen load purity of foraging bees, which reflects the sum of its foraging choices during a foraging trip (e.g. [25,26]). 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 due to 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 [5,6]. Artificial flower setups solve many of these challenges (e.g. [8,19,22,27]), but they are feasible only for a small number of pollinators and artificial setups work best with sugar solution as a reward. Pollinators are likely of modify their strategies depending on whether they collect pollen or nectar, *e.g.* by being more specialised, when collecting pollen [9,18].

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 [4] 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 (Fig. 1) [14,28–39].

(a) Interspecific pollen transfer (IPT)

Inconstant pollinators will frequently transfer pollen from one species to the stigmas of a different species. This interspecific pollen transfer (IPT) is ubiquitous [33–35,40–43] and can reduce plant fitness through a variety of mechanisms [31,35,43–46]. 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 [29,31,35,37,47,48]. Pollen misplacement can also lower outcrossing rate, thereby reducing not only offspring quantity but also quality [48].

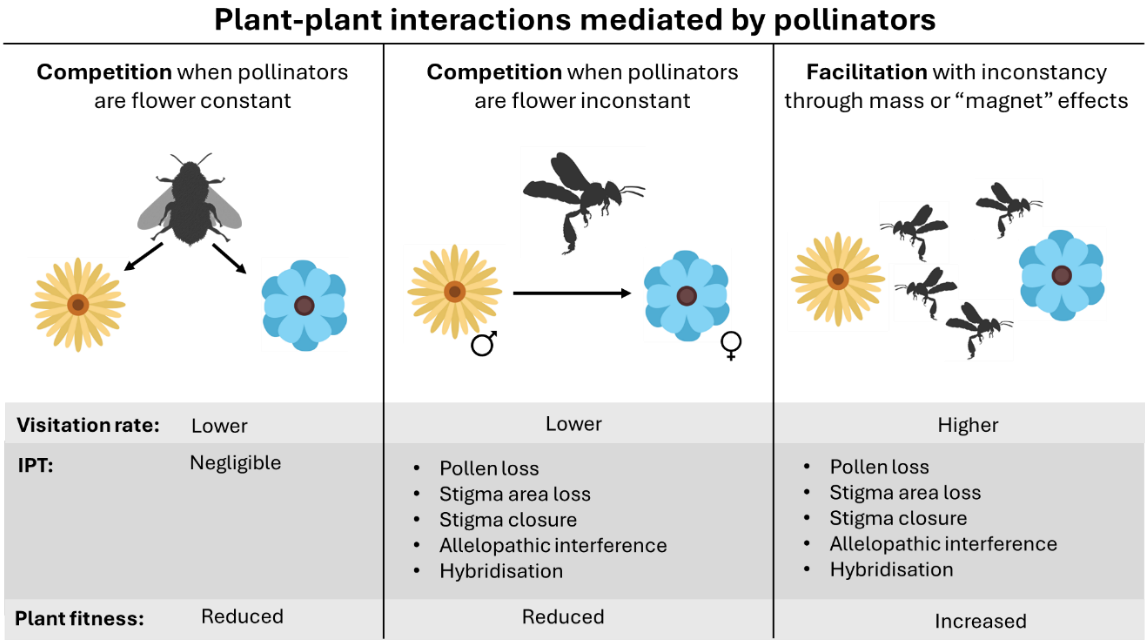

Figure 1. Pollinator behaviour affects interactions between plants. If plants from different species share the same pollinator, then this will likely affect the fitness of plants through different mechanisms, depending on whether pollinators are flower constant or not. While sharing pollinators will often have a negative impact on flowers through competition, there may be circumstances when the sharing of inconstant pollinators benefits plants through facilitation [32,34–37,49,50]. Plants visited by inconstant pollinators may still pay some costs due to interspecific pollen transfer, but these costs are outweighed by the benefits of increased visitation.

For the plant receiving heterospecific pollen, the deposition of this pollen can impair seed set [29,31,37], 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 hybridisation (see [31] for 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 [28,31,37,46,51,52], which could increase the risk of extinction of rare plants [31,53]. Interspecific pollen transfer from invasive to native plants has the potential to reduce the reproductive success of native plants ([31,43]; but see [40,41,54]). Flower constancy affects the strength of this effect, for example, the solitary bee *Rhodanthidium septemdentatum* switched more often from an 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 [55]. This highlights how different types of pollinators create different interaction pollen transfer networks (see also [56]). More flower constant pollinators reduce the risk of ITP and facilitate cross-pollination [57], but they may also increase repeat visits to flowers of the same plant, thereby increasing self-pollination (geitonogamy), which can impair plant fitness [58].

The costs of these interspecies pollen transactions can select for greater divergence in floral traits, e.g. different habitat choice, flowering times or floral morphology (e.g. morphology, colour or scent; see Section 4) and self-pollination [14,28–31,33,35,44,59]. A striking example are the closely related plants *Phlox drummondii* and *P. cuspidate*, 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 hybridisation [14]. 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 [14]. This example highlights how flower constancy can drive evolutionary divergence in closely related sympatric lineages (see also [60,61]).

(b) Facilitation

Not all studies, however, find that pollinator sharing has negative effects on plant fitness. Floral infidelity can be neutral or even beneficial for co-flowering plant species through facilitation (Fig. 1) [34,36,49,50,62], *i.e.* an increase in visitation rate due to the presence of co-flowering plants, for example through a "magnet effect". For example, nonrewarding orchids benefit from [63] or provide benefits to [64] co-flowering rewarding plants (see also [65,66]). In high-altitude plant communities where pollinators are scarce, this facilitation could be common [34]. More generally, when plant abundance is low and pollination services are limited, sharing inconstant pollinators with co-flowering plants species could increase visitation rates due to a "mass effect", *i.e.* the attraction of pollinators to the area (or the survival of pollinators in an area) [34,37,50,67]. Similarly, in environments experiencing widespread pollinator decline, inconstant pollinators may be of increasing value to plants.

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 [35]. In sum, 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 [68,69]).

3. The pollinator perspective

Pollinators are expected to maximise energy intake – either in terms of rate [70] or efficiency [71] – while making sure they also collect all required nutrients for a healthy diet [72,73]. The first requirement is primarily achieved by collecting nectar, 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 [74] due to time (increased foraging trip duration) and opportunity (missed rewards) costs [74], sub-optimal flower choice [5,75] and increased flight distances [76]. 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 [74]. In addition, focusing on a particular plant species risks missing out on important nutrients [77].

So why would a pollinator be flower constant? One common 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 [6]. Due to limitations of these cognitive tools, pollinators switching between plants would be less efficient at extracting rewards [5–7,78,79]. An alternative view is that flower constancy is the economically most successful foraging strategy given the limited information a pollinator has about its environment [7,20].

(a) Cognitive limitations

Darwin [4] and von Frisch [80] suggested that flower constancy is favoured due to the benefits of learning: a bee that has learned how to extract nectar from, for example, linden (*Tilia*) blossoms is a more efficient forager than a bee unfamiliar with this flower [2,14] (an idea sometimes misleadingly been called “Darwin’s interference hypothesis” [81,82]). 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 [5,83–85]. However, research on the learning efficiency of pollinators 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 [12] and naïve *Bombus impatiens* bees collecting pollen from four plant reached a plateau in pollen collection efficiency within the first 20 visits [85]. On the other hand, *B. terrestris* collecting pollen from poppy flowers (*Papaver rhoeas*) improved their foraging efficiency over several foraging trips that included visiting hundred flower visits [84], 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 *Bombus impatiens* foragers [85]. Overall, observations suggests that bees and butterflies quickly learn how to handle a range of flower types, 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 [5,6,19]. Working memory, on the other hand, is prone to rapid decay and interference from competing information, such as new floral traits [6,12,86,87]. Inter-flower flights of inconstant bumblebees tended to be longer (~1-3 seconds) than flights between flowers of the same species [21,88]. These delays in inconstant flights could be due to a transient working memory that is stable for only a few seconds or they could indicate that inconstant bees need time to access long-term memory about an alternative, in case the forager has already experience with the second flower type. These time delays in inter-floral flights and learning how to extract nectar are likely to accelerate flower visitation rate due to flower constancy while also facilitating information consolidation from working- to long-term memory [21]. Overall, however, time costs due to inconstancy appear to be low. Laverty [89], for instance, found that *Bombus fervidus* experienced no time costs when switching between two types of flower with simple morphologies and only a ~1sec delay when switching between flower types with more complex morphologies, similar to the small increases in handling time found by Raine & Chittka [21] and Goulson et al. [13]. Importantly, even small time gains during flights between conspecific flowers can add up to a substantial amount of time saved as pollinators 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 (>30sec with each visit in the simulations) to make flower constancy more successful than inconstancy due to the costs of inconstancy [74]. I am not aware of any empirical studies comparing the time costs of switching flower type – due 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 [82]. Search images are thought to be useful when looking for cryptic targets, *i.e.* those that are difficult to find [90,91]. In contrast, flower constancy tends to be stronger when flowers become easier to detect or flower species become easier to differentiate (see Section 4a). Convincing evidence that “search images” cause of flower constancy is currently missing, but more research into visual background effects on flower constancy and attention priming [90,91] is needed to assess the roles of search “search images” in 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 (Section 4). This suggests that ecological and social interactions shape the cognitive tools and behavioural strategies pollinators follow.

(b) Informational limitations

The costly information hypothesis [6,7] posits that flower constancy is the best strategy in an uncertain environment given that acquiring information about better plant species would cost time and energy. Assessing the profitability of alternative flower species may require sampling a large number of flowers given that different flowers of the same plant species offer variable rewards [92]. Flower constancy might then be the best option if the rewards currently experienced by a pollinator are above a threshold. Honey bees are indeed almost fully flower constant when the rewards they receive are above a reward threshold [22,93]. As the number of plant species in an environment increases, so do the sampling costs to obtain reliable information, thus favouring flower constancy [6,7]. While I have found this hypothesis intuitively appealing in the past [7], computer simulations have since convinced me that flower constancy becomes more costly as plant species diversity increases [74]. This is because the time and opportunity costs of bypassing flowers also increase when alternative options are 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 [74]. Empirical evidence is mixed, however. While Gervais et al. [94] and Martínez-Bauer et al. [95] found that increasing plant diversity was indeed associated with lower flower constancy in bumble bees, Austin et al. [96] found that bumble bees became more flower constant when there are more options available. The first two studies were performed under natural conditions, whereas Austin et al. [20] used artificial flower arrays and lab 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 Section 2) suggest that pragmatism and flexibility guide flower choice in the pollinator world. We would expect an optimal pollinator with multiple options to divide her time between exploiting familiar flowers and sampling alternative ones [97,98]. The impression that bees are commonly flower constant may have resulted from the focus on the honey bee *Apis mellifera*, a highly flower constant species [3,75,99], but even honey bees show flexibility in their floral choices in response to reward characteristics [7]. These two findings – variation between species and flexibility within species – suggest that there is ample scope for natural selection to drive flower choice strategies [7]. Below I discuss three types of drivers of 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 [88,100–105]. Bumble bees preferentially foraged on more complex flowers only if it offered sucrose solution of higher concentration than simple flowers in experimental setups [102,103]. Bumble bees foraging naturally on different shrubs preferred the species with higher daily sucrose production per flower [106]. The small skipper butterfly was twice as likely to switch plant species after receiving a below-average reward quantity [13]. Even the highly flower constant honey bee *Apis 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 [22].

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 in the number of traits [5,19,27,45,79,88,99,101,107–109]. The link between flower constancy and pollinator perception is likely due 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 Section 2). Bees also increase flower constancy as flower size and floral display size (*i.e.* larger number of inflorescences per plant) increase [110,111]. Since flower and display size have been shown to correlate positively with reward size [112], pollinators may use flower and display size 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 [85,105,108,113,114]. For example, while bumble bees needed only a few minutes to learn how to efficiently extract nectar from flowers with simple morphologies, they needed up to an hour to become competent foragers on flowers with complex morphologies [83] (see also Section 3). In addition, visiting complex flowers is associated with longer handling times (up to 25 seconds *vs.* a few seconds for simple flowers) [85,113,114]. One might, therefore, predict that pollinators prefer simple flowers. Evidence, however, is mixed: while *Bombus impatiens* preferred the simpler of two artificial flower types [102], naïve *Bombus terrestris* foraging on natural flowers preferred complex types [113]. Similarly, *Bumbus fervidus* were only flower constant when visiting plants with complex morphologies [89]. What could explain these counterintuitive observations? First, bees might be discouraged to switch to an alternative type due to 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 [115,116]. Visiting a complex flowers could be beneficial for pollinators experiencing intense competition, while plants might benefit if flower morphology filters out ineffective pollinators [116].

(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 [19,23]. 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 [17]. Abundance and degree of clustering of co-flowering plants determine the distances pollinators need to fly between flowers. As distances increase, both honey bees and bumble bees become less flower constant and switching to the nearest flower type becomes more common [19,23,27,88,117–119]. Pollinators could gauge these distances based on travel costs [5] or based on floral visual angles [111]. Computer simulations similarly found that flower constancy reduces energy intake when flower density is low [74] 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 and cognitive limitations (working memory instability) arguments [6,119]. 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 (Fig. 2) [19,120].

For plants, on the other hand, the more frequent switching in more evenly mixed situations could be costly due to increased IPT.

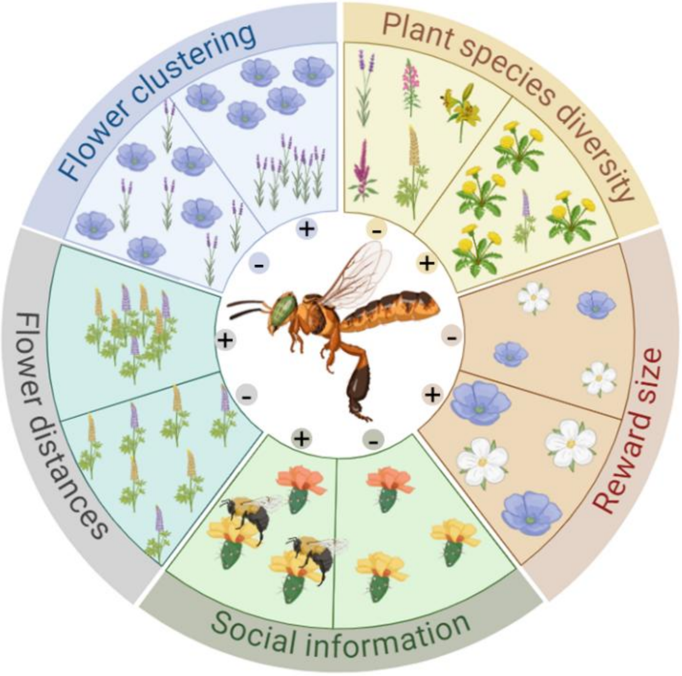

Figure 2. Factors affecting behavioural flexibility and the strength of flower constancy. Flower constancy depends on floral features like reward size [22], ecological factors like the arrangement of flowers in space (e.g. [19,23,120]), flower diversity [94,95] or social factors like social information [74,121]. Plus and minus symbols indicate whether a particular factor is expected to increase or decrease flower constancy.

(c) Interspecies variation and the effects of sociality

Different observers have noticed that pollinator species can vary considerably in how flower constant they are [2,5,7,39,77,122]. Bateman [123] and Waser [5], observing bees moving between flowers, found that honey bees were more flower constant than bumble bees. Furthermore, honey bees returning to their hive have mostly pure pollen loads [3], whereas those of bumble bees are commonly mixed (Fig. 3) [124]. In controlled laboratory experiments, *Bombus impatiens* foragers were also quicker to switch from a deteriorating sugar solution to an alternative one than *Apis mellifera* [125]. Even within bumble bees (*Bombus*) there appear to be considerable interspecific differences: in the South American *B. atratus* and *B. bellicosus,* 80% and 84% of pollen foragers visited just one plant during a foraging trip [9], whereas only 23% of pollen foragers showed flower constancy in the European *B. terrestris* [126]. 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.

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 [42,55,123,127]. In a comparative study of pollen loads of 56 bee species in a temperate bee community, Smith et al. [122] found that social bees were more flower constant than solitary bees. Three explanations for this sociality effect have been proposed: the resource-partitioning hypothesis [6,7,100], the communication hypothesis [6,74,121] and the diet breadth hypothesis [77,128]. 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 specialising on different flower species [6,100,126]. However, if a subset of nestmates specialises on a subset of flowers then they still compete within their group, while now also paying the energy, time and opportunity costs of flower constancy.

Fig. 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: CG).

Sociality could favour flower constancy in bees due because many social bees communicate about food sources [74,121]. Since social bees share information selectively about high quality food sources, nestmates using social information are likely to discover more profitable food sources [129–133]. For example, honey bees use the waggle dance and some stingless bees lay pheromone trails to food sources [129,131,133–136]. 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 [130–132,135,137,138]. This selective information sharing lowers the risk of specialising on flowers offering low-quality rewards and, therefore, reduces the benefits of sampling alternative types. Virtual bee colonies with communication and flower constancy indeed collected more energy than those without communication because selective information sharing allowed colonies to specialise on the most profitable flower species in their environment [74]. 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 [74]. As plant diversity increased, inconstancy became the best strategy (see Section 3b). Thus, while communication about profitable flower types reduces one cost of flower constancy, specialising on sub-optimal flower species, it does not affect the time, energy and opportunity 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 [72,73,139]. Nectar is the main source of carbohydrates, while pollen provides most of the proteins, lipids and micronutrients [72,139]. As pollen from different plant species differ in their nutrient composition [72], collecting a small number of pollen types risks nutritional imbalances [140,141], with potentially negative fitness consequences [142–144]. In social bees, nectar and different types of pollen are often collected by different colony members as a form of division of labour [145–147]. A solitary bee, on the other hand, needs to collect both nectar and pollen by herself. Williams & Tepedino [128] 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.

Since different colony members exploit different flower species in social species, flower constancy might not lower diet breadth [74,126,128]. Pollen analysis confirms that colonies of highly flower constant species exploit many plant species simultaneously [148–150]. However, only a small number of pollen types, usually <5, is collected in significant quantities. Thus, social bees may still face the risk nutritional deficiencies due to flower constancy, especially in environments with low plant diversity. Accordingly, simulated flower constant colonies with less than 50 foragers often exploited less than half of the plant species exploited by inconstant colonies [77]. A larger colony size increased the number of flower types visited even if colonies were flower constant, which could help explain why bumble bees, which have small colony sizes than honey bees and most stingless bees [77] are less flower constant than the latter two groups [151].

5. 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. Likewise, social and solitary pollinators are likely to experience different costs and benefits due to flower constancy. As a result, interests of plants and pollinators may align in some situations, yet contrast in others (Fig. 4): for example, when a plant is abundant, flower visitation and flower constancy increase [17,152,153], which is likely to favour both plants and pollinators in terms of seed set for the former [153] and energy intake rate for the latter [74] (*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 (*Scenario 2*). These costs could outweigh the benefits of reduced interspecific pollen transfer due to flower constancy under some circumstances (Fig. 1). In plant species-rich habitats with a relatively even abundance and distribution, interspecific pollen transfer due 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 (*Scenario 3*) [6,74]. Finally, when plants and pollinators are scarce, flower constancy could reduce pollinator visits to plants and reward rates for pollinators, thus negatively impacting the fitness of both plants and pollinators (*Scenario 4*).

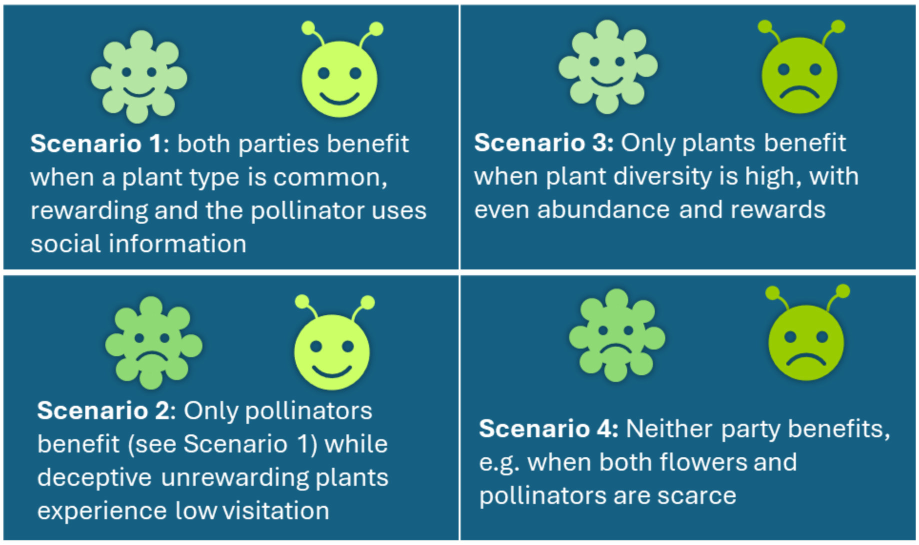

Fig 4. Interests of both plants and their pollinators when pollinators are *flower constant*. Four Scenarios (1-4) are suggested that reflect different situations.

While some empirical and theoretical support for these scenarios exists, the interests of plants and pollinators remain far from understood. Our knowledge gaps, especially when considering rare plants, are a blind spot for plant conservation: it has been suggested that rare plants experience higher costs due to IPT [28,31,52,53], but whether and when these costs outweigh the benefits of facilitation [34,37,50] is poorly understood. Rare plants might even encourage pollinator inconstancy by offering particularly valuable nutrients [39]. Other important gaps remain, for example, we know little about the dietary requirements and foraging strategies, including flower constancy, of the vast majority of pollinators, especially in small-bodied pollinators and those in the tropics [18,35,39]. Research in both controlled environments and natural communities is needed to better understand how different behavioural strategies 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.

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