

Flower sharing and pollinator health: a behavioural perspective

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Abstract

Disease is an integral part of any organisms' life, and bees have evolved immune responses and a suite of hygienic behaviours to keep them at bay in the nest. It is now evident that flowers are another transmission hub for pathogens and parasites, raising questions about adaptations that help pollinating insects stay healthy while visiting hundreds of plants over their lifetime. Drawing on recent advances in our understanding of how bees of varying size, dietary specialisation and sociality differ in their foraging ranges, navigational strategies and floral resource preferences, we explore the behavioural mechanisms and strategies that may enable foraging bees to reduce disease exposure and transmission risks at flowers by partitioning overlapping resources in space and in time. By taking a novel behavioural perspective, we highlight the missing links between disease biology and the ecology of plant-pollinator relationships, critical for improving the understanding of disease transmission risks and the better design and management of habitat for pollinator conservation.

Keywords

Bees, foraging, nutrition, behaviour, navigation, disease

1. Introduction

As with all multicellular organisms, pollinating insects face threats from the pathogens that they have co-evolved alongside for millenia. A fine balance between the geographical distribution, prevalence and infectivity of pathogens defines the health of pollinator populations, and we are just beginning to understand the impacts of disease on plant-pollinator interactions and whole ecosystem dynamics [1]. In the field of pollinator disease ecology, much of the current research focus is on conserving wild pollinator populations and maintaining healthy populations of managed pollinators that are bred and distributed by humans [2], as well as minimising the risk posed by the latter to the former. One less understood question however is how pollinating insects might use *behavioural* defences to avoid infection and illness caused by pathogens when visiting flowers.

Commercially-managed bees carry a wide range of parasites (*e.g. Varroa* mites) and pathogens, including viral (*e.g. deformed wing virus*), fungal (*e.g. Nosema ceranae*), bacterial (*e.g. Paenibacillus larvae*) and protozoan (*e.g. Crithidia bombi*) infectious agents, some of which can spread to wild insect pollinators [3]. Such spillover effects in pollinator communities can occur through direct and indirect transmission [4], and the number, route, mode of transmission, and stability of an infectious agent outside the host will determine its infectivity. Direct transmission occurring through contact with infected individuals happens mostly under conditions where insects spend a substantial amount of time together, such as within nests or mating aggregations. Social bees are among the best-studied pollinators and are known to have evolved a suite of hygienic behaviours, both at the individual and social level, to keep disease transmission at bay in the nest [reviewed by 5-6]. Indirect transmission can occur through exposure to contaminated surfaces or food, and for pollinators this is mostly likely to occur during foraging on flowers [7-9, see Table S1]. Much less is known about how the foraging behaviour and choices of individual bees affects the risk of disease transmission and infection, raising the question of whether pollinators have behavioural adaptations that help them stay healthy when visiting hundreds of plants over their lifetime.

Previously it has been suggested that bees may be able to recognise and actively avoid landing on flowers containing pathogens or offering nectar that has been modified by bacteria [10-13]. Yet in most cases the purpose of flower visits is the extraction of food which requires handling of the flower, and foraging pollinators risk exposure to pathogens with each flower contact. The frequency, duration and type of floral contacts determines the likelihood of contamination and infection, as well as the prevalence and survival of infectious pathogens on

flowers. Foraging and floral handling behaviour therefore may not only be under selection to increase a forager's success in acquiring food, but also selected to reduce disease exposure and infection risk. The types and levels of infection risk that foraging pollinators can tolerate remain unclear.

Here we explore whether behavioural adaptations that are commonly assumed to be driven by floral reward quality and availability, such as patterns of flower choices and patch-leaving decisions, are also beneficial in reducing the frequency of exposure to pathogens. We focus on bees because it is a diverse group of insect pollinators but also the best-studied behaviourally. We consider female social and solitary bees exclusively in our discussion, but acknowledge that male bees in most bee species are also flower visitors collecting food for themselves within defined home ranges and learning the locations of flowers [14-16]. Males are typically not considered to be central-place foragers. and so such differences could potentially also have significant effects on disease transmission at flowers. It is also relevant to note that not all microbes found on flowers are pathogenic, yet are still relevant to pollinator health through important roles in multitrophic relationships (see Table S2 for an overview).

2. Overlap in plant utilisation increase the risk of indirect disease transmission in pollinators

The relationships between pollinating insects and flowering plants are complex. They are best understood in the context of communities and whole networks that incorporate a variety of individual interactions between diverse partners over time, in particular locations and/or types of habitat [for a review see 17]. Flowers vary in their morphology, advertisement cues and rewards, typically *including* rather than excluding diverse pollinators, even if that comes at a higher cost of rewarding less effective species of insect pollinator [e.g. 18-18]. Therefore, there is significant overlap in the floral resources pollinators utilise, even in species-rich networks and habitats where biotic interactions are increased. While this should lead to *more* partitioning and specialisation [22], in reality most plant-pollinator relationships are predominantly generalist and highly overlapping [23-21]. Typically bees collect pollen and nectar from many different plant species, benefitting from such generalist collection strategies by diversifying both the range of nutrients consumed and by diluting exposure to plant toxins [25-23].

The generalised nature of plant-pollinator relationships therefore generates a high potential for multiple indirect contacts between insect flower visitors. When foragers of the same or different species overlap in space and time, visiting the same individual flowers within short time windows, flower-sharing contacts become a prominent source for indirect pathogen

transmission [10, 27] (Figure 1). Pathogens are deposited when pollinators defecate on flowers, and this seems to be the most likely mechanism of indirect transmission, both within and between species [28-31]. Pollen collection can increase pathogen presence on the bee body and may also be a potential route for infection, though grooming may reduce infection risk, and pathogen-contaminated pollen has been found on the body of healthy bees [32-34]. Some bees regurgitate small drops of nectar to moisten pollen during collection, and it is possible that surface contamination of flower organs occurs through salivary deposits or contact with pollen sacs on the bee legs, though this has not yet been shown directly [35-37].

The risk of infection via indirect contact with pathogens is more variable than risks associated with direct contact and depends on the amount of time elapsed between pollinator visits, and whether pollinators make sufficient contact with the contaminated surface. Also important is the pathogen's ability to survive on the flower, withstanding various macro- and microclimatic conditions and exposure to potentially harmful phytochemicals. The longevity of the flower is another factor. Thus, what matters in terms of disease exposure and transmission are those visits to the same individual flower that occur within a critical time window during which the pathogen remains viable. Contacts must also be of sufficient duration to cause infection. Although contact patterns will depend to a large degree on the abundance of insects and flowers within a given area, factors which are commonly measured and modelled in ecological disease studies, sometimes in combination with broad sampling of insect visits [37, 38], we argue that it is also imperative to consider the specific movements and actions of individual foraging pollinators, including visitation sequences at finer temporal and spatial scales.

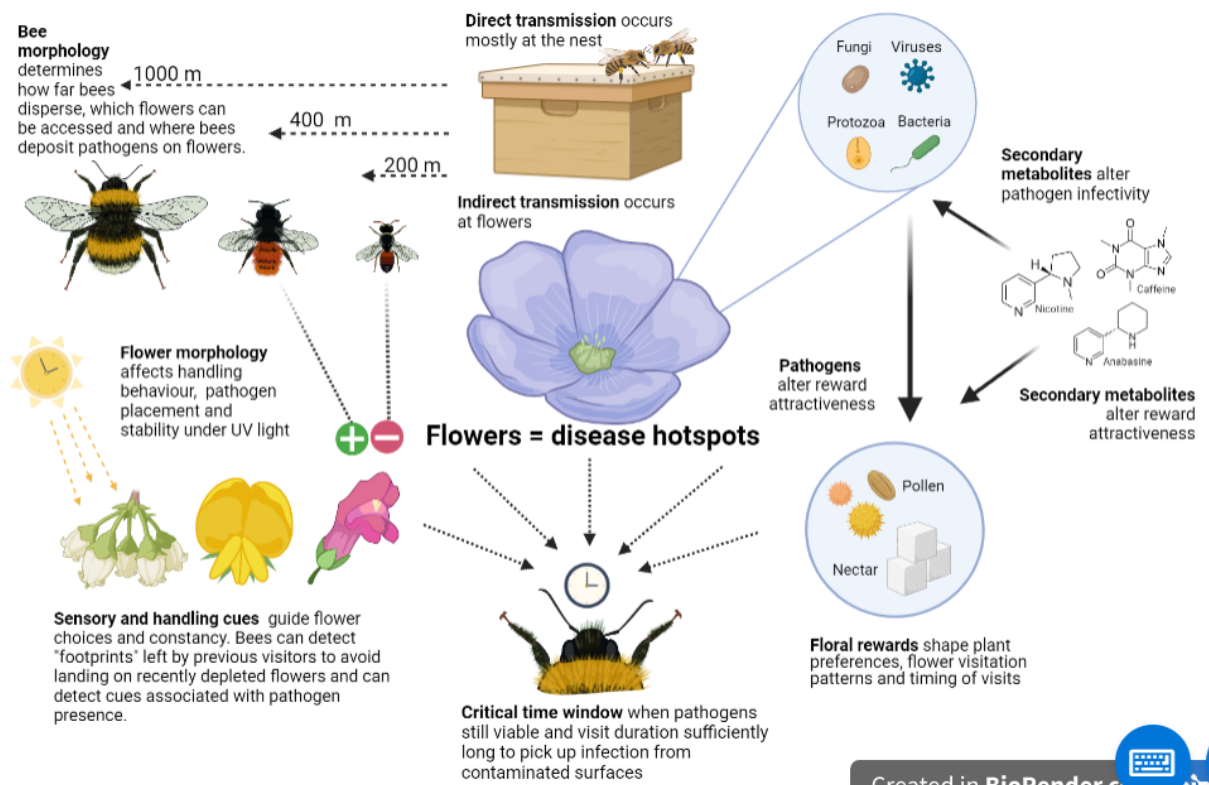


Figure 1. Flowers are hotspots for indirect transmission of disease. Various factors, including both flower and bee morphology, determine the placement of pathogens on flowers and the duration which they remain viable, leading to a critical time window for flower visits that lead to infection, where bees make sufficient contact with contaminated surfaces and pathogens remain infective. While dietary specialisations and preferences drive flower choices and resource partitioning, individual foragers use many different sensory and handling cues to guide flower choices within a patch, and can avoid landing on flowers that have been recently visited by another pollinator or reject flowers on the basis of cues associated with pathogen presence. These behavioural adaptations may serve to reduce their susceptibility to infection by pathogens present on flowers. Figure created with BioRender.com. Bee images credited to Jose Luis Ordóñez and Ignasi Bartomeus, used under CC-by-NC licence.

3. Dietary specialisations and preferences drive flower choices and can reduce flower sharing

Although the majority of bees are generalists, diet breadth varies considerably between species. The larvae of certain solitary bees can only develop on the pollen of one or two closely related plants, and even the larvae of generalist bees exhibit better survival when fed one type of pollen over another [see 21]. When foraging, individual bees are known to develop preferences for certain plant species over another, and do not visit and collect resources equally from all available flowers

When collecting nectar, the main source of carbohydrate for bees, foragers assess the nutritional value of this reward instantaneously and over the duration of several foraging bouts, by measuring the flow rate and sugar content [39]. Generally more concentrated nectar is preferred by bees, providing it is not too viscous [40], and bees learn floral cues and spatial information better when the sugar content is higher [e.g. 41-39, 43]. Nectar also contains amino acids and other phytochemicals, such as caffeine or nicotine, that have been shown to alter bees' flower visitation preferences and ability to learn floral cues [44-47].

For pollen the factors driving flower visitation preferences are less well understood [reviewed by 21], owing both to the nutritional complexity of pollen as a floral reward, and the fact that unlike nectar, pollen is not actively ingested at the flower during pollen collection, raising questions about the mechanism(s) of reward evaluation. Individual bees concentrate their effort on a smaller selection of plant species compared to nectar foraging. There is evidence that bumblebee foragers appear to favour plants providing pollen with high protein:lipid ratios [48], and that macronutrient ratio preferences vary according to bee species [49-46]. However, the majority of the work on bees' individual pollen foraging preferences has been conducted in social bees, which rely on a large foraging workforce to ensure that a suitable range of nutrients is secured by the colony [reviewed by 25]. Solitary female foragers in contrast, must also lay eggs, build the nest and collect all food for developing larvae, and as yet very little is known about how the drivers of foraging decisions differ between social and solitary bees [but see 51-52].

Differences in floral food reward preferences, both between species and individuals, can therefore lead to spatial segregation in flower visitation patterns, reducing the overlap in flower contacts between pollinating insects, and thus potentially lowering the risk of contamination of food and flower surfaces, and pathogen transmission and infection.

4. Flower visitation patterns within a patch

Aside from the nutritional suitability of food rewards offered by flowers, there are many additional factors which affect a bee's decision to land on a particular flower or not. These can

be broadly divided into i) *sensory cues* arising from the display of the flower and ii) *handling cues* related to flower morphology. Many pollinators exhibit 'flower constancy' within a foraging bout, visiting flowers of the same species or limited range of species and ignoring others within the same patch, even if they provide approximately equal food rewards [53]. Both sensory and handling cues contribute to flower constancy, which is thought to maximise foraging efficiency by minimising the handling and cognitive costs associated with switching between different flower morphologies, and by reducing the cost of information acquisition [54-58]. Flower constancy, or majoring and minoring [59], varies in different species, forager types and contexts, and even an individual that is highly flower constant to one particular plant species may occasionally deviate from that flower type during a foraging bout to assess and compare the profitability of alternative floral resources [60]. This means that every flower in a particular location or 'patch' does not have an equal likelihood of being visited by a particular bee species or individual forager, meaning the risk of indirect disease transmission through contact with contaminated plant tissue or consumption of contaminated food rewards is variable.

Sensory cues, of which visual and olfactory cues are most salient and well studied, but also other cues, such as temperature, electric fields and humidity patterns [61-63] help bees to distinguish between flowers and remain constant to a particular plant species. However, such multi-modal displays can also lead bees to generalise between flowers of a similar type on the basis of traits such as petal colour, fragrance and flower morphology [64-66], which could lead to more overlap between visitors and an increase in flower contacts within a given location. Such generalising between similar flowers could further be influenced by environmental 'noise' such as changeable weather conditions affecting the bees' ability to detect and respond to floral signals [67]. This means it can be hard to predict how individual bees will distribute themselves and select flowers within a foraging bout in a multi-species patch based solely on the knowledge of the plant species present alone. Detailed examination of visitation patterns of individual bees within a foraging bout as well as plant-pollinators networks are needed. This will allow the detection of contact patterns and the degree of overlap between individuals which when overlaid with information regarding the virulence and infectivity of pathogens deposited on flowers, will determine the true exposure risk of foraging in a particular area.

Differences in flower morphology shape bees' foraging preferences and the degree of constancy due to the handling time required to extract rewards. However, flower morphology itself can also influence the risk of disease transmission. For example, the type of behaviour required to extract a floral reward from a flower can affect pathogen dispersal, as shown for bumblebee pollen-scrabbling behaviour which led to a 23% higher acquisition of microbes

from monkeyflowers, compared to nectar collection [34]. When comparing 14 different plant species, Adler and colleagues [68] showed that the number of reproductive structures per inflorescence predicted both the risk and intensity of infection with the trypanosome parasite *Crithidia* in *Bombus impatiens* workers. Flower morphology also directly affects which bees or insects can visit a particular flower, due to mismatches in bee body size or tongue length, which again leads to partitioning of floral resources among insect visitors. The shape of flowers and size of bees visiting them affects where faeces are deposited on the flower [28, 29], which in turn can affect not only the likelihood of other bees making contact with pathogens present in faeces, but also how long the pathogen remains infectious on plant tissue, since many pathogens are affected by prolonged exposure to UV light [69]. Furthermore, although the oral-faecal transmission is arguably the most common route for bee pathogens, both within colonies and between bee species [27, 29], some bee pathogens, such as Chronic Bee Paralysis Virus (CBPV) and Israeli Acute Paralysis Virus (IAPV), can also be transmitted by topical contact through bee cuticle [70, 71]. Therefore, close bodily contact of bees with pathogen-contaminated flower parts owing to flower shape and/or bee handling behaviour may also influence the likelihood of viral transmission.

As discussed above, bees will pass by many flowers without approaching them. At times they may approach a flower but then reject it after inspection, without landing on it. This decision is based on the presence or absence of particular sensory cues. Insects can detect the presence and/or size of nectar rewards in flowers using scent cues, humidity gradients and even the CO₂ emitted during nectar production [72-74], which may inform their decision of whether to land on a particular flower or not. Also, "footprints" (hydrocarbons) left behind by previous insect visitors, for example, can provide olfactory cues used by bees to assess how recently a flower has been visited or identify a particular reward context [75-77], and may even be able to determine information about the identity of the visitor [78]. Crucially the decay of these footprint signals is thought to occur within a similar timeframe to floral reward replenishment [75], meaning bees already have an in-built sensory and behavioural system to avoid landing on flowers that have been recently visited by other insects, which potentially serves a dual purpose of avoiding wasting handling time on empty flowers, as well as minimising contact with diseases. Furthermore, the presence of pathogens themselves may alter floral traits and attractiveness, providing sensory cues that could allow bees to avoid landing and feeding from contaminated flowers [7, 13]. Fouks & Lattorff [79], for example, showed that when given a choice, bees preferentially feed on non-contaminated flowers, rather than those contaminated with *Crithidia bombi*, which they attribute to bees' detection of olfactory cues emanating from the pathogen-contaminated nectar [80].

Within a given location bumblebees and honeybees tend to follow individual flight paths developing a persistent flight geometry as they move from flower to flower [81-84]. The frequency and sequence in which bees visit individual flowers can change and vary over time, particularly as bees become more experienced on the flowers [85]. Within and between foraging bouts, individual bees may switch between *exploiting* floral resources, and *exploring* new resources (i.e. exhibit a decrease in flower constancy)[60]. This can happen in response to dwindling rewards and resource availability or through increased competition [86, 87]. Following exploration of alternative resources, a bee may choose to switch to a different floral resource and remain longer within a given location, or to move out of a patch to find better rewards. Bumblebees tend to stay in the same foraging site where possible, switching to new plants or foraging on more than one plant species within that site [88]. Plants may also exploit and manipulate the local behaviour of visiting bees by strategic allocation of rewards to different flowers within an inflorescence [89].

In summary, bees have behavioural adaptations, based on sensory and morphological traits, that help them maximise the efficiency of reward extraction through minimising unnecessary contact with flowers, which can simultaneously help to reduce exposure to freshly contaminated surfaces or food. When foraging within a patch of preferred floral resources, bees will not visit every flower of a particular species in that patch, nor indeed every flower on a particular plant, therefore the risk of pathogen exposure and infection are not evenly distributed across a flower patch.

5. Foraging ranges, trap lining and navigation between patches

Bees exhibit a high degree of spatial fidelity which enhances their foraging efficiency. This is best demonstrated for various species of social bees where foragers frequently return to locations where they have discovered a reward, typically also at the same time of the day. Besides, movements between plants in a patch are directional and influenced by the type and quality of reward they experience on subsequent visits, and bees will spend more or less time in a patch depending on this experience. When homing in on individual flowers bees rely on wider views of the patch, because they cannot detect single flowers from a long distance with their low-resolution eyes. Already at a distance of just 10-50cm the appearance of flowers changes dramatically, rendering small details of their displays and inflorescences undetectable [90]. Instead, bees are guided by views that are optically merged, and thus floral displays of many flowers and inflorescences are shared. As bees leave the patch, they memorise global views, which will include large landmark objects or contrasting visual features, such as the skyline or tree edges, and follow individual routes [91]. Jointly with compass information, bees are well equipped with effective navigational mechanisms that

allow them to direct and maintain movements over longer distances, such as between patches. Over a few foraging trips they develop preferred travel routes [92]. Their movements between patches have considerable impact on the visitation patterns and hence the risks of disease transmission (Figure 2).

How far bees are willing to travel to reach a flower patch differs substantially between species, mainly as a function of body size and level of sociality. Foraging female bees are central-place foragers; they depart and return to a single permanent location, their nest. However, social bees tend to fly further away, typically around 1-2km [93-97]. The Western honeybee and buff-tailed bumblebee have been found to follow rich sources up to 12-15km, although at diminishing rates of return with many bees being lost to the colony at such extreme distances [43, 98]

Travelling further away from the nest goes against the predictions of optimal foraging theory which posits that a pollinator should minimise their flight distance and time, and thus energetic costs incurred when travelling between patches (Heinrich 1976). On the other hand, it helps a colony to disperse its workers over a larger area, and an economic model by Cresswell and colleagues [99] clearly demonstrates that this is an adaptive approach to resource gathering. The waggle dance is a well-documented recruitment system in honeybees that is dependent on distance-based profitability assessments [43, 97]. The likelihood and intensity of dancing decreases when bees travel over longer distances which results in different density distributions in foraging areas. For foraging patches less than 100m away colony dances do not indicate specific locations [43], with the aim of spreading out foragers within the immediate radius of the hive, as well as encouraging independent exploration. Stingless bee, such as *Melipona panamica* or *M. quadrifasciata*, recruit their hive mates to locations and are able to communicate distance information with vibrational signals similar to honeybees [100-102].

Solitary bees typically forage over much shorter distances. Moving host plants instead of artificial feeders, Zurbucher and colleagues [103] found that the maximal distance over which females would forage was between 1.1-1.4km depending on body size and bee species. The preferred range was much shorter than the maximal distance, typically between 100 and 300m. The strong relationship between the body size of a bee and its foraging range [104] is linked to the physical capacity to endure movement through air, which for insects is an unsteady and viscous medium [105]. Several size-related factors affect speed and energy requirements, such as mass-specific metabolic rate, wing size, wing beat frequency, ability to control body posture and orientation in air turbulence, and thermoregulatory abilities needed to remove excessive heat [106-108].

In social bee species where individuals differ strongly in body size within a colony, such as bumblebees or some stingless bees, larger-sized individuals have longer flight ranges and also differ in their cognitive and flower foraging strategies [42, 109]. Given these dramatic differences in foraging behaviour, it is logical that sizes and numbers of visited patches will differ substantially among species, and therefore influence their specific movement patterns, proximity to the nest and numbers of flowers visited during a foraging trip which in turn will vary the risk of exposure to pathogens and parasites.

Pollinators fly over variable distances yet plants grow with a finite density, and situations will arise where pollinators aggregate in larger numbers in high-density or highly-rewarding patches. However, it is difficult to predict when and where aggregations will occur, as contrasting boundaries and heterogeneous structures between adjacent patches in the landscape will influence the different routes followed by pollinators. Adjacent patches separated by such structures may present high and low abundances of the same or different flowers, such as crop fields and species-rich field margins. On route, pollinators will decide whether to stay within a crop field or margin, or whether to switch from one to the other. Modelling reveals that spatial parameters as well as flower abundances in the multispecies margins and other floral resources influence which patches will be preferred by bees moving between them [110, 111].

Variations in flight ranges and trajectories spread pollinators in space and time in a dynamic way that is not completely random but also not predictably uniform. Taken together, the spatial behaviour of bees has evolved such that they spread out between patches over large areas. This reduces the levels of close contacts within the critical time period where visits occur in short succession and expose the pollinator to a virulent pathogen or parasite.

6. Conclusions

Here we have argued that understanding pollinator behaviour is crucial to predicting how some diseases spread through the environment. Bees foraging behaviour has evolved to deal adaptively with the varying spatial and temporal distribution of floral resources that differ in their heterogeneity. Such adaptive behaviours may be challenged in areas in which plants are scarce or extremely uniform over a large area, such as in deserts, pastures or large crop fields. The limitation of measuring disease risks from abundances of flowers and/or pollinators is that this can only show association and will strongly vary depending on context, landscape scale and focus of investigation leading to conclusions that biodiverse habitats can both

improve and impair disease threats for pollinators [112]. Flower diverse patches offer more opportunities for partitioning among diverse pollinators that differ in their flower choices and movements, leading to a 'dilution effect'. While dilution effects are typically described as decreases in transmission due to increases in host diversity [113], increasing flower density in some cases results in a similar effect [37]. This suggests that increasing both flower abundance and diversity should synergistically reduce pathogen transmission risks in pollinator communities.

There are limitations for pinpointing transmission mechanisms and causal health risks at the individual and nest/colony level. We argue that this is the missing link that would help to effectively estimate fitness costs at the population level. As well as targeted work in the field to identify and quantify transmission events, modelling offers a useful tool for exploring the process and impacts of flower-mediated pathogen contact. Given that this system involves an understanding of pollinator movement behaviour and contact dynamics, it is likely that suitable models would need to be spatially explicit (considering complex floral environments that accommodate the flight ranges of multiple nests of pollinators), going beyond a standard compartmental epidemiological model. Network theory gives us links into understanding how interactions between individuals of the same and different species could drive infection [114], and models exist that consider the links between pollinator networks, individual behaviour and infection [38, 115]. However, given that pollinator behaviour is highly dependent upon the location of flowers, the configuration of the pollinator's landscape is likely to be highly influential on infection. Individual-based modelling offers us a means of bringing movement rules, landscape form, and population processes together (Figure 2), by simulating the behaviour of multiple autonomous agents within a complex environment. Individual-based models (IBMs) already exist considering bee movement and population processes [e.g. 116-110], and IBMs are being used more frequently to understand disease epidemiology [e.g. 118-112].

IBMs are often complex, particularly when they are designed to model real systems (where many specific assumptions are made). For the questions raised here, we suggest that it would be enlightening to explore the value of modelling assumptions through the creation of deliberately basic models that simplify the landscape and movement behaviour of the pollinators, to avoid masking the effects of the pathogen's transmission strategy. The pollinator-plant-pathogen system is particularly unusual in that the pathogen is distributed through the environment in many discrete locations where onward contact is not guaranteed, and where the hotspots are potentially extremely short-lived. This is partly analogous to the models created by Nunn and colleagues [120] exploring faecally-transmitted parasites in

primates and which could be extended to animals grazing on a replenishing resource, in analogy to depleting flowers. Inevitably, however, the floral system does not allow pathogens to remain present in the environment beyond the short critical time window defined by several factors (Figure 1), which should be a strong selective force on the pathogens, giving what is arguably a novel system in epidemiology [1]. In the Supplementary Material (<https://figshare.com/s/4df1fceb538e240a19e8>) we provide an example of a simplified model, which sets out to explore how individual differences in behaviour within a nest could influence the spread of a florally-transmitted disease.

Finally, we should acknowledge that our focus on bees does not completely cover all the variation in flower visitation behaviour that applies to full diversity of insect pollinators. Some, typically less well studied, insects visit flowers for purposes other than collecting floral rewards, such as eating the flower or using it as a mating site, and this will affect where and how they interact with flowers and the risks of disease transmission. A finer distinction between types of pollinators, their behaviour and life-history traits and their functional position in plant-pollinator networks will help to identify which behavioural adaptations defend against disease exposure on flowers.

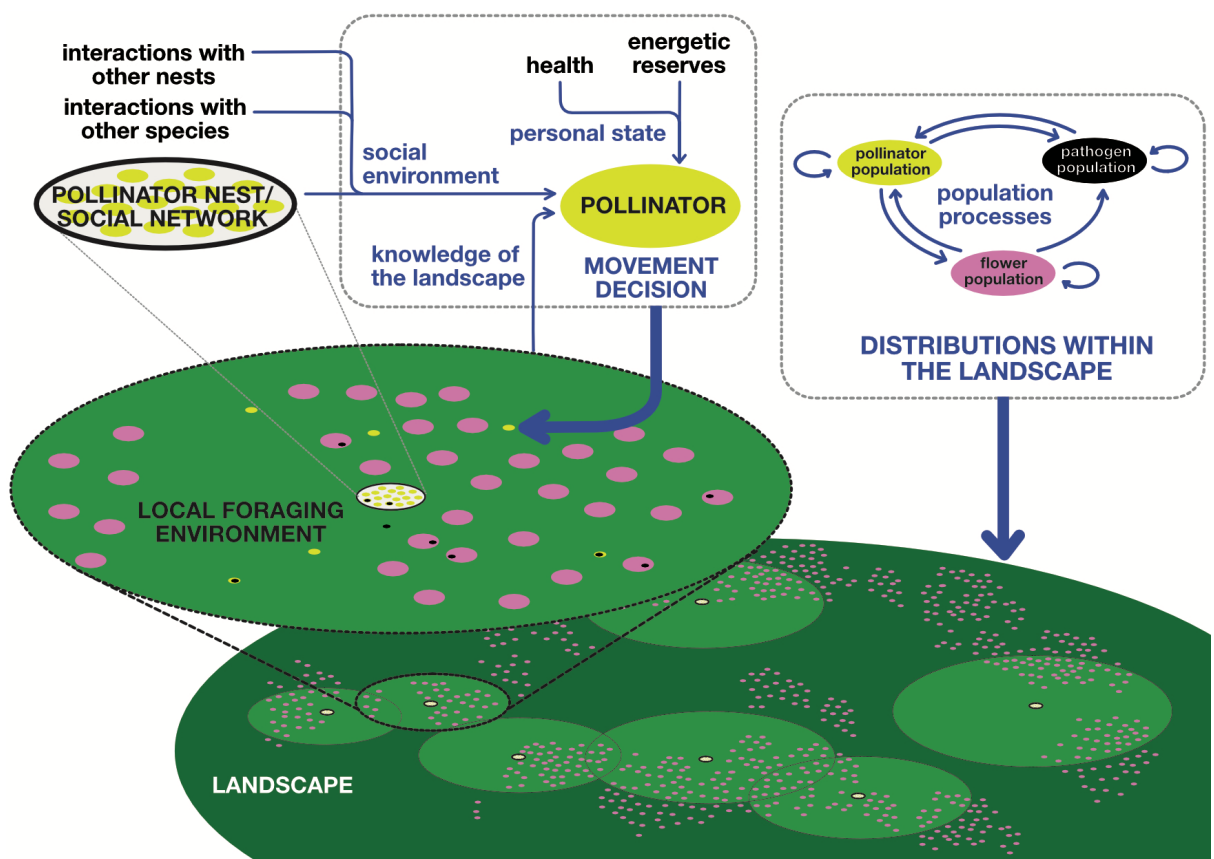


FIGURE 2. *A cartoon of the assumptions required for a functioning model describing how plant-pollinator-disease dynamics are influenced by both the environment and the behaviour of the pollinators. The landscape is likely to be highly heterogeneous, and may consist of different patches of flowers of different species. We sketch an example with central-place foraging pollinators (such as female bees, which return to a central nest at the end of each foraging trip), which assumes that all the individuals based in a nest have a limited distance over which they can forage, here denoted as the ‘local foraging environment’. Within the landscape, different nests have different local areas, and where these overlap are the points at which infections can spread. The movement of each pollinator is likely to be dependent upon its own knowledge of the environment and information it gains both from the environment and socially (from both its nestmates and other pollinators within the environment), as well as its own personal state (such as its energetic or nutritional requirements, or its current health). Because each individual is likely to differ in both experience and personal state, and because the environment is changing dynamically, the behaviour of a nest (or several nests) will be complex, and relevant models are likely to use a spatially-explicit modelling technique such as individual-based modelling. However, because the populations of both pollinators, flowers and pathogens are also going to be changing dynamically over the course of a simulation, it is likely that concepts from epidemiological population modelling may also need to be considered and applied to the spatially-explicit framework.*

Funding

EN acknowledges support from UK Research and Innovation (Future Leaders Fellowship awarded to E.N., MR/T021691/1), NHI from BBSRC (research grant number BB/N000625/1) and CB from Consejería de Educación, Cultura y Deportes of Junta de Castilla – La Mancha (European Regional Development Fund SBPLY/19/180501/000342)

Author statement

All authors worked jointly and contributed equal efforts to this paper. EN and NHI conceived the idea for it and wrote the first draft of the manuscript. SAR performed the modelling. All authors worked on various iterations of the manuscript and approved its final version.

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