Can foraging in pesticide-treated patches become an ecological trap for pollinators? Modelling visitation patterns on a simulated landscape

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Abstract

Understanding the risks of pesticide exposure in agricultural environments is crucial for maintaining essential agroecosystem services. Behaviour often plays a pivotal role in determining how well species cope with human-altered environments, but in pollinators, its significance in mitigating the exposure level to pesticides and, consequently, the accumulation of associated sub-lethal effects has received little attention. In this study, I extended the individual-based model implemented in the simulation tool BEE-STEWARD to investigate how previously overlooked behavioural processes, such as preference for mass-flowering crop, inadvertent social information (ISI) use, and a foraging bias induced by the pesticide applied on the crop may affect nectar and pollen visit rates in a common pollinator species, the buff-tailed bumblebee (*Bombus terrestris*), on far and closely located crop patches. All investigated behavioural processes increased foragers' visit rate on crop patches but their impact differed substantially in magnitude and context. As expected, preference for the crop was strongly positively associated with both visit rates. ISI use increased the visit rate during nectar foraging in interaction with preference on the close crop patches, and the modelled pesticide-induced foraging bias substantially enhanced pollen visits on both close and far crop patches. Simulation results indicate that if a pesticide applied to the crop causes a behavioural alteration that reduces foragers' ability to assess the level of patch depletion correctly, an ecological trap may emerge for pollinators in pesticide-treated agricultural landscapes.

Keywords: bumblebees; foraging; pesticide exposure; sub-lethal effects; individual-based modelling

Introduction

Pesticide use is an integrated element of intensive agriculture aiming for global food security. However, its environmental impact can threaten human health [1], biodiversity [2] and various ecosystem services [3]. Even though environmentally friendly agricultural approaches have been advocated by both governing and conservation organisations in the last decades, the majority of plant health programs are still based on chemical control [4], so pollinators and natural predators of pests are often at risk due to their frequent exposure to agrochemicals. As exposure risk can negatively impact population stability and species interactions at the ecosystem level [5,6], a better understanding of pesticides' adverse effects on non-target organisms and the way these effects are mitigated is essential to maintain key agroecosystem services and achieve sustainable food production.

The amount of pesticides found in agricultural landscapes is highly inconsistent, and it is not well understood if pollinators can influence their exposure risk when pesticide contamination varies spatially and temporally [7]. Evidence suggests that some pollinating insects, such as honeybees and bumblebees, cannot detect even the lethal concentrations of pesticides in nectar [8,9], so foraging individuals cannot behaviourally mitigate their pesticide exposure level by avoiding contaminated food sources (but see [7] for a lepidopteran counterexample). If so, exposure patterns are most likely determined by how pesticide-treated food patches are distributed within pollinators' foraging range. However, intrinsic and induced preference for specific food sources can modify such distribution-based exposure levels. Natural preference for certain types of flowers (e.g., [10,11]) may enhance exposure risk if those plant species are more often treated with pesticides than alternative food sources. Besides, mass-flowering crops can attract pollinators disproportionally to their patches during seasonal blooms [12]. Pesticide-induced preference may also emerge through physiological dependence, due to the addictive nature of some active ingredients or co-formulants. For instance, experimental findings proved that pollinators can develop a preference for food treated with neonicotinoid pesticides [8,13], and similarly induced preferences were also observed for other substances like alcohol and caffeine [14,15]. Finally, pesticide exposure may alter some specific aspects of foraging behaviour that lead to a shift in optimal food preferences. For instance, prolonged exposure to pesticides may hinder locating the floral scent source [16], or induce biases that result in visiting food sources located further apart [17] or foraging less persistently [18]. Pesticide exposure may also reduce activity [19] or motivation to forage [20,21], or directly alter pollinators' natural preference for the flower types they usually exploit [22,23]. Such

behavioural changes can also result in higher pesticide exposure if the more frequently visited food patches are more likely to receive – directly or indirectly [24] – regular pesticide treatments. Natural and pesticide-induced preferences are not mutually exclusive and may dynamically shape actual exposure patterns together.

The ecological significance of inadvertent social information ('ISI' henceforward) use lies in the possibility of inducing strong correlations in the behaviours and space use of many individuals [25]. ISI use is a well-known phenomenon in pollinating insects [26], but its contribution to exposure risk during foraging has remained unexplored. Bees often rely on social cues when they do not have personal information about surrounding food sources or finding them would be more costly [27,28], and so ISI use facilitates the localisation and exploitation of new food sources [29,30] and helps to avoid predators [31]. The presence of conspecifics can also provide a cue about the quantity of resources in the visited flowers [32]. However, relying on social information may also limit the time spent searching for alternative food sources and making independent foraging decisions, resulting in sub-optimal foraging [33]. For instance, attracting conspecifics to the same foraging patches could facilitate the spread of foraging biases or induce preference among colony members.

Ecological traps are maladaptive consequences of naturally adaptive behaviour in human-altered environments [34], and ISI use has previously been shown to be responsible for the emergence of such traps in group-living mammals (e.g., [35,36]). In pesticide-treated agricultural landscapes, the interaction between preference for pesticide-treated food patches and ISI use could lead to elevated exposure patterns. Visiting pesticide-treated food patches represents a sub-optimal foraging choice if the associated sub-lethal effects negatively affect individual behaviour, physiology or colony growth. These adverse effects can be further amplified if ISI use facilitates the exploitation of such patches and thus copying the patch choice of conspecifics increases colony exposure to the pesticide's sub-lethal effects, ultimately leading to severe reductions in fitness (e.g., [37,38]).

In this study, I conducted a theoretical investigation about how ISI use, preference for the crop, and a recently demonstrated pesticide-induced foraging bias can influence the pesticide exposure risk of pollinators on an agricultural landscape. I used the buff-tailed bumblebee (*Bombus terrestris*) as the model species, an important pollinator of both crops and wildflowers in temperate regions [39], and a common visitor of the used mass-flowering crop,

oilseed rape (*Brassica napus*; 'OSR' henceforward), the dominant oil crop in Europe [40]. I included the above behavioural processes in the individual-based model implemented in BEE-STEWARD, a research and decision-supporting simulation tool that enables researchers, policymakers and practitioners to predict the impact of land-use characteristics and interventions on colony and population dynamics in various bumblebee species [41]. I examined how patch visitation – and thereby the level of exposure – change with the presence of ISI use and different parameter values of preference for OSR in a landscape consisting of a grassland (i.e., natural nesting and foraging habitat) and eight OSR (i.e., foraging habitat during the crop's flowering period) patches. Moreover, a recent study showed that chronic exposure to a formulation containing a neonicotinoid insecticide frequently applied in OSR cultivations [42,43] reduced buff-tailed bumblebees' ability to orient toward the floral blend-containing scent source [16]. By incorporating a similar effect into the model, I also explored how a pesticide-induced behavioural alteration may further modulate foragers' pesticide exposure on this simulated landscape. I assessed the magnitude of the effect of these three parameters on the visit rate of OSR patches at two different distances (i.e., in close or far OSR patches) during nectar and pollen foraging (i.e., proportion of nectar visits and proportion of pollen visits, respectively). In addition, I evaluated the relationship between these visit rates and proxies for pollination capacity and colony fitness under the default model settings.

Results

Nectar visits on OSR patches

Both preference for OSR and ISI use influenced which patches bees exploited during the OSR flowering period, but differently. Preference for OSR substantially increased the proportion of nectar visits to closely located OSR patches (Fig. 2a). In the baseline scenario (i.e., using the original model setting), as well as in the 'only ISI use' and 'only foraging bias' scenarios, the relationship between OSR preference and nectar visit proportion was best described by a second-order polynomial approximation. However, when both ISI use and foraging bias were present, this relationship was linear (Table S1). When the preference for OSR was set to zero, the proportion of nectar visits (predicted value [95% CI]) ranged between 0.271 [0.26; 0.282] and 0.376 [0.363; 0.388] across the four scenarios, with the lowest value observed in the baseline scenario. At 100% OSR preference, this proportion increased to between 0.497 [0.486; 0.508] and 0.633 [0.62; 0.646]. ISI use also increased nectar visits to close OSR patches, and the magnitude of its contribution linearly increased with preference; this trend was observed both in the absence (*intercept* [95% CI]=0.11 [0.1; 0.12]; β [95% CI]=0.0003

[0.0001; 0.0005]) and presence of foraging bias (*intercept*=0.07 [0.05; 0.08]; β=0.0003 [0.0001; 0.0006]; Fig. 1a inset). In the absence of both OSR preference and ISI use, foraging bias increased the proportion of nectar visits to a level equivalent to a scenario where 27.5% of bees preferentially foraged on close OSR patches. This resulted in a modest increase in nectar visits to these patches (from 0.271 [0.26; 0.282] to 0.311 [0.299; 0.322]). However, when ISI use was present, foraging bias had no additional effect on visitation rates.

On far OSR patches, the proportion of nectar visits increased linearly with preference for OSR (Fig. 2b; Table S1). The smallest increase occurred in the 'baseline' scenario (from 0.064 [0.06; 0.067] to 0.116 [0.112; 0.121] (back-transformed values)), while the largest increase was observed in the 'both ISI use and foraging bias' scenario (from 0.082 [0.078; 0.086] to 0.137 [0.132; 0.142]). Overall, ISI use had a minor effect on the proportion of nectar visits and did not increase with OSR preference in the absence of foraging bias (*intercept*=0.02 [0.01; 0.03]; β=0.0001 [-0.01; 0.01]). In the presence of foraging bias, its contribution was marginal, showing a slight increase with preference (*intercept*=0.007 [0.0007; 0.0129]; β=0.0088 [-0.0015; 0.019]; Fig. 2b inset). When both OSR preference and ISI use were absent, foraging bias led to only a slight increase in nectar visits to far OSR patches (0.064 [0.06; 0.067] vs. 0.075 [0.072; 0.077]), similar to a scenario where 23.8% of bees preferentially visited OSR patches. However, when ISI use was included in the model, foraging bias had no additional effect.

Pollen visits on OSR patches

Preference for OSR substaintially increased the proportion of pollen visits across all OSR patches. On close OSR patches (Fig. 3a), this preference nearly quadrupled the proportion of pollen visits in the 'baseline' scenario (from 0.111 [0.091; 0.131] at zero preference to 0.392 [0.372; 0.412] at 100% preference) and almost doubled it when both ISI use and foraging bias were present (0.341 [0.327; 0.355] vs. 0.579 [0.564; 0.593]). In contrast, ISI use had little impact on pollen visits to close OSR patches (Fig. 3a inset). In the absence of foraging bias, its highest contributions were predicted when OSR preference was either zero (0.036 [0.008; 0.066]) or 100% (0.043 [0.014; 0.071]), with a minimum value of 0.013 [-0.004; 0.03] at 47.3% preference. When foraging bias was present, ISI use contributions did not change with preference (*intercept* = 0.03 [0.01; 0.05]; β = 0.006 [-0.03; 0.04]). Most notably, foraging bias increased pollen visits to close OSR patches to levels comparable to scenarios where 78.1% (without ISI use) or 79.8% (with ISI use) of bees preferred OSR. As a result, the proportion of

pollen visits rose from 0.111 [0.091; 0.131] to 0.311 [0.297; 0.325] in the absence of ISI use and from 0.148 [0.127; 0.168] to 0.341 [0.327; 0.355] in its presence.

The positive effect of OSR preference on pollen visits was also evident on far OSR patches (Fig. 3b). In all scenarios, the proportion of pollen visits increased linearly with preference (Table S1), leading to a substantial rise from 0.023 [0.02; 0.027] (back-transformed values) to 0.104 [0.097; 0.112] in the 'baseline' scenario and from 0.09 [0.083; 0.097] to 0.148 [0.139; 0.157] in the 'both ISI use and foraging bias' scenario. ISI use had a negligible effect on pollen visits, regardless of foraging bias. In the absence of foraging bias, its maximum predicted contribution was just 0.006 [-0.006; 0.018] at 0% preference, while in its presence, the contribution remained minimal (*intercept*= 0.001 [-0.011; 0.013]; $\beta_{\text{preference}}$=0.002 [-0.018, 0.022]; Fig. 3b inset). Notably, foraging bias alone had a strong effect on pollen visits to far OSR patches, even when preference for OSR was absent. This effect was comparable to scenarios where 85.7% of foraging bees preferred OSR without ISI use (increasing from 0.023 [0.02; 0.027] to 0.089 [0.084; 0.095]) and 83.5% preferred OSR with ISI use (increasing from 0.027 [0.024; 0.031] to 0.09 [0.083; 0.097]).

3.3. Relationship between the proportions of visits and the proxies for pollination capacity and fitness

In the 'baseline' scenario, the proportion of pollen visits across all OSR patches was positively related to the total number of adult workers (β=469.37 [79.35; 859.4]) and the number of colonies (β=55.63 [16.77; 94.5]), but did not increase the total number of hibernating queens (β=352.4 [-57.92; 762.7]; Fig. 4, Fig. S4). The proportion of nectar visits across all OSR patches had no such effect on either measure (total number of adult workers: β= 448.9 [-199.1; 1096.93]; number of colonies: β= 27.98 [-37.4; 93.36]; total number of hibernating queens: β= 561.5 [-124.99; 1247.99]).

Discussion

The extent to which ecological traits can modify foragers' pesticide exposure and its subsequent impacts is less known in non-*Apis* bees [44]. Simulation results indicated that all investigated behavioural processes increased foragers' visit rate on OSR patches in the simulated landscape where the buff-tailed bumblebee population existed in equilibrium. Still, their effect differed substantially in magnitude and context. The original model predicted that, on average, 33.9% of nectar and 14.2% of pollen visits occurred on the close and far OSR

patches. As expected, preference for the crop notably increased both visit rates, so when all bees preferred collecting resources from OSR during its flowering period, 61.8% of nectar and 49.8% of pollen visits occurred on these patches. The maximum exposure, however, was observed when ISI use and the modelled foraging bias was also present, increasing the visit rates further to 76% in nectar and 73.3% in pollen foraging, respectively. A decisive result is that the foraging bias alone significantly increased the rate of pollen visits (from 13.4-17.4% to 40-43.1%) on the crop patches, potentially amplifying this exposure pathway to the pesticide's additional adverse effects. Under the original model settings, the proportion of pollen visits on all OSR patches was positively associated with colony growth measures representing the population's capacity for pollination but not with reproductive performance. This observation corroborates with the findings of previous field studies that the presence of a mass flowering crop within the colonies' foraging range does not necessarily translate into a higher production of sexual offspring [45,46]. Because of that, a preference for mass-flowering OSR crops is unlikely to be strongly favoured by natural selection. However, if the pesticide applied to the crop induces a foraging bias – among other effects – that impairs bees' ability to accurately assess patch depletion, an ecological trap may emerge in pesticide-treated foraging patches, leading to more pronounced sub-lethal effects on colony growth. This finding implies that even in the presence of alternative food sources during crop bloom [47,48], bumblebees may collect resources disproportionally from contaminated resource patches and the resulting risk of exposure can be prolonged if crops with different pesticide application schedules (e.g., consecutive in time) are present within their foraging range.

Chronic pesticide exposure often leads to multiple sub-lethal effects [17,49,50]. Previous studies showed that exposure to field-realistic concentrations of acetamiprid following application (>3360 ppb; see in [51]) can result in various colony- and individual-level symptoms in bumblebees including significant reductions in drone count [52,53], drone weight [53,54], number of pupae [53], number of interactions in the colony, immune response, worker body size (dependent also on food quality [55]), and biased foraging-related parameters (some dependent also on weight [16,51]). The conducted simulations indicate that even a single pesticide-induced foraging bias can change the patch exploitation pattern of bumblebees in a way that makes other sub-lethal effects more likely to appear. There are various forms of pesticide-induced biases in cognition or foraging behaviour, such as the impairment of spatial memory [56], disruption of odour coding and discrimination ability [57], foraging less persistently [18] or visiting food sources located further apart than

unexposed individuals [58], which might have similar exposure-enhancing effects in bumblebees. This finding strongly suggests that induced foraging biases may have far-reaching consequences in pollinating insects, not necessarily on overall consumption but on the level of pesticide exposure and the likelihood of developing multiple sub-lethal effects.

Exposure to pesticides is known to disrupt within-nest social networks and social interactions in bumblebees [38,55,59], but the extent to which social information use modulates patch visitation patterns represents a crucial gap in knowledge (unlike in honeybees [60]). These simulations provide the first evidence that ISI use increases visitation rates on specific resource patches (predicted values ranging between 0.007 [0.001; 0.013] and 0.144 [0.132; 0.156]). In accordance with initial expectations and previous findings, ISI use enhanced the impact of natural preference for the crop during nectar foraging, but its effect was mitigated by the pesticide-induced foraging bias. In this study, ISI use was modelled as simply as possible to obtain conservative estimates of its impact, i.e., patches visited by others were preferred to unoccupied patches irrespective of the number, condition or foraging success of those conspecifics. However, insects can follow various strategies regarding when to use social information and whom they should copy [26], so incorporating more complex decision rules in the model, if characteristic of buff-tailed bumblebees, could refine the obtained predictions. Second, a few but large patches in the simulated landscape represented a coarse-scale resolution of resources for the foraging bees. While such spatial distribution of crop patches is not unrealistic in modern agricultural environments, the contribution of ISI use to exploitation patterns could be considerably higher than the observed one at a fine-scale resolution of small resource patches.

Simulations showed a substantial discrepancy in how the modelled foraging bias and ISI use affected the visit rates on OSR patches during nectar and pollen foraging. Patch choice decisions related to these two resources differ in the Bumble-BEEHAVE model incorporated in BEE-STEWARD: the calculation of handling time for nectar foragers follows the model of Harder [61] and the energetic efficiency of exploiting a patch (i.e., energy gained compared to the energy needed to exploit given layer) plays a crucial role in determining the most profitable food source, whereas pollen foraging, in the lack of detailed data and existing models, is modelled to maximise foraging rate. In addition, the priority of nectar and pollen foraging is also different in the model, and individuals always search for nectar if the stimulus for this task in the bee's colony is higher than the bee's associated threshold, regardless of the

stimulus-threshold relationship of the other tasks (including pollen foraging). Since these differences do not necessarily explain the observed asymmetry in the effect of the investigated parameters, the possible mechanisms behind the pattern should be explored further, especially as exposure routes via syrup and pollen may lead to distinct sub-lethal effects. For instance, in a study where both routes of exposure to acetamiprid were examined within the same experimental setup [53], exposure via nectar resulted in fewer drones in the examined bumblebee colonies, while the pollen exposure route significantly reduced drone weight. Besides, although bees may consume more syrup than pollen, pesticide intakes via the two routes will depend on the pesticide concentrations in these two resources, thus their capacity to exert sub-lethal effects may vary [62]. Nevertheless, Lonsdorf et al. [63] recently proved that pesticide exposure via pollen foraging in bumblebees can be satisfyingly predicted by a spatially explicit model characterised only by the pesticide level and a distance-based foraging process from the colony locations. This finding implies that this exposure pathway could be robustly estimated across heterogeneous agricultural landscapes, even if the available information is limited.

This study provides *in silico* evidence that previously overlooked aspects of pollinator behaviour do not mitigate but increase pesticide exposure risk and corroborates with field observations that mass-flowering crops can competitively dilute pollinator densities in agricultural landscapes [12,64]. In particular, simulation results imply that a pesticide-induced foraging bias may lead to greater exploitation of crop patches, increasing bumblebees' exposure level to the pesticide in pollen without changing overall pollen consumption. Through positive feedback, such shifts in preference may facilitate the accumulation of sub-lethal effects of pesticides in real-world scenarios. Future efforts should extend the BEE-STEWARD model to more behavioural aspects of pollinator foraging that could potentially influence visitation patterns to differently treated resource patches. In addition, if more sub-lethal effects could be included in the model, it would allow an evaluation of the conditions under which their accumulation is likely to occur and the magnitude of their overall impact on colonies. In that way, we could have an even more powerful tool for predicting the impact of pesticide exposure on bumblebee population dynamics and exploring intervention options to mitigate the pesticide-associated risks for pollinators in agricultural landscapes.

Materials and methods

Description of the applied model

Simulations were run in BEE-STEWARD (www.beesteward.co.uk [41]), a software into which the landscape exploration module of BEESCOUT [65] and the individual-based model of Bumble-BEEHAVE [66] has been integrated. Pollinator behaviour is determined by stimuli and thresholds that scale up to colony-level processes, enabling the simulation of population survival and performance on the landscape level over multiple years. The underlying parts of the software are parameterised with empirical data from the UK, describing colony dynamics of six bumblebee species and plant species characteristics, including details on flower shape, resource production, and flowering period. The model also incorporates energy budgets and depletion of resources to facilitate the emergence of competition both within and between pollinator species. With sensitivity analysis and validation, the Bumble-BEEHAVE model has been demonstrated to make realistic predictions for buff-tailed bumblebee colonies within the boundaries of independent empirical observations [66]. For a detailed description of the underlying models and procedures, see Becher et al.'s [65,66] supplementary materials (Appendices S02 and S05, respectively).

In short, the simulated landscape is 2-dimensional, consisting of 300 × 210 grid cells and comprises patches that provide foraging and/or nesting opportunities. Patches are spatially explicit and implemented as one or more food sources, each representing a single plant species. If a patch contains multiple food sources, these can be layered, i.e. placed at the same location and linked with each other. The simulations start at the beginning of the year with an initial number of hibernating queens that, after emerging from hibernation, search for suitable nest sites in semi-natural habitats (exact dates drawn from a characteristic distribution). Queens that survived the searching process and successfully founded a colony must collect resources to lay the first batch of eggs, then forage and care for the brood simultaneously until the first adult workers emerge. After that, the queen's activity is limited to egg laying, while the workers are responsible for nursing and foraging. Foragers' choices on which patch to exploit are based on maximising the foraging rate for pollen and the energetic efficiency for nectar, primarily determined by the distance from the colony, handling time, and the amount of the given resource available in the patch [67]. Colony growth depends on resource collection, whereas population dynamics result from the number of mated queens that leave the colony and enter into hibernation until the following spring [66].

Model extensions

I modified the original code by incorporating the parameters ‘ISI use’, ‘preference for OSR’ and ‘foraging bias’ into the model (Table 1). I also included additional functions in the extended version to obtain patch-specific nectar and pollen visitation data. To reduce the computational time of the simulations, the code of the original model was converted from NetLogo 5.3.1 to 6.4.0 [68].

In the original foraging module, the model sorts the list of known foraging patches by their distances to the bee’s colony. In the presence of ‘ISI use’, foragers’ choice of where to collect nectar or pollen is influenced by the presence of conspecifics. Individuals’ known patches are first divided into two types: one type is where others are currently foraging, and the other type is the unoccupied patches. Then, both lists are sorted by the distances of patches and the bee’s colony, and the lists are compiled so the occupied patches appear first in the compiled list (see the ‘Foraging_SortKnownPatchesListREP’ function in the supplemented code). The modified function is later called during both nectar and pollen foraging.

When foragers’ activity is set to ‘searching’, unexperienced foragers and those unsatisfied with their previous patch search for a new flower patch. In the original model, foragers’ chance of finding a patch is determined by a default detection probability function based on the distance between a given food source and the colony’s location (‘DetectionProbREP’ [65]). If ‘preference for OSR’ is set to a non-zero value, the ‘foraging_searchingProc’ procedure (which utilises the detection probability function) is modified in a way that a given proportion of bees (represented by the provided non-zero value) search for a patch from the list of available OSR patches during the OSR flowering period, while others bees’ patch-finding process is unaffected by the type of flower present in the patch.

The foraging bias included in the extended model is based on a recent finding of Kárpáti et al. [16]. This study examined the peripheral olfactory detection of a floral blend and foraging behaviour of buff-tailed bumblebee workers exposed to acetamiprid, a neonicotinoid insecticide. One of the main results was that treated bumblebees had a decreased likelihood of finding the floral blend source (that was associated with the presence of syrup during the chronic pesticide treatment), resulting in a random choice between the control and blend scent sources in the behavioural trials. This finding suggests that exposed individuals could not correctly assess which presented scent source was rewarding. As scent is generally associated with the presence of resources in flowers [69], I mimicked a similar effect by modifying the

‘Foraging_bestLayerREP’ function that reports the most profitable layer within the currently used flower patch based on minimal handling time. In the original model, handling time (‘handlingTimePerFlower_s’ function) for nectar foraging is determined by the time needed to travel to the next flower plus the time to test whether it contains nectar, divided by the filling level of the flower, plus the time needed to collect the nectar once a filled flower is found. During pollen foraging, handling time is calculated from the time needed to travel to the next flower multiplied by the number of flowers needed to be visited, divided by the filling level of the flower, plus the time needed to collect the pollen once a flower with pollen is found. In the presence of ‘foraging bias’, filling levels are set to 1, so handling times are not dependent on actual filling levels when bumblebees are exposed to a pesticide. Still, only those patches are considered where the filling level > 0. For simplicity, I assumed that all bees are affected by the pesticide application on OSR patches irrespective of the patch individuals exploit (as the resources stored within the colonies can also be contaminated), but only during the OSR flowering period (i.e., from day 114 to day 136).

Simulated agricultural landscape with foraging patches

The landscape consisted of one grassland and eight oilseed rape (*Brassica napus*) patches (Fig. 1). The central grassland patch can provide nectar and pollen for the bumblebees year-around and also serves as a nesting habitat where queens can establish new colonies after emerging from winter hibernation. This patch is a good-quality habitat for bumblebees containing 22 different flowering plant species [66]. The OSR patches represent habitats that are unsuitable for nesting and solely consist of oilseed rape crop that flowers from day 114 until day 136 in each simulation year. All patches had a 200 m radius, resulting in a 125 663.7 m^2 patch area. Due to the spatial distribution of OSR patches around the grassland patch, four OSR patches were closer to the central patch (distance between patch edges: 15 m) than the diagonally located OSR patches (186.9 m). The former patches were termed ‘close OSR patches’, whereas the latter ‘far OSR patches’. The exploitation of close and far OSR patches was examined separately.

Characteristics of the simulation runs

Simulations were run over 50 years in 50 iterations to determine if the default number of total hibernating queens (set to 500) is appropriate for the model and from which year the population can be assumed to be in equilibrium [70] (Fig. S1A). Based on the results, I took year 10 as the year when the bumblebee population was likely to reach equilibrium in the

simulated landscape and thus subsequently analysed the data obtained in the 10th year. The initial number of hibernating queens was also 500 in all iterations. I ran the simulations 50 times in all combinations of 'ISI use' (absent or present), preference for OSR (ranging from 0 to 1 by 0.1) and foraging bias (present or absent), totalling 2200 simulations. Models were run individual-based under the 'intermediate foraging mortality' scenario. I also used the setting where males were not unlimited.

I evaluated the model by its ability to reproduce the following patterns. First, as semi-natural habitats support pollinators by providing nectar, pollen and nesting resources over the whole season [46,71], the simulated bumblebee population reaches equilibrium if only the grassland patch is present (Fig. S1B). Second, preference for OSR and ISI use do not substantially affect the number of pollen and nectar visits, i.e., these parameters have little impact on bees' general foraging activity (Fig. S2). Third, preference for OSR and ISI use do not considerably alter the bumblebee population's pollination capacity and fitness either (Fig. S3).

Analysis of model outputs

All simulations and calculations were performed using R 4.3.2 [72] and RStudio v2024.04.2.764 [73]. Instead of applying frequentist hypothesis testing during the analysis, I evaluated the magnitude of differences between simulation runs with different parameter settings and reported parameter estimates with corresponding uncertainty following the recommendations of White et al. [74]. The extended model, the R script for the analysis of model outputs and data supporting the results are archived and available at Figshare (https://figshare.com/s/acee9613adfc7757267b).

From the simulation outputs, I assembled the following data from the 10th simulation year for subsequent analysis: the number of visits associated with nectar foraging on each patch between day 114 and day 136 (i.e., during the OSR flowering period), the number of visits related to pollen foraging on each patch between day 114 and day 136, total number of adult workers and number of colonies on day 149, and total number of hibernating queens on day 365. I calculated the proportions of nectar and pollen visits from the patch visits data for the close and far OSR patches. Then, I used these variables to characterise the magnitude of exploitation and, with it, the exposure level to the pesticide on these two types of OSR patches. The sum of the proportions determined for the close and far OSR patches represented the total exposure in the simulated landscape during nectar and pollen foraging. The total

number of adult workers and the number of colonies variables were used as proxies for the pollination capacity of the simulated bumblebee population, and the total number of hibernating queens was considered a proxy for fitness (as in [67]).

I fitted linear polynomial models on the proportion of nectar and pollen visits on the close and far OSR patches with the preference for OSR as a predictor in four scenarios. In the 'baseline' scenario, bumblebees' foraging decisions followed the original model settings (i.e., no ISI use or foraging bias). In the 'only ISI use' scenario, conspecifics' presence in the patches could affect bees' foraging decision on where to collect resources. In the 'only foraging bias' scenario, bees suffered a foraging-related behavioural alteration due to the simulated exposure to acetamiprid on the OSR patches. In the 'both ISI use and foraging bias' scenario, ISI use and foraging bias was present and could influence bees' foraging behaviour. In one iteration, the bumblebee population died out before day 136 of the 10th year (in the 'only foraging bias' scenario), and in an additional one, it went extinct before the end of the 10th year (in the 'baseline' scenario); simulation results from these iterations were excluded from the corresponding analyses. To better illustrate the role of ISI use, I also fitted linear polynomial models on the contribution of ISI use to the proportion of nectar and pollen visits calculated as mean differences between the two scenarios with the absence and presence of ISI use at each preference value in far and close OSR patches. To obtain differences for these calculations, I randomly paired corresponding iterations from the two scenarios. For all models, the optimal number of degrees was determined by calculating the AICc value for each candidate model (with *k* ranging from 1 to 3) using the 'AICcmodavg' R package [75]. Model assumptions were checked by plot diagnosis using the 'DHARMa' R package [76]. The final models were the most parsimonious from the candidate model set with appropriate diagnostics and a good fit (i.e., ΔAICc<2). From these models, I evaluated the magnitude of differences between simulation runs with different parameter settings and calculated parameter estimates with 95% CI to characterise the effect of predictors on specific dependent variables. In the case of second-order polynomial regressions, critical values were computed with the help of the 'mosaic' R package [77]. Inverse estimations from the fitted models were calculated using the 'investr' R package [78].

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Author contribution statement

The author confirms sole responsibility for the following: conceptualisation, methodology, data curation, formal analysis, investigation, validation, visualisation, and writing.

Data availability statement

The extended model, the R script for the analysis of model outputs and data supporting the results are archived and available at Figshare (https://figshare.com/s/acee9613adfc7757267b) and are available from the corresponding author on reasonable request.

Competing interests statement

The author has no conflict of interest to declare.

Ethics approval

Not applicable.

References

1. Smagghe, G., Hayrabedya, S., Hayrabedyan, K., Topping, C., Kahru, A., Hardy, I. C. W., ... & Norton, M. Neonicotinoids and their substitutes in sustainable pest control. EASAC policy report 45. Schaefer Druck und Verlag GmbH. (2023).
2. Sánchez-Bayo, F., & Wyckhuys, K. A. Worldwide decline of the entomofauna: A review of its drivers. *Biol. Conserv.* **232**, 8-27. (2019).
3. Rumschlag, S. L., Mahon, M. B., Hoverman, J. T., Raffel, T. R., Carrick, H. J., Hudson, P. J., & Rohr, J. R. Consistent effects of pesticides on community structure and ecosystem function in freshwater systems. *Nat. Commun.* **11**, 6333; https://doi.org/10.1038/s41467-020-20192-2 (2020).
4. Deguine, J. P., Aubertot, J. N., Flor, R. J., Lescourret, F., Wyckhuys, K. A., & Ratnadass, A. Integrated pest management: good intentions, hard realities. A review. *Agron. Sustain. Dev.* **41**, 38; https://doi.org/10.1007/s13593-021-00689-w (2021).
5. Richman, S. K., Maalouf, I. M., Smilanich, A. M., Marquez Sanchez, D., Miller, S. Z., & Leonard, A. S. A neonicotinoid pesticide alters how nectar chemistry affects bees. *Funct. Ecol.* **36**, 1063-1073. (2022).

6. Nicholson, C. C., Knapp, J., Kiljanek, T., Albrecht, M., Chauzat, M. P., Costa, C., ... & Rundlöf, M. Pesticide use negatively affects bumble bees across European landscapes. *Nature* **628**, 355-358. (2024).

7. Olaya□Arenas, P., Scharf, M. E., & Kaplan, I. Do pollinators prefer pesticide□free plants? An experimental test with monarchs and milkweeds. *J. Appl. Ecol.* **57**, 2019-2030. (2020).

8. Kessler, S. C., Tiedeken, E. J., Simcock, K. L., Derveau, S., Mitchell, J., Softley, S., ... & Wright, G. A. Bees prefer foods containing neonicotinoid pesticides. *Nature* **521**, 74-76. (2015).

9. Parkinson, R. H., Scott, J., Dorling, A. L., Jones, H., Haslam, M., McDermott-Roberts, A. E., & Wright, G. A. Mouthparts of the bumblebee (*Bombus terrestris*) exhibit poor acuity for the detection of pesticides in nectar. *eLife* **12**, RP89129; https://doi.org/10.7554/eLife.89129.2 (2023).

10. Lanterman Novotny, J., Lybbert, A., Reeher, P., Mitchell, R. J., & Goodell, K. Bumble bee banquet: Genus□and species□level floral selection by Midwestern Bombus. *Ecosphere* **14**, e4425; https://doi.org/10.1002/ecs2.4425 (2023).

11. Huang, W., Vallejo-Marín, M., Inouye, D. W., Yang, C. F., & Ye, Z. M. Bumblebees' flower preferences are associated with floral abundance and buzz frequency when buzz-pollinating co-flowering plants. *Entomol. Gen.* **44**, 133-141. (2024).

12. Riggi, L. G., Raderschall, C. A., Fijen, T. P. M., Scheper, J., Smith, H. G., Kleijn, D., ... & Lundin, O. Early□season mass□flowering crop cover dilutes wild bee abundance and species richness in temperate regions: A quantitative synthesis. *J. Appl. Ecol.* **61**, 452-464. (2024).

13. Arce, A. N., Ramos Rodrigues, A., Yu, J., Colgan, T. J., Wurm, Y., & Gill, R. J. Foraging bumblebees acquire a preference for neonicotinoid-treated food with prolonged exposure. *Proc. R. Soc. B* **285**, 20180655; https://doi.org/10.1098/rspb.2018.0655 (2018).

14. Arnold, S. E., Dudenhöffer, J. H., Fountain, M. T., James, K. L., Hall, D. R., Farman, D. I., ... & Stevenson, P. C. Bumble bees show an induced preference for flowers when primed with caffeinated nectar and a target floral odor. *Curr. Biol.* **31**, 4127-4131. (2021).

15. Ostap-Chec, M., Opalek, M., Stec, D., & Miler, K. Discontinued alcohol consumption elicits withdrawal symptoms in honeybees. *Biol. Lett.* **17**, 20210182; https://doi.org/10.1098/rsbl.2021.0182 (2021).

16. Kárpáti, Z., Szelényi, M. O., & Tóth, Z. Exposure to an insecticide formulation alters chemosensory orientation, but not floral scent detection, in buff-tailed bumblebees (*Bombus terrestris*). *Sci. Rep.* **14**, 14622; https://doi.org/10.1038/s41598-024-65388-4 (2024).

17. Siviter, H., Johnson, A. K., & Muth, F. Bumblebees exposed to a neonicotinoid pesticide make suboptimal foraging decisions. *Environ. Entomol.* **50**, 1299-1303. (2021a).

18. Ohlinger, B. D., Schürch, R., Durzi, S., Kietzman, P. M., Silliman, M. R., & Couvillon, M. J. Honey bees (Hymenoptera: Apidae) decrease foraging but not recruitment after neonicotinoid exposure. *J. Insect Sci.* **22**, 16; https://doi.org/10.1093/jisesa/ieab095 (2022).

19. Baines, D., Wilton, E., Pawluk, A., de Gorter, M., & Chomistek, N. Neonicotinoids act like endocrine disrupting chemicals in newly-emerged bees and winter bees. *Sci. Rep.* **7**, 10979; https://doi.org/10.1038/s41598-017-10489-6 (2017).

20. Lämsä, J., Kuusela, E., Tuomi, J., Juntunen, S., & Watts, P. C. Low dose of neonicotinoid insecticide reduces foraging motivation of bumblebees. *Proc. R. Soc. B* **285**, 20180506; https://doi.org/10.1098/rspb.2018.0506 (2018).

21. Muth, F., & Leonard, A. S. A neonicotinoid pesticide impairs foraging, but not learning, in free-fying bumblebees. *Sci. Rep.* **9**, 4764; https://doi.org/10.1038/s41598-019-39701-5 (2019).

22. Gill, R. J., & Raine, N. E. Chronic impairment of bumblebee natural foraging behaviour induced by sublethal pesticide exposure. *Funct. Ecol.* **28**, 1459-1471. (2014).

23. Phelps, J. D., Strang, C. G., Gbylik-Sikorska, M., Sniegocki, T., Posyniak, A., & Sherry, D. F. Imidacloprid slows the development of preference for rewarding food sources in bumblebees (*Bombus impatiens*). *Ecotoxicology* **27**, 175-187. (2018).

24. Ward, L. T., Hladik, M. L., Guzman, A., Winsemius, S., Bautista, A., Kremen, C., & Mills, N. J. Pesticide exposure of wild bees and honey bees foraging from field border flowers in intensively managed agriculture areas. *Sci. Total Environ.* **831**, 154697; https://doi.org/10.1016/j.scitotenv.2022.154697 (2022).

25. Gil, M. A., Hein, A. M., Spiegel, O., Baskett, M. L., & Sih, A. Social information links individual behavior to population and community dynamics. *Trends Ecol. Evol.* **33**, 535-548. (2018).

26. Grüter, C., & Leadbeater, E. Insights from insects about adaptive social information use. *Trends Ecol. Evol.* **29**, 177-184. (2014).

27. Dawson, E. H., Avarguès-Weber, A., Chittka, L., & Leadbeater, E. Learning by observation emerges from simple associations in an insect model. *Curr. Biol.* **23**, 727-730. (2013).

28. Jones, P. L., Ryan, M. J., & Chittka, L. The influence of past experience with flower reward quality on social learning in bumblebees. *Anim. Behav.* **101**, 11-18. (2015).

29. Worden, B. D., & Papaj, D. R. Flower choice copying in bumblebees. *Biol. Lett.* **1**, 504-507. (2005).

30. Avarguès-Weber, A., & Chittka, L. Local enhancement or stimulus enhancement? Bumblebee social learning results in a specific pattern of flower preference. *Anim. Behav.* **97**, 185-191. (2014).

31. Dawson, E. H., & Chittka, L. Bumblebees (*Bombus terrestris*) use social information as an indicator of safety in dangerous environments. *Proc. R. Soc. B* **281**, 20133174; https://doi.org/10.1098/rspb.2013.3174 (2014).

32. Leadbeater, E., & Chittka, L. Bumble-bees learn the value of social cues through experience. *Biol. Lett.* **5**, 310-312. (2009).

33. Avarguès-Weber, A., Lachlan, R., & Chittka, L. Bumblebee social learning can lead to suboptimal foraging choices. *Anim. Behav.* **135**, 209-214. (2018).

34. Robertson, B. A., & Hutto, R. L. A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* **87**, 1075-1085. (2006).

35. Donaldson, R., Finn, H., Bejder, L., Lusseau, D., & Calver, M. The social side of human–wildlife interaction: wildlife can learn harmful behaviours from each other. *Anim. Conserv.* **15**, 427-435. (2012).

36. Sigaud, M., Merkle, J. A., Cherry, S. G., Fryxell, J. M., Berdahl, A., & Fortin, D. Collective decision□making promotes fitness loss in a fusion□fission society. *Ecol. Lett.* **20**, 33-40. (2017).

37. Baron, G. L., Jansen, V. A., Brown, M. J., & Raine, N. E. Pesticide reduces bumblebee colony initiation and increases probability of population extinction. *Nat. Ecol. Evol.* **1**, 1308-1316. (2017).

38. Crall, J. D., De Bivort, B. L., Dey, B., & Ford Versypt, A. N. Social buffering of pesticides in bumblebees: agent-based modeling of the effects of colony size and neonicotinoid exposure on behavior within nests. *Front. Ecol. Evol.* **7**, 51; https://doi.org/10.3389/fevo.2019.00051 (2019).

39. Hutchinson, L. A., Oliver, T. H., Breeze, T. D., Bailes, E. J., Brünjes, L., Campbell, A. J., ... & Garratt, M. P. Using ecological and field survey data to establish a national list of

the wild bee pollinators of crops. *Agric. Ecosyst. Environ.* **315**, 107447; https://doi.org/10.1016/j.agee.2021.107447 (2021).

40. Perrot, T., Bretagnolle, V., Acar, N., Febvret, V., Matejicek, A., Grégoire, S., & Gaba, S. Bees improve oil quality of oilseed rape. *Basic Appl. Ecol.* **76**, 41-49. (2024).

41. Twiston□Davies, G., Becher, M. A., & Osborne, J. L. BEE□STEWARD: A research and decision□support software for effective land management to promote bumblebee populations. *Methods Ecol. Evol.* **12**, 1809-1815. (2021).

42. Kathage, J., Castañera, P., Alonso□Prados, J. L., Gómez□Barbero, M., & Rodríguez□Cerezo, E. The impact of restrictions on neonicotinoid and fipronil insecticides on pest management in maize, oilseed rape and sunflower in eight European Union regions. *Pest Manag. Sci.* **74**, 88-99. (2018).

43. Dworzańska, D., Moores, G., Zamojska, J., Strażyński, P., & Węgorek, P. The influence of acetamiprid and deltamethrin on the mortality and behaviour of honeybees (*Apis mellifera carnica* Pollman) in oilseed rape cultivations. *Apidologie* **51**, 1143-1154. (2020).

44. Raine, N.E., & Rundlöf, M. Pesticide exposure and effects on non-*Apis* bees. *Annu. Rev. Entomol.* **69**, 551-576. (2024).

45. Westphal, C., Steffan□Dewenter, I., & Tscharntke, T. Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *J. Appl. Ecol.* **46**, 187-193. (2009).

46. Williams, N. M., Regetz, J., & Kremen, C. Landscape□scale resources promote colony growth but not reproductive performance of bumble bees. *Ecology* **93**, 1049-1058. (2012).

47. Rundlöf, M., Stuligross, C., Lindh, A., Malfi, R. L., Burns, K., Mola, J. M., ... & Williams, N. M. Flower plantings support wild bee reproduction and may also mitigate pesticide exposure effects. *J. Appl. Ecol.* **59**, 2117-2127. (2022).

48. Carturan, B. S., Siewe, N., Cobbold, C.A., & Tyson, R. C. Bumble bee pollination and the wildflower/crop trade-off: When do wildflower enhancements improve crop yield? *Ecol. Modell.* **484**, 110447; https://doi.org/10.1016/j.ecolmodel.2023.110447 (2023).

49. Desneux, N., Decourtye, A., & Delpuech, J. M. The sublethal effects of pesticides on beneficial arthropods. *Annu. Rev. Entomol.* **52**, 81-106. (2007).

50. Tosi, S., Sfeir, C., Carnesecchi, E., & Chauzat, M. P. Lethal, sublethal, and combined effects of pesticides on bees: A meta-analysis and new risk assessment tools. *Sci. Total Environ.* **844**, 156857; https://doi.org/10.1016/j.scitotenv.2022.156857 (2022).

51. Tóth, Z., & Kovács, Z. Chronic acetamiprid exposure moderately affects the foraging behaviour of buff-tailed bumblebees (*Bombus terrestris*). *Ethology* **130**, e13425; https://doi.org/10.1111/eth.13425 (2024).

52. Camp, A. A., Williams, W. C., Eitzer, B. D., Koethe, R. W., & Lehmann, D. M. Effects of the neonicotinoid acetamiprid in syrup on Bombus impatiens (Hymenoptera: Apidae) microcolony development. *PLoS ONE* **15**, e0241111; https://doi.org/10.1371/journal.pone.0241111 (2020a).

53. Weitekamp, C. A., Koethe, R. W., & Lehmann, D. M. A comparison of pollen and syrup exposure routes in Bombus impatiens (Hymenoptera: Apidae) microcolonies: implications for pesticide risk assessment. *Environ. Entomol.* **51**, 613-620. (2022).

54. Camp, A. A., Batres, M. A., Williams, W. C., Koethe, R. W., Stoner, K. A., & Lehmann, D. M. Effects of the neonicotinoid acetamiprid in pollen on Bombus impatiens microcolony development. *Environ. Toxicol. Chem.* **39**, 2560-2569. (2020b).

55. Straub, F., Birkenbach, M., Leonhardt, S. D., Ruedenauer, F. A., Kuppler, J., Wilfert, L., & Ayasse, M. Land-use-associated stressors interact to reduce bumblebee health at the individual and colony level. *Proc. R. Soc. B* **290**, 20231322; https://doi.org/10.1098/rspb.2023.1322 (2023).

56. Samuelson, E.E., Chen-Wishart, Z. P., Gill, R. J., & Leadbeater, E. Effect of acute pesticide exposure on bee spatial working memory using an analogue of the radial-arm maze. *Sci. Rep.* **6**, 38957; https://doi.org/10.1038/srep38957 (2016).

57. Andrione, M., Vallortigara, G., Antolini, R., & Haase, A. Neonicotinoid-induced impairment of odour coding in the honeybee. *Sci. Rep.* **6**, 38110; https://doi.org/10.1038/srep38110 (2016).

58. Siviter, H., Richman, S. K., & Muth, F. Field-realistic neonicotinoid exposure has sub-lethal effects on non-Apis bees: A meta-analysis. *Ecol. Lett.* **24**, 2586-2597. (2021b).

59. Crall, J. D., Switzer, C. M., Oppenheimer, R. L., Ford Versypt, A. N., Dey, B., Brown, A., ... & de Bivort, B. L. Neonicotinoid exposure disrupts bumblebee nest behavior, social networks, and thermoregulation. *Science* **362**, 683-686. (2018).

60. Hasenjager, M. J., Hoppitt, W., Cunningham□Eurich, I., Franks, V. R., & Leadbeater, E. Coupled information networks drive honeybee (*Apis mellifera*) collective foraging. *J. Anim. Ecol.* **93**, 71-82. (2024).

61. Harder, L. D. Flower handling efficiency of bumble bees: morphological aspects of probing time. *Oecologia* **57**, 274-280. (1983).

62. Azpiazu, C., Bosch, J., Viñuela, E., Medrzycki, P., Teper, D., & Sgolastra, F. Chronic oral exposure to field-realistic pesticide combinations via pollen and nectar: effects on feeding and thermal performance in a solitary bee. *Sci. Rep.* **9**, 13770; https://doi.org/10.1038/s41598-019-50255-4 (2019).

63. Lonsdorf, E. V., Rundlöf, M., Nicholson, C. C., & Williams, N.M. A spatially explicit model of landscape pesticide exposure to bees: Development, exploration, and evaluation. *Sci. Total Environ.* **908**, 168146; https://doi.org/10.1016/j.scitotenv.2023.168146 (2024).

64. Holzschuh, A., Dormann, C. F., Tscharntke, T., & Steffan-Dewenter, I. Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proc. R. Soc. B* **278**, 3444-3451. (2011).

65. Becher, M. A., Grimm, V., Knapp, J., Horn, J., Twiston-Davies, G., & Osborne, J. L. BEESCOUT: A model of bee scouting behaviour and a software tool for characterizing nectar/pollen landscapes for BEEHAVE. *Ecol. Modell.* **340**, 126-133. (2016).

66. Becher, M. A., Twiston□Davies, G., Penny, T. D., Goulson, D., Rotheray, E. L., & Osborne, J. L. Bumble□BEEHAVE: A systems model for exploring multifactorial causes of bumblebee decline at individual, colony, population and community level. *J. Appl. Ecol.* **55**, 2790-2801. (2018).

67. Knapp, J. L., Becher, M. A., Rankin, C. C., Twiston□Davies, G., & Osborne, J. L. *Bombus terrestris* in a mass□flowering pollinator□dependent crop: A mutualistic relationship? *Ecol. Evol.* **9**, 609-618. (2019).

68. Wilensky, U. NetLogo. Center for Connected Learning and Computer-Based Modeling. Northwestern University, Evanston, IL. http://ccl.northwestern.edu/netlogo (1999).

69. Wright, G. A., & Schiestl, F. P. The evolution of floral scent: the influence of olfactory learning by insect pollinators on the honest signalling of floral rewards. *Funct. Ecol.* **23**, 841-851. (2009).

70. Hui, C. Carrying capacity, population equilibrium, and environment's maximal load. *Ecol. Modell.* **192**, 317-320. (2006).

71. Rundlöf, M., Persson, A. S., Smith, H. G., & Bommarco, R. Late-season mass-flowering red clover increases bumble bee queen and male densities. *Biol. Conserv.* **172**, 138-145. (2014).

72. R Core Team R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ (2023).

73. Posit Team RStudio: Integrated Development Environment for R. Posit Software, PBC, Boston, MA. http://www.posit.co/ (2024).

74. White, J. W., Rassweiler, A., Samhouri, J. F., Stier, A. C., & White, C. Ecologists should not use statistical significance tests to interpret simulation model results. *Oikos* **123**, 385-388. (2014).

75. Mazerolle, M. J. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3.3, https://cran.r-project.org/package=AICcmodavg (2023).

76. Hartig, F. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.4.6, https://CRAN.R-project.org/package=DHARMa (2022).

77. Pruim, R., Kaplan, D. T., & Horton, N. J. The mosaic Package: Helping Students to 'Think with Data' Using R. *R J.* **9**, 77-102. (2017).

78. Greenwell, B. M., & Schubert Kabban, C. M. investr: An R Package for Inverse Estimation. *R J.* **6**, 90-100. (2014).

Table 1. Additional parameters in the extended BEE-STEWARD model.

Parameter	**Description**	**Range (unit)**
Preference for OSR	When this parameter is set above zero, a corresponding proportion of bees search for a patch from the list of available OSR patches during the OSR flowering period.	0-1 (0.1)
ISI use	When using ISI, foragers collect nectar or pollen from patches where conspecifics are present, provided such foraging sites are known.	0-1 (1)*
Foraging bias	With foraging bias, filling levels (if >0) are set to 1, making handling times independent of actual filling levels when bumblebees are exposed to a pesticide during the OSR flowering period.	0-1 (1)*

*either absent (0) or present (1)

Figure legends

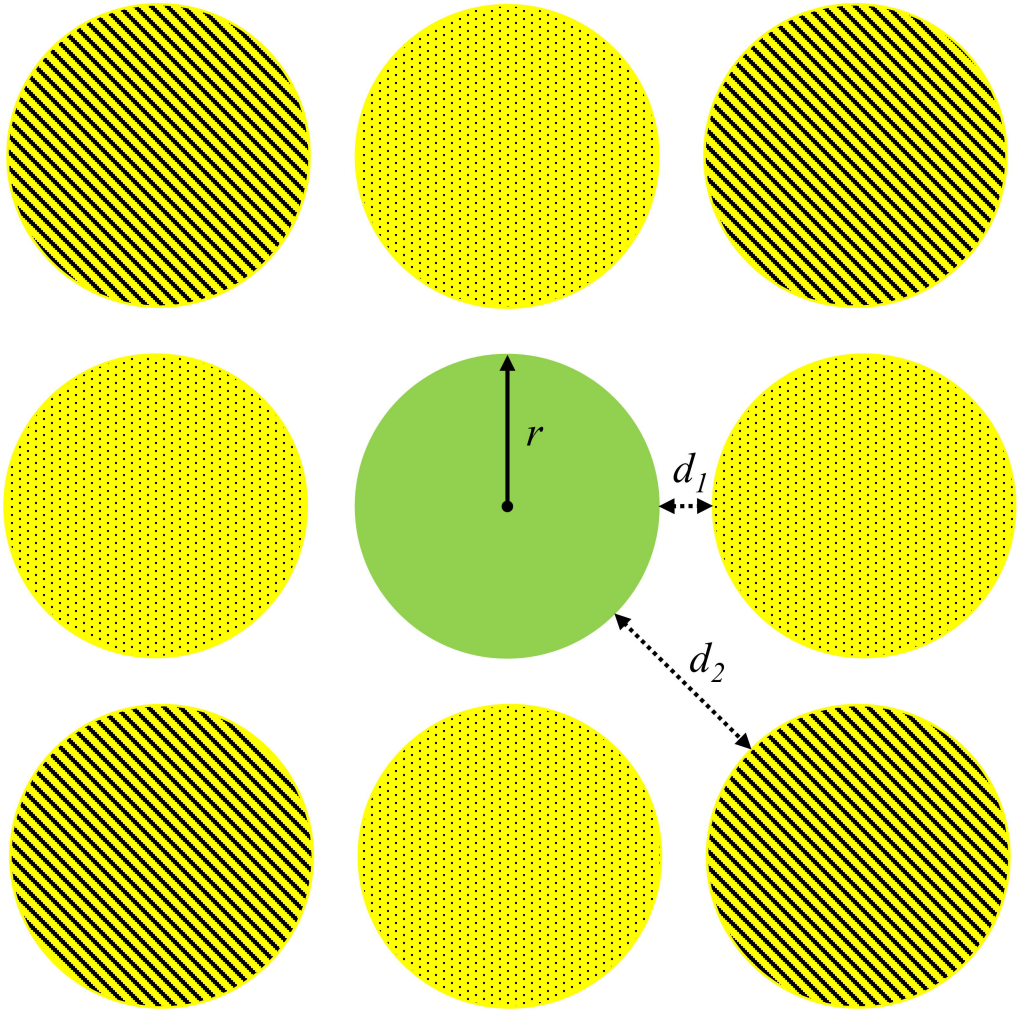
Figure 1. Schematic diagram of the simulated landscape consisting of a grassland (green) and multiple oilseed rape (OSR) patches (yellow). All patches had a 200 m radius (*r*), resulting in a 1256.64 m^2 patch area. Due to the spatial distribution of OSR patches around the grassland patch, four OSR patches were closer to the central patch (d_1: 15 m) than the diagonally located OSR patches (d_2: 186.9 m). The former patches were termed 'close OSR patches' (with dotted pattern), whereas the latter 'far OSR patches' (with diagonal pattern). Distances on the diagram are not on scale.

Figure 2. Relationship between the preference for OSR and the proportion of nectar visits on the close (A) and far (B) OSR patches in the examined four scenarios ('Baseline': light blue; 'Only ISI use': dark blue; 'Only foraging bias': yellow; 'Both ISI use and foraging bias': dark grey). Insets indicate the contributions of ISI use to this measure fitted against preference in the absence (blue) and presence of foraging bias (brown). Symbols in the insets represent mean differences (i.e., the mean difference in the proportion of nectar visits between the two scenarios with the absence and presence of ISI use at each preference value), and vertical lines show the corresponding SEs. All trend lines were fitted using polynomial approximations with the degree of the corresponding final models. In the main panels, light red arrows show at which preference value the predicted proportion of nectar visits in the 'baseline' scenario matches the value predicted in the 'only foraging bias' scenario at zero preference (in the presence of ISI use, foraging bias did not increase the proportion of nectar visits on either close or far OSR patches; Table S2). In panel b, the y-axis is on the square-root scale because models were fitted to square-root transformed data.

Figure 3. Relationship between the preference for OSR and the proportion of pollen visits on the close (A) and far (B) OSR patches in the examined four scenarios ('Baseline': light blue; 'Only ISI use': dark blue; 'Only foraging bias': yellow; 'Both ISI use and foraging bias': dark grey). Insets indicate the contributions of ISI use to this measure fitted against preference in the absence (blue) and presence of foraging bias (brown). Symbols in the insets represent mean differences (i.e., the mean difference in the proportion of pollen visits between the two scenarios with the absence and presence of ISI use at each preference value), and vertical lines show the corresponding SEs. All trend lines were fitted using polynomial approximations with the degree of the corresponding final models. In the main panels, red

arrows show at which preference value the predicted proportion of nectar visits in the 'baseline' scenario matches the value predicted in the 'only foraging bias' scenario at zero preference (in the absence of ISI use: light red; in the presence of ISI use: dark red; Table S2). In panel b, the y-axis is on the square-root scale because models were fitted to square-root transformed data.

Figure 4. Forest plot for the standardised parameter estimates (with corresponding 95% CI) of the proportion of nectar visits and the proportion of pollen visits on all OSR patches calculated from the linear regressions fitted on the proxies for pollination capacity and fitness. The total number of adult workers and the number of colonies were measured on day 149, whereas the total number of hibernating queens was measured on day 365 of the 10th simulation year.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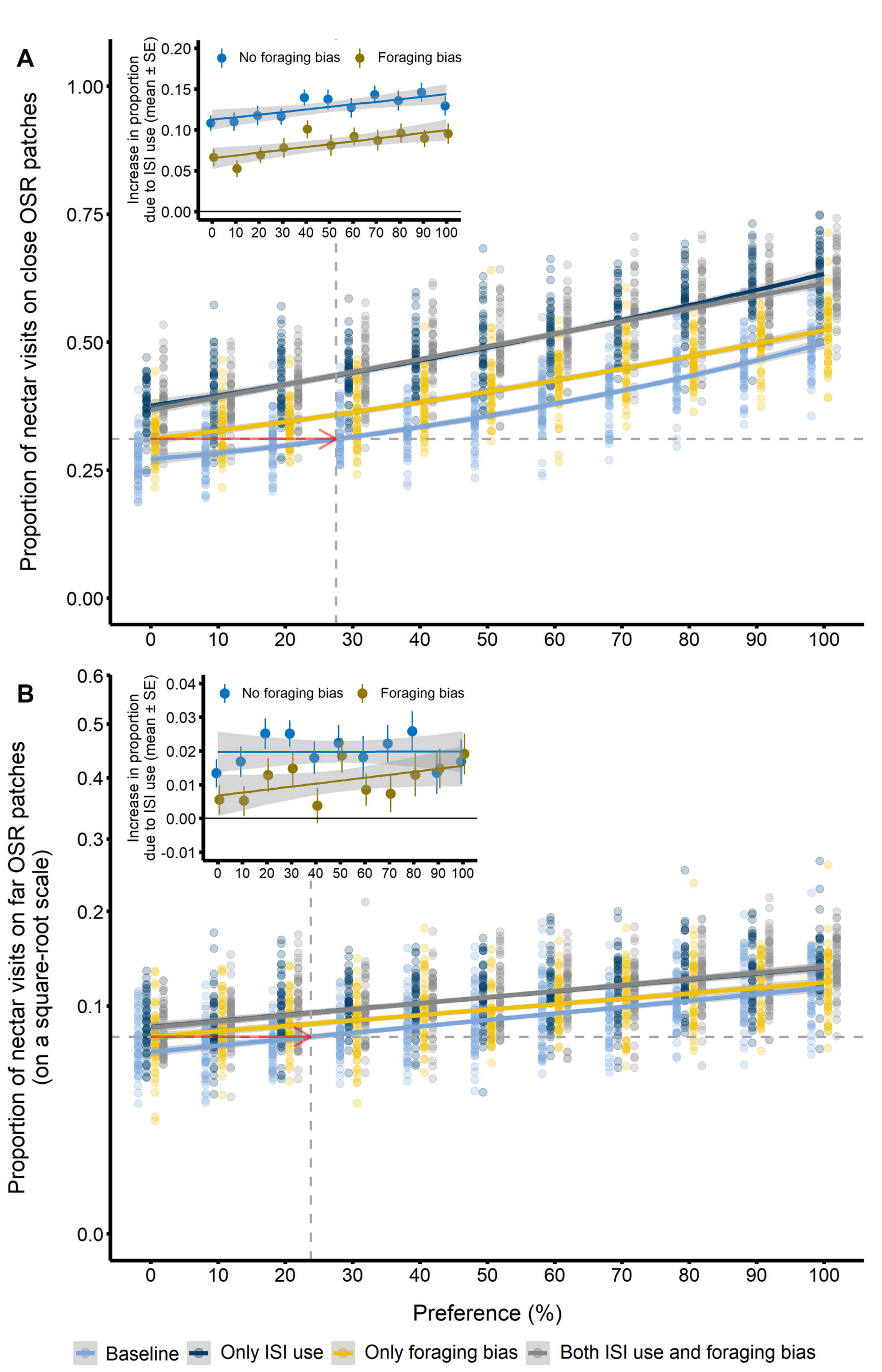
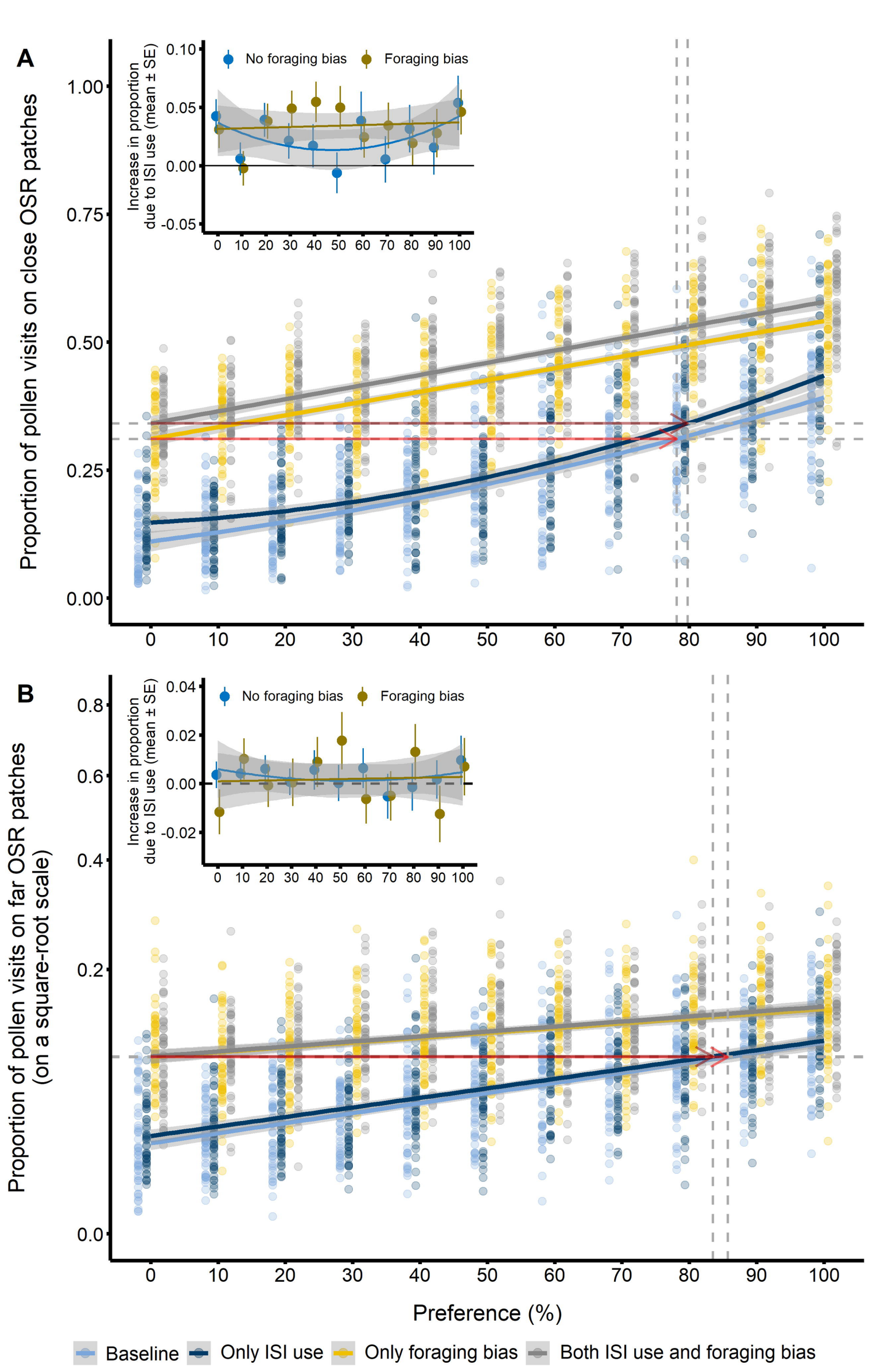
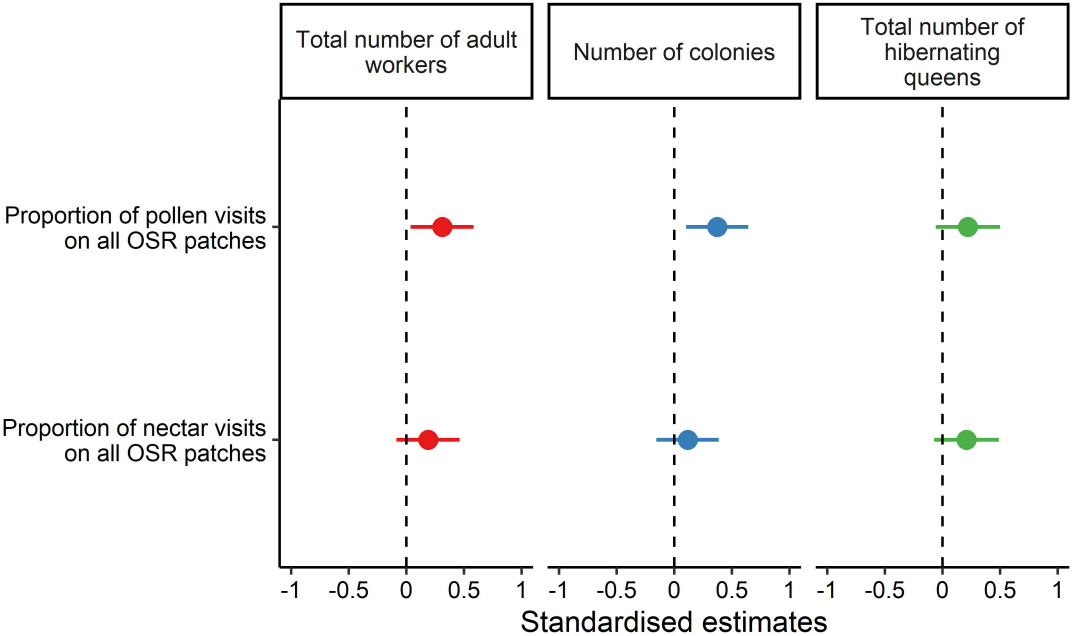

A
Proportion of nectar visits on close OSR patches
1.00
0.75
0.50
0.25
0.00
0 10 20 30 40 50 60 70 80 90 100
Increase in proportion due to ISI use (mean ± SE)
0.20
0.15
0.10
0.05
0.00
No foraging bias
Foraging bias
B
Proportion of nectar visits on far OSR patches (on a square-root scale)
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Increase in proportion due to ISI use (mean ± SE)
0.04
0.03
0.02
0.01
0.00
-0.01
Preference (%)
Baseline
Only ISI use
Only foraging bias
Both ISI use and foraging bias


A
Proportion of pollen visits on close OSR patches
1.00
0.75
0.50
0.25
0.00
0
10
20
30
40
50
60
70
80
90
100
Increase in proportion due to ISI use (mean ± SE)
0.10
0.05
0.00
-0.05
No foraging bias
Foraging bias
B
Proportion of pollen visits on far OSR patches (on a square-root scale)
0.8
0.6
0.4
0.2
0.0
Increase in proportion due to ISI use (mean ± SE)
0.04
0.02
0.00
-0.02
No foraging bias
Foraging bias
Preference (%)
Baseline
Only ISI use
Only foraging bias
Both ISI use and foraging bias


Total number of adult workers
Number of colonies
Total number of hibernating queens
Proportion of pollen visits on all OSR patches
Proportion of nectar visits on all OSR patches
-1
-0.5
0
0.5
1
Standardised estimates