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REVIEW

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Pesticide impacts on honey bee foraging behaviour: a field-relevant scoping review

Ming Wang^{1*} , Volker Grimm^{1,2} , Fabrice Requier³ , Jürgen Groeneveld^{1,4} , Holger Bargaen⁵,
Silvio Knaebe⁵  and Richard Odemer^{6*} 

Abstract

Honey bees (*Apis* spp.) play a crucial role in agricultural productivity and ecosystem functioning through pollination. However, their foraging behaviour is increasingly affected by pesticide exposure, including insecticides, acaricides, fungicides, and herbicides. Reported effects range from adverse to negligible or even stimulatory, depending on the compound, dose, and experimental design. To support more ecologically realistic risk assessments, we conducted a targeted scoping review of 26 studies examining pesticide impacts on honey bee foraging under semi-field and field-realistic conditions. These studies were evaluated based on pesticide type, exposure route and duration, *Apis* species, foraging type (nectar vs. pollen), behavioural endpoint, level of observation (individual vs. colony), and proposed mechanisms. Our synthesis reveals a pronounced research bias toward neonicotinoid insecticides and *Apis mellifera*, with minimal investigation of other pesticide classes, chronic exposures, or non-*mellifera* species such as *A. cerana* and *A. dorsata*. Most studies assessed individual-level effects and nectar foraging, while colony-level endpoints and pollen foraging remain underexplored. Additionally, small and inconsistent sample sizes reduce the statistical robustness and generalisability of many findings. We identify critical gaps in current pesticide risk assessments and call for standardised experimental methodologies, including harmonised behavioural metrics, consistent dosing protocols, and endpoints that link individual- to colony-level responses. Strengthening colony-level indicators under field-realistic exposures is essential for improving the predictive power of regulatory assessments, guiding targeted mitigation strategies, and promoting more sustainable pesticide use in agroecosystems.

Keywords *Apis mellifera*, Foraging behavior, Pesticide exposure, Field realism, Ecotoxicology, Risk assessment, Chronic exposure, Pollen foraging, Ecosystem services, Biodiversity

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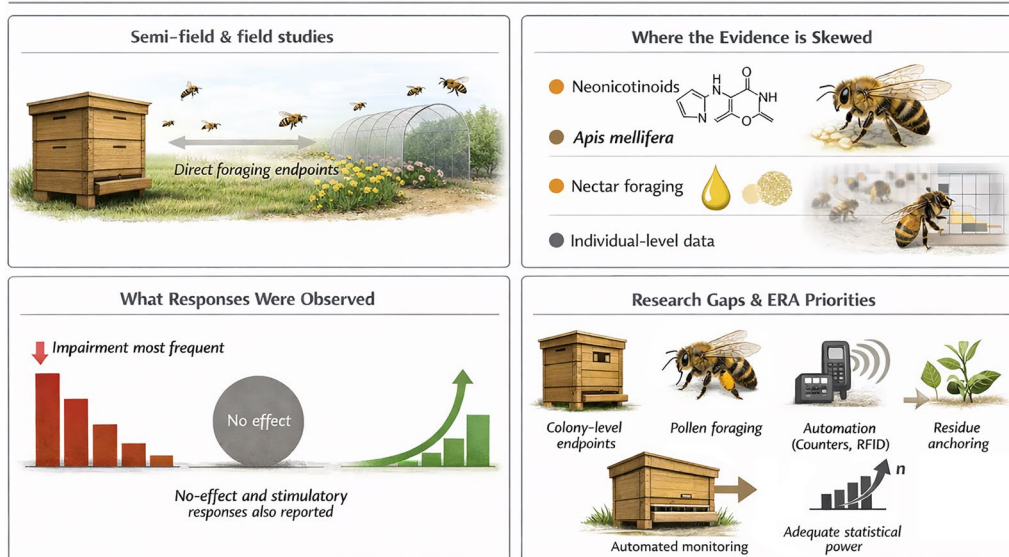
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Graphical Abstract

Pesticide Impacts on Honey Bee Foraging under Field-Realistic Conditions



Current evidence is informative but biased — advancing ERA requires colony-level, pollen-focused, automated, and residue-anchored field studies.

Background

To ensure colony maintenance and long-term viability, worker honey bees (*Apis mellifera* L.) perform two distinct tasks: nectar and pollen collection. These foraging activities are functionally and behaviourally differentiated and are typically performed by physiologically and behaviourally specialised worker cohorts [30]. Nectar, later ripened into honey, serves as a critical energy source and must be stored in large quantities to sustain feeding during winter and other non-foraging periods [8, 20, 76]. In contrast, pollen provides proteins, lipids, vitamins, and minerals required for brood development and the nutrition of young adult bees [8, 20, 76]. This nutritional contrast is reflected in the distinct behavioural and physiological traits associated with nectar and pollen foraging.

As non-target organisms, honey bees encounter a broad range of pesticides—including insecticides, fungicides, herbicides, and acaricides—across agricultural and natural landscapes [25, 29, 47]. In this review, we therefore distinguish between two levels of terminology: (i) “pesticide categories,” referring to these broad use-based groups, and (ii) “chemical classes,” referring to specific groups of active substances such as neonicotinoids, pyrethroids, organophosphates, or triazoles. This distinction allows us to summarise both coarse and fine-grained patterns in the literature in a consistent manner. Among these chemical classes, neonicotinoids

have most frequently been reported to adversely affect honey bee foraging [5, 69]. Documented effects include prolonged foraging trips [53, 80], impaired homing ability [16, 21, 60], reduced foraging frequency [43, 65], and altered behaviours such as inefficient task performance [48, 57] and disrupted social communication [65].

However, not all studies report adverse outcomes. Some find no detectable effects [19, 63], while a minority describe stimulatory responses consistent with hormesis, such as increased nectar foraging after exposure to methyl parathion [18] or imidacloprid [35]. Interestingly, even when identical compounds and similar nominal doses were tested, results often diverged both within and across studies. For example, sublethal doses of imidacloprid were reported to impair cognitive processes involved in foraging [53, 64, 80], whereas Karahan et al. [28] observed no such effect. Similarly, Shi et al. [56] documented a decline in homing success after exposure to acetamiprid, whereas Capela et al. [9] reported improved homing at sublethal concentrations. Ma et al. [32] found that thiamethoxam exposure reduced homing ability, yet in a separate flight-mill study the same doses enhanced flight performance (e.g., velocity, duration, distance). The implications of which for foraging under natural conditions remain unclear. In addition, Decourtye et al. [14] demonstrated that behavioural effects of deltamethrin

exposure were detectable at the individual level but not when assessed at the colony level.

From a risk-assessment perspective, foraging behaviour is the primary interface between individual bees and colony-level functioning. Foragers determine the colony's inflow of nectar and pollen, which constrains brood production, worker replacement, and overall colony performance. Because current Environmental Risk Assessment (ERA) frameworks define their protection goals at the colony or population level—such as maintaining colony strength and ensuring sufficient nutritional provisioning for brood—any pesticide-induced alteration of foraging behaviour may have cascading consequences beyond the individual worker [15, 58]. Establishing a clear link between behavioural effects and these colony-level endpoints is therefore essential for evaluating whether regulatory protection goals are met under field-realistic exposure conditions.

Despite decades of research, evidence remains fragmented for risk-assessment purposes. To our knowledge, no synthesis has focused explicitly on foraging endpoints under field-realistic exposure across the genus *Apis* in a way that would support ecotoxicological assessment. Several key questions remain: which pesticide classes and *Apis* species have been most intensively studied? What exposure levels are typically tested? Which foraging behaviours are most affected? What mechanisms underlie the observed effects? And how are these impacts measured and interpreted?

We therefore reviewed the literature on pesticide effects on honey bee foraging across chemical classes, species, exposure types and levels, endpoints, and methods. Recognising that foraging connects individual impairment to colony function and pollination services, we focus on field-realistic outcomes from semi-field and field studies across *Apis*. In doing so, we highlight systematic skews in chemical scope, observation level, and target behaviours (including the relative neglect of pollen foraging), which set up the research gaps (Sect. "Synthesis and identified research gaps") and forward-looking recommendations (Sect. "Future directions"). Our synthesis maps common patterns and gaps in a way aligned with regulatory assessment endpoints, clarifying where evidence is strong or sparse at both individual and colony levels and outlining priorities for future higher-tier studies.

Methods

Scope and operational definitions

Our objective was not to provide an exhaustive bibliography of all pesticide effects on bees, but to synthesise foraging-related functional endpoints measured under field-realistic exposure. We therefore restricted inclusion

to semi-field and field studies, as well as explicitly field-mimicking designs that allowed free-flying foraging. Eligible endpoints comprised direct foraging measures (e.g., trip frequency or duration, resource return, homing, recruitment/dance activity), whereas studies reporting only physiological proxies without quantified foraging behaviour were excluded. We use "semi-field" to describe controlled outdoor conditions with human interventions (e.g., tents or tunnels, including OECD 75-style designs) and "field-realistic" for exposure scenarios intended to reflect plausible field doses, routes, and temporal patterns.

Exclusion terms were applied to remove records focused exclusively on physiological proxies, lab-only assays, or non-foraging topics (e.g., molecular endpoints, nutrition, thermoregulation, modelling) when no foraging behaviour was quantified. This ensured alignment with our predefined scope and avoided dilution by multi-topic studies lacking resolvable foraging metrics.

To anchor the term "field-realistic," we interpret dose labels in relation to European residue monitoring: pollen and nectar typically contain ≤ 0.001 mg/kg following neonicotinoid seed treatments, with background levels generally ranging between 0.001 and 0.01 mg/kg and occasional spray-period spikes up to ~ 4.5 mg/kg in daily pollen series. EU-compliant field trials similarly report low residues relative to acute oral thresholds, with thiacloprid often representing the dominant pollen signal when detected [17, 27, 49, 62]. In this review, "field-realistic" is therefore used as an operational descriptor—plausible within monitored residue ranges—rather than a regulatory judgement on representativeness across all crops or exposure scenarios.

The term "pesticide class" reflects the chemical grouping reported in the original studies; substances were not reassigned to alternative classification frameworks (e.g., IRAC/FRAC/HRAC).

Search strategy and screening

We executed a prespecified Web of Science query (All Databases) combining *Apis* spp., pesticides (insecticides, acaricides, fungicides, herbicides), and foraging-related behaviours with the aforementioned exclusion terms specified in Section S2 of the Supplementary Information (full Boolean search string). The search returned 33 records in Dataset 1 [72], of which 26 studies met all eligibility criteria after title/abstract and full-text screening (PRISMA, see Fig. S1). We conducted the prespecified search on 23 February 2023. Although a verification run in September 2025 identified a small number of later eligible records, sensitivity checks did not change any Chi-square (χ^2) conclusions (see Supplementary Information).

Eligibility criteria

Inclusion. (i) Honey bees (*Apis* spp.); (ii) semi-field/field or explicitly field-mimicking designs permitting free foraging; (iii) direct foraging endpoints quantified at the individual and/or colony level; (iv) pesticide exposure defined by compound/class, formulation where applicable, route (oral/contact/treated plants), and exposure duration (acute/chronic).

Exclusion. (i) Lab-only assays without free-foraging; (ii) studies lacking quantified foraging outcomes; (iii) reviews, opinions, meta-analyses; (iv) non-chemical stressors without pesticide exposure.

Clarification. Studies that involved a laboratory exposure or tagging phase were included when the behavioural endpoints (e.g., foraging, homing) were subsequently quantified under semi-field or field conditions permitting free flight.

Data extraction

To enable structured comparison and synthesis, we applied a predefined data-extraction protocol to all included studies. For each article, information was recorded according to a fixed set of evaluation criteria (Table 1). These criteria captured the study type (field, semi-field, or mixed), the honey bee species or subspecies investigated, the pesticide category (insecticide, fungicide, herbicide, acaricide), and chemical-specific details such as pesticide class (e.g., neonicotinoid, organophosphate), the active compound, and whether a formulated

product or technical-grade active ingredient was used. In addition, we documented the dose level (as reported), exposure route (oral exposure, contact exposure, or via sprayed plants), the target life stage (e.g., adult foragers, larvae, whole colony), and exposure duration (acute vs. chronic).

Behavioural endpoints were classified with attention to the type of foraging (nectar, pollen, both, or unspecified), the observed outcome (e.g., reduced trip frequency, impaired homing, increased foraging time), the observation level (individual bee or colony), and the measurement method (e.g., RFID, mark–release tracking, manual observation). Where applicable, we also extracted the authors' proposed biological/physiological mechanisms underlying observed effects. This protocol provided the basis for quantitative and qualitative synthesis and supported the identification of knowledge gaps. A study-by-study summary is provided in Supplementary Table S1 (studies listed in Refs. [1, 3, 4, 9, 11, 14, 18, 19, 22, 28, 32, 33, 43, 48, 52, 53, 56, 57, 59, 63–65, 68, 75, 77, 80]). The full, machine-readable extraction is available in Dataset 2, and harmonised category labels match those used in Dataset 3 for plotting and Chi-square (χ^2) summaries [72].

Data analysis

To evaluate whether certain study attributes (e.g., pesticide class, observation method, behavioural outcome) were reported more frequently than others, we applied

Table 1 Variables and harmonised categories used for data extraction and summaries

Criteria	Example
Study type*	Field study, semi-field study, laboratory + semi-field/field study
Species studied	<i>Apis mellifera</i> , <i>Apis cerana</i> , etc
Pesticide category	Insecticides, fungicides, acaricides, herbicides
Pesticide class	Neonicotinoid, pyrethroid, organophosphate, etc
Pesticide name	Imidacloprid, clothianidin, flumethrin, glyphosate, etc
Pesticide type	Formulated product, non-formulated (pure active ingredient) product
Applied dose	Lethal, sublethal doses
Application method	Spraying, oral intake, contact exposure
Target organism or life stage	Adult foragers, young adults, larvae, whole colony, etc
Exposure duration	Acute (single exposure), chronic (multiple days or developmental stage)
Observed effect type	Lethal, sublethal, positive, no observable effects
Observed foraging behaviour	Nectar foraging, pollen foraging, both nectar and pollen foraging, foraging (not specified)
Observed outcome	Increased trip duration, reduced trip frequency, reduced homing success, etc
Observation level	Individual bee, and colony levels
Observation method	RFID tracking, mark-release tracking, manual observation, etc
Interpretation of results	Cognitive dysfunction, motor deficits, altered behaviours, neurological disruption, etc

*Studies involving human interventions (e.g., RFID tagging, marking bees, feeder training, etc.) were classified as semi-field studies

Articles can contribute multiple mentions across categories; therefore, totals in some figures exceed the number of included studies. Category labels match those in Dataset 3 [72]

Chi-square (χ^2) goodness-of-fit tests to compare proportions across categories. Where expected counts were small, Monte-Carlo computation of P -values was used. Because counts are based on study-level “mentions” and multiple mentions can originate from the same study, we interpret χ^2 as a descriptive/heuristic indicator of uneven representation rather than a strict inferential test assuming independence across all observations. All statistical analyses and visualisations were performed in R [50] using base R and the packages *tidyverse* [73], *ggstatsplot* [45], and *cowplot* [74]. The source data used for all statistical analyses and figures are provided in Dataset 3 [72].

Figures produced with *ggstatsplot* display, alongside χ^2 test results, ancillary indicators (e.g., effect-size estimates with confidence intervals and, where available, the natural logarithm of Bayes factors, $\log_e \text{BF}_{01}$). These diagnostics aid interpretation of distributional differences but are not the focus of our inference; accordingly, we describe patterns in the text and present the χ^2 outputs and ancillary indicators in the figure panels without duplicating numeric values in the main text.

Given the heterogeneous and unbalanced distribution of studies in the underlying literature, all χ^2 -based summaries are used strictly as descriptive, exploratory tools to illustrate skewed representation across categories. They are not intended as formal inferential tests, and we do not interpret the resulting P -values or effect-size diagnostics as evidence for statistical significance. Their sole purpose is to support transparent, descriptive synthesis of the available evidence.

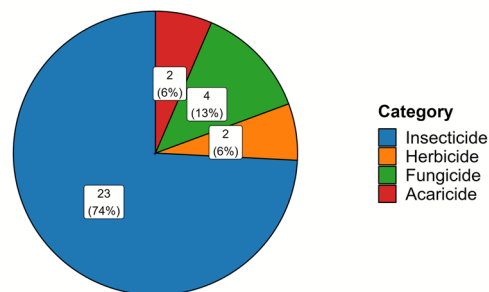
Pesticide categories and compounds studied

Across the 26 included studies, sample sizes within several categories were small or uneven; accordingly, χ^2 outputs in the following sections are intended as descriptive summaries of proportions rather than confirmatory hypothesis tests. Because the figures in this section are intended to provide a high-level overview of the relative frequency of study attributes, we used pie-chart visualisations to summarise category proportions in a compact, easily interpretable format. All underlying numerical values are reported in the supplementary dataset for readers who wish to inspect exact proportions in detail.

In the context of pesticide effects on honey bee foraging, most studies focused on insecticides, which accounted for 74% of mentions (Fig. 1A). Acaricides, fungicides, and herbicides together comprised 26% (Fig. 1A), with similar representation among these non-insecticide categories [acaricides: 2, fungicides: 4, herbicides: 2]. Among pesticide classes (excluding “Others”), neonicotinoids were the most extensively studied (30%), followed by pyrethroids (8%), organophosphates (7%), triazoles (7%), anilinopyrimidines (5%), and sulfoximines (5%),

A Pesticide category

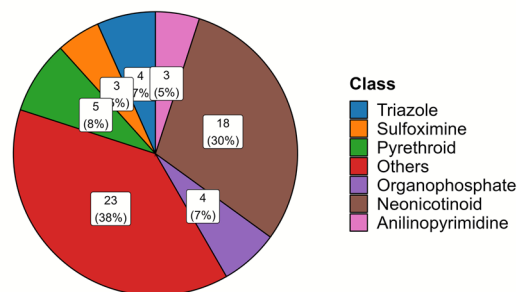
$$\chi_{\text{Gof}}^2(3) = 40.35, p = 8.96\text{e-}09, \hat{C}_{\text{Pearson}} = 0.75, \text{CI}_{95\%} [0.63, 1.00], n_{\text{obs}} = 31$$



$$\log_e(\text{BF}_{01}) = -11.34, a_{\text{Gunnell-Dickey}} = 1.00$$

B Pesticide class

$$\chi_{\text{Gof}}^2(6) = 48.27, p = 1.05\text{e-}08, \hat{C}_{\text{Pearson}} = 0.67, \text{CI}_{95\%} [0.53, 1.00], n_{\text{obs}} = 60$$



$$\log_e(\text{BF}_{01}) = -5.38, a_{\text{Gunnell-Dickey}} = 1.00$$

Fig. 1 Pesticide categories and classes investigated in the reviewed literature. **A** Most mentions concern insecticides ($n = 23$); herbicides ($n = 2$), fungicides ($n = 4$), and acaricides ($n = 2$) are rarer. **B** Neonicotinoids predominate ($n = 18$), followed by pyrethroids ($n = 5$), organophosphates ($n = 4$), triazoles ($n = 4$), anilinopyrimidines ($n = 3$), sulfoximines ($n = 3$), and Others ($n = 23$). Pie slices represent mentions at the study level; totals can exceed the number of included studies when a paper reports multiple compounds/classes/endpoints

with class representation skewed toward neonicotinoids (Fig. 1B).

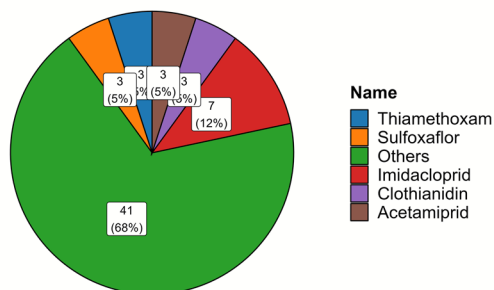
Note: Classes mentioned more than twice are shown individually; the remainder are grouped as “Others.”

Compounds and formulation types

Among frequently mentioned active ingredients, the most common were imidacloprid (12%), acetamiprid (5%), sulfoxaflor (5%), clothianidin (5%), and thiamethoxam (5%) (Fig. 2A), with similar representation across these compounds [imidacloprid: 7, acetamiprid: 3, sulfoxaflor: 3, clothianidin: 3, thiamethoxam: 3]. These five compounds accounted for 32% of all mentions. The proportion of formulated products (37%) was similar to non-formulated active ingredients (63%) (Fig. 2B).

A Pesticide name

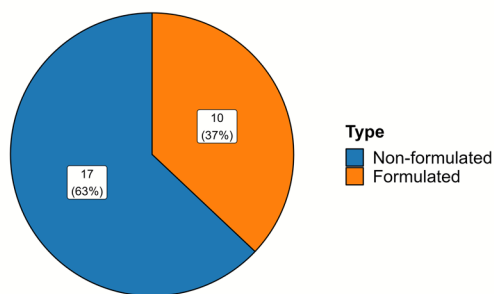
$$\chi_{\text{gof}}^2(5) = 116.60, p = 1.65\text{e-}23, \widehat{C}_{\text{Pearson}} = 0.81, \text{CI}_{95\%} [0.76, 1.00], n_{\text{obs}} = 60$$



$$\log_e(\text{BF}_{01}) = -29.32, a_{\text{Günzel-Dickey}} = 1.00$$

B Pesticide type

$$\chi_{\text{gof}}^2(1) = 1.81, p = 0.18, \widehat{C}_{\text{Pearson}} = 0.25, \text{CI}_{95\%} [0.00, 1.00], n_{\text{obs}} = 27$$



$$\log_e(\text{BF}_{01}) = 0.97, a_{\text{Günzel-Dickey}} = 1.00$$

Fig. 2 Frequency of specific pesticide compounds and formulation types. **A** The most frequently studied active ingredients were imidacloprid ($n = 7$), acetamiprid ($n = 3$), sulfoxaflor ($n = 3$), clothianidin ($n = 3$), and thiamethoxam ($n = 3$); all remaining compounds are grouped as Others ($n = 41$). **B** Slightly more mentions involved non-formulated active ingredients ($n = 17$) than formulated products ($n = 10$); counts were similar overall. Pie slices represent mentions at the study level; totals can exceed the number of included studies when a paper reports multiple compounds/classes/endpoints

Note: Compounds mentioned more than twice are shown individually; the remainder are grouped as “Others.”

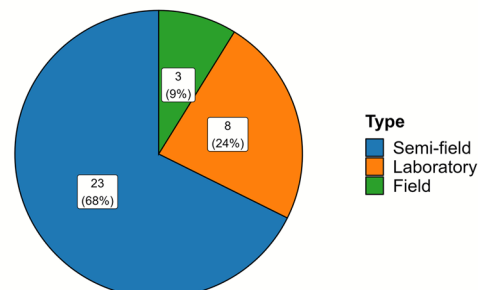
Species focus and study types

For the genus *Apis*, semi-field designs constituted 68% studies and predominated over field studies (9%) (Fig. 3A); laboratory experiments (24%) typically occurred in combination with semi-field or field work (Fig. 3A).

The western honey bee (*A. mellifera*), including its subspecies (e.g., *A. m. anatoliaca*, *A. m. carnica*, *A. m. iberiensis*, *A. m. ligustica*, *A. m. mellifera*), was the most frequently studied, accounting for 83% of species

A Study type

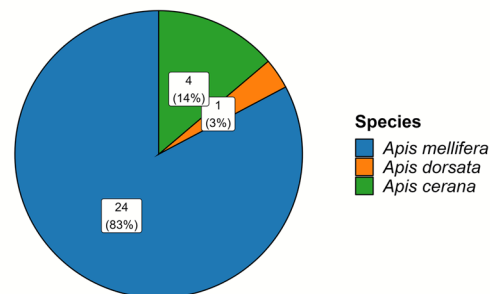
$$\chi_{\text{gof}}^2(2) = 19.12, p = 7.06\text{e-}05, \widehat{C}_{\text{Pearson}} = 0.60, \text{CI}_{95\%} [0.40, 1.00], n_{\text{obs}} = 34$$



$$\log_e(\text{BF}_{01}) = -5.55, a_{\text{Günzel-Dickey}} = 1.00$$

B Species studied

$$\chi_{\text{gof}}^2(2) = 32.34, p = 9.47\text{e-}08, \widehat{C}_{\text{Pearson}} = 0.73, \text{CI}_{95\%} [0.59, 1.00], n_{\text{obs}} = 29$$



$$\log_e(\text{BF}_{01}) = -12.44, a_{\text{Günzel-Dickey}} = 1.00$$

Fig. 3 Study types and *Apis* species represented. **A** Most studies are semi-field ($n = 23$), with fewer laboratory ($n = 8$) and field ($n = 3$) studies. **B** The majority focus on *A. mellifera* ($n = 24$), with fewer on *A. cerana* ($n = 4$) or *A. dorsata* ($n = 1$). Pie slices represent study-level mentions; totals can exceed the number of included studies when a paper reports multiple compounds/classes/endpoints

mentions (Fig. 3B). In contrast, other *Apis* species, such as *A. cerana* (incl. *A. c. indica*) and *A. dorsata*, were rarely examined (14% and 3%, respectively), i.e. ~ five-fold less often than *A. mellifera*.

Exposure routes, dosage regimes, and targeted life stages

Most studies used oral exposure (60%) (Fig. 4A), typically via contaminated sugar solutions at feeders. Contact exposure (27%) and plant-based exposure (sprayed flowering plants; 13%) were less common (Fig. 4A).

Exposure regimes predominantly involved sublethal doses (90%) (Fig. 4B)—often low $\mu\text{g L}^{-1}$ or $\mu\text{g kg}^{-1}$ concentrations or a few ng bee^{-1} —designed to reflect field-realistic conditions. Only a small proportion explicitly tested lethal doses (10%) (Fig. 4B).

Acute exposures (single events) were more common (73%) than chronic exposures (multiple days or

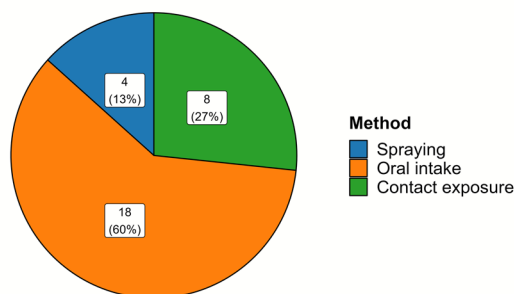
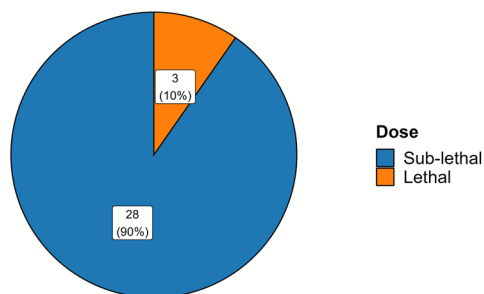
A Applied method
 $\chi^2_{\text{gor}}(2) = 10.40, p = 5.52e-03, \widehat{C}_{\text{Pearson}} = 0.51, \text{CI}_{95\%} [0.24, 1.00], n_{\text{obs}} = 30$

 $\log_e(\text{BF}_{01}) = -1.24, a_{\text{Gunnel-Dickey}} = 1.00$
B Applied dose
 $\chi^2_{\text{gor}}(1) = 20.16, p = 7.12e-06, \widehat{C}_{\text{Pearson}} = 0.63, \text{CI}_{95\%} [0.46, 1.00], n_{\text{obs}} = 31$

 $\log_e(\text{BF}_{01}) = -9.67, a_{\text{Gunnel-Dickey}} = 1.00$

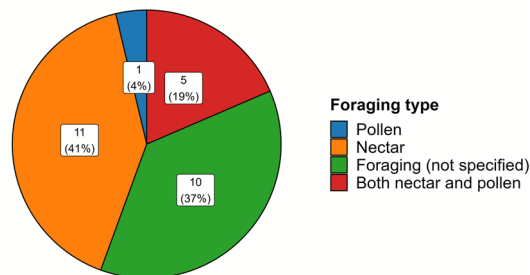
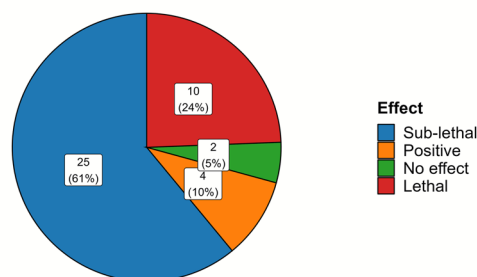
Fig. 4 Exposure routes and dose levels. **A** Oral exposure is most common ($n = 18$), followed by contact ($n = 8$) and sprayed plants ($n = 4$). **B** Sublethal doses dominate ($n = 28$), with few lethal applications ($n = 3$). Pie slices represent study-level mentions; totals can exceed the number of included studies when a paper reports multiple compounds/classes/endpoints

developmental stages; 27%) [acute: 22 vs. chronic: 8; see χ^2 in Fig. S2]. Regarding targeted life stages/organisms, adult foragers (63%) and young adults (27%) predominated, whereas larvae (3%), adult worker bees (3%), and whole hives (3%) were rarely examined [adult foragers: 19; young adults: 8; larvae: 1; adult worker bees: 1; hive: 1; see χ^2 in Fig. S3].

Effects of pesticides on foraging behaviour

Nectar foraging (41%) and unspecified foraging (37%) were most frequently examined, together representing 78% (Fig. 5A). Studies explicitly focusing on both nectar and pollen foraging accounted for 19%, while pollen-only foraging comprised 4% (Fig. 5A).

Note: “Unspecified” denotes studies that evaluated foraging activity without distinguishing nectar versus pollen.

A Foraging studied
 $\chi^2_{\text{gor}}(3) = 9.59, p = 0.02, \widehat{C}_{\text{Pearson}} = 0.51, \text{CI}_{95\%} [0.16, 1.00], n_{\text{obs}} = 27$

 $\log_e(\text{BF}_{01}) = -0.24, a_{\text{Gunnel-Dickey}} = 1.00$
B Observed effect
 $\chi^2_{\text{gor}}(3) = 31.68, p = 6.10e-07, \widehat{C}_{\text{Pearson}} = 0.66, \text{CI}_{95\%} [0.51, 1.00], n_{\text{obs}} = 41$

 $\log_e(\text{BF}_{01}) = -8.94, a_{\text{Gunnel-Dickey}} = 1.00$
Fig. 5 Foraging behaviours assessed and observed effect types. **A**

Most studies investigated nectar foraging ($n = 11$) or unspecified foraging ($n = 10$); pollen foraging was rare ($n = 1$). Five studies assessed both nectar and pollen. **B** Sublethal effects were most frequent ($n = 25$), followed by lethal ($n = 10$); a few reported no effect ($n = 2$) or stimulatory responses consistent with hormesis ($n = 4$). Pie slices represent study-level mentions; totals can exceed the number of included studies when a paper reports multiple compounds/classes/endpoints

Pesticide exposure was commonly associated with sub-lethal effects on foraging (61%) (Fig. 5B). Reported outcomes included decreased trip frequency, increased trip duration, impaired homing, reduced foraging time, and altered behaviours (e.g., increased resting, changes in communication, elevated abnormal behaviours). Lethal effects were reported in 24%; no-effect outcomes in 5%; and stimulatory responses in 10% (e.g., increased foraging activity/performance) (Fig. 5B).

Individual-level observations predominated relative to colony-level assessments under field-realistic conditions [individual: 26 vs. colony: 9; see χ^2 in Fig. S4].

Mechanistic insights into observed effects

To contextualise the reported behavioural outcomes, we synthesised the mechanistic pathways proposed across studies. Mechanistic interpretations of pesticide-induced

changes in honey bee foraging behaviour varied widely but nonetheless converged on a small number of consistent functional patterns.

The most frequently proposed pathways involved cognitive impairment, including disrupted learning, memory, or spatial orientation (e.g., [53, 60, 80]). Such impairments directly affect navigation, route optimisation, and the ability of bees to return reliably to their colonies. Closely related were reports of altered behavioural regulation, such as reduced foraging motivation, inefficient resource acquisition, or extended rest periods (e.g., [48, 57]). Together, cognitive and behavioural pathways accounted for nearly half of all mechanistic explanations identified (Fig. 6).

Motor and neurological disturbances were also frequently mentioned. Studies reported motor deficits and neurological disruption that can limit flight capacity, impair antennal sensory integration, slow reaction times, or reduce coordination—all of which can extend foraging trips or increase the risk of homing failure (e.g., [41, 60]). These findings are consistent with the idea that social buffering within colonies can partially mask or compensate for individual impairments, at least under natural foraging conditions [79].

Multiple studies also described physiological disruptions, including impaired detoxification capacity (e.g., reduced P450 activity), oxidative stress, metabolic dysfunction, and energetic constraints [10, 12, 31, 48, 80].

These mechanisms highlight that behavioural effects frequently emerge from underlying physiological burdens, potentially interacting with environmental and nutritional stressors.

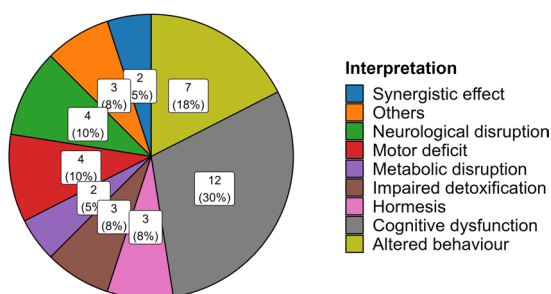
A smaller but ecologically important set of studies identified synergistic effects from mixed pesticide exposure, particularly combinations of insecticides and fungicides (e.g., [48, 52, 55]). Such interactions can amplify behavioural disruption even when individual compounds are applied at sublethal doses. Although mechanistic detail was variable, the existence of multiple interacting pathways highlights the complexity of sublethal responses under field conditions.

By contrast, a minority of studies described stimulatory responses consistent with hormesis [34] (e.g., [32, 66]). Increases in flight duration or speed may reflect transient hyperactivity rather than improved foraging efficiency, and such stimulation may incur physiological costs or accelerate behavioural maturation. Consequently, the ecological relevance of stimulatory effects remains uncertain and requires colony-level dose–response designs for meaningful interpretation.

Overall, mechanistic explanations span cognitive, behavioural, neurological, and physiological pathways, often interacting or co-occurring. A critical challenge for pesticide risk assessment is determining how such individual-level impairments translate—or fail to translate—to colony-level consequences. The well-documented buffering capacity of the colony as a superorganism [54, 61, 78, 79] may mask some impairments under natural conditions, while amplifying others under nutritional stress. These complexities reinforce the need for mechanistic, multi-level interpretation of sublethal effects within realistic ecological contexts.

Mechanistic insights into observed effects

$\chi^2_{\text{Gof}}(8) = 18.50, p = 0.02, \hat{C}_{\text{Pearson}} = 0.56, \text{CI}_{95\%} [0.20, 1.00], n_{\text{obs}} = 40$



$\log_e(\text{BF}_{01}) = 14.36, \theta_{\text{Gunnel-Dickey}} = 1.00$

Fig. 6 Proposed mechanisms underlying observed pesticide effects on honey bee foraging behaviour. The most frequently cited mechanism was cognitive dysfunction ($n = 12$), followed by altered behaviour ($n = 7$), motor deficits ($n = 4$), and neurological disruption ($n = 4$). Other proposed mechanisms included impaired detoxification ($n = 3$), hormesis ($n = 3$), synergistic effects ($n = 2$), metabolic disruption ($n = 2$), and a small number of other physiological or environmental interactions ($n = 3$). Pie slices represent study-level mentions; totals can exceed the number of included studies when a paper reports multiple compounds/classes/endpoints

Synthesis and identified research gaps

Understanding how diverse sublethal mechanisms scale from individual impairments to colony-level outcomes remains a central challenge for pesticide risk assessment. This review focuses specifically on foraging-related endpoints in *Apis* spp. under semi-field and field-realistic exposure conditions. The patterns and gaps we identify therefore pertain to this foraging-focused evidence base, situated within—but narrower than—the broader literature on pollinator ecotoxicology.

Importantly, the structural biases revealed by our analysis are not unique to foraging behaviour. Two recent reviews reached similar conclusions when synthesising sublethal pesticide effects across a broader range of endpoints. Tosi et al. [67] documented pronounced taxonomic and chemical skews—including overrepresentation of neonicotinoids and *A. mellifera*—while Pamminger et al. [44] found that methodological

heterogeneity and inconsistent reporting prevented a formal meta-analysis across chemical classes and behaviours. Our findings parallel these assessments and indicate that the empirical landscape for foraging endpoints reflects broader systemic patterns in bee ecotoxicology.

More broadly, difficulties in extrapolating from individual-level impairments to colony-level outcomes align with ecotoxicological theory emphasising multi-level translation, emergent properties, and biological buffering [2, 51]. Integrating these perspectives helps explain why consistent patterns remain elusive and underscores the need for harmonised, colony-linked study designs capable of spanning mechanistic, behavioural, and ecological scales.

To orient readers, Box 1 summarises the most recurrent evidence gaps observed across the included studies.

Together, the patterns in Box 1 show a literature tilted toward acute, individual-level outcomes in simplified settings; to start, the chemical scope is narrow.

Most reviewed studies focused on insecticides, particularly neonicotinoids such as imidacloprid, thiamethoxam, and clothianidin. Other classes, such as sulfoximines, pyrethroids, and especially fungicides, herbicides, and acaricides, were studied far less frequently. This pronounced focus on neurotoxic insecticides likely reflects historical concern about their effects on pollinators but has led to a narrow understanding of the full chemical spectrum [13]. The sublethal and interactive effects of non-insecticidal compounds remain largely uncharacterised. For instance, monitoring studies in neonicotinoid-treated sugar beet fields suggest that exposure through flowering weeds may still pose sublethal risks in certain regions, despite regulatory restrictions [39].

Second, exposure types, endpoints, and target organisms show a similar skew. The majority of studies assessed short-term oral exposure in adult worker bees, with foraging performance typically measured at the individual

level. This focus on adult bees overlooks potential buffering processes within the colony. For example, recent field-based evidence suggests that nurse bees may act as a biological filter, substantially reducing fungicide transfer from stored food to larvae during trophallaxis, which could mitigate some exposure effects at the brood level [78]. Colony-level endpoints were rare, and pollen foraging behaviour, a critical determinant of brood development, was almost completely neglected. These patterns suggest a methodological and conceptual bias that constrains our capacity to detect long-term or colony-scale disruptions.

Moreover, this skew extends to taxonomic coverage. Nearly all studies investigated *A. mellifera* or its subspecies, whereas *A. cerana* and *A. dorsata* were examined only sporadically. This limitation restricts the ecological relevance of current findings, particularly in regions where non-*mellifera* species dominate pollination services.

Many experiments were conducted under semi-field conditions, but often included direct human interventions such as feeder training or RFID tagging. While valuable for isolating behavioural effects, these designs do not fully capture the complexity of foraging under natural conditions. Field-based studies with intact colonies and chronic pesticide exposure under realistic conditions have shown that colony-level outcomes may differ substantially from individual-level predictions [42]. Recently developed, automated, non-invasive monitoring tools offer promising alternatives. When deployed under field-realistic exposure scenarios, they could improve the resolution of colony-level assessments without interfering with social dynamics or requiring disruptive manipulation [7, 40].

A small fraction of studies reported stimulatory responses consistent with hormesis (Fig. 5B); their ecological significance remains unresolved, prioritising

Box 1 Main identified evidence gaps in honey bee foraging studies

-
- **Chemical scope bias:** Strong focus on neonicotinoids; sparse coverage of sulfoximines, pyrethroids, fungicides, herbicides, acaricides; realistic mixtures rarely tested
 - **Endpoint skew:** Predominantly individual-level metrics (trip duration/frequency, homing); colony-level readouts (flight activity, pollen inflow, brood area) seldom included
 - **Exposure realism:** Short-term oral exposures dominate; chronic, field-realistic regimens underrepresented
 - **Pollen foraging overlooked:** Metrics of pollen collection/pollen-laden returns rarely quantified despite direct relevance to brood nutrition
 - **Taxonomic narrowness:** Evidence centred on *A. mellifera*; limited work on *A. cerana*, *A. dorsata* and other *Apis* species
 - **Design constraints:** Semi-field studies with feeder training/RFID useful but simplify ecological context and social buffering
 - **Scaling uncertainty:** Limited co-measurement of individual impairment and colony function over adequate time scales
 - **Statistical power:** Many studies have low–medium sample sizes; power/effect-size reporting inconsistent
 - **Hormesis/stimulation:** Occasional stimulatory responses; ecological significance unresolved without colony-level dose–response tests
 - **Residue context:** Behavioural outcomes often unanchored to residue bands or in-hive transfer dynamics (e.g., nurse-bee filtering)
-

field-realistic, colony-level dose–response tests to distinguish transient overstimulation from durable performance gains.

Sample size is a critical factor in evaluating the reliability of reported pesticide effects. In our analysis, we categorised group sizes as low ($n=2–20$), medium ($n=20–50$), or high ($n>50$). Only 29% of studies used high sample sizes, while 71% fell into low or medium categories, indicating an imbalance (see χ^2 in Fig. S5). Some studies relied on extremely small cohorts (e.g., $n<10$), raising concerns about statistical power and generalisability. These limitations should be considered when interpreting reported effects, especially where strong outcomes are based on minimal replication.

Taken together, these findings underscore a strong research bias toward *A. mellifera*, acute neonicotinoid exposure, and individual-level endpoints under simplified conditions. This leaves substantial gaps in our understanding of pesticide effects on colony-level foraging dynamics, non-insecticidal compounds, mixed exposures, chronic sublethal impacts, and non-*mellifera* species. These gaps motivate the forward-looking recommendations outlined in Sect. "Future directions". Much of the apparent heterogeneity in reported effects therefore reflects not only biological variability but also the way study designs and endpoints are clustered within the literature.

Future directions

Pesticide effects on honey bee foraging and flight behaviour remain difficult to generalise, with studies reporting sublethal impairments, stimulatory responses, or no measurable change depending on compound, exposure type, and experimental design (e.g., [4, 18, 19, 35, 43, 63, 80]). Individual-level impairments do not necessarily translate to colony-level consequences [14, 63], and responses such as altered foraging onset or trip duration frequently diverge across studies (e.g., [11, 48]).

Because these sources of variation directly affect the ecological realism and interpretability of ERA, addressing the identified gaps is an immediate priority for the field (Box 2).

Reducing uncertainty requires harmonised experimental protocols, including standardised dosing regimes, clearly defined behavioural endpoints, and consistent observation methods across studies. Whole-colony designs under field-realistic exposure conditions should be prioritised because they capture ecological feedbacks that cannot be replicated in individual-level assays. In parallel, mechanistic modelling—especially agent-based approaches—can simulate heterogeneous exposure routes and complement field studies by linking behavioural changes to colony-level population dynamics [58].

Building on the chemical and taxonomic skews summarised in Sect. "Synthesis and identified research gaps", future research should broaden its chemical scope—particularly to non-insecticidal classes and realistic mixtures [26]—and extend beyond *A. mellifera* to better reflect global *Apis* diversity [36]. Such expansion will improve the generalisability of findings across agroecosystems and support ERA frameworks that consider region-specific exposure regimes.

ERA benefits from endpoints that scale meaningfully from individual behaviour to colony performance. Consistent with evolving regulatory guidance [15], higher-tier studies should pair individual-level foraging metrics (e.g., trip frequency/duration, homing success) with colony-level readouts such as flight activity, pollen inflow, brood-area trajectories, and the proportion of pollen-laden returns. Pollen-foraging metrics warrant routine inclusion because pollen underpins brood nutrition and temporal delays in brood development may arise even when adult-level effects appear subtle [23, 24, 46]. Task-specific physiology may further lead nectar and pollen foragers to respond differently to the same stressor [70, 71], underscoring the need for differentiated endpoints.

Box 2 Main challenges and priorities for research and risk assessment

-
- **Define field-realistic exposure:** Region-appropriate dose bands, routes, timing; report residue ranges alongside effects
 - **Standardise protocols & endpoints:** Harmonised dosing, clearly defined behavioural endpoints, consistent observation methods
 - **Elevate colony-level assessment:** Pair individual metrics with colony-linked readouts (flight activity, pollen inflow, brood area) in chronic designs ($\geq 7–14$ d)
 - **Broaden chemistry & mixtures:** Include non-insecticidal classes and realistic co-application mixtures
 - **Expand taxa:** Incorporate *A. cerana*, *A. dorsata* and other *Apis* spp. to improve generalisability
 - **Anchor to residues & in-hive transfer:** Interpret behaviour relative to measured residues and nurse-bee filtering dynamics
 - **Harmonise automation:** QA/QC, calibration and reporting standards for automated counters and AI/video systems
 - **Power & transparency:** A priori power analyses; effect sizes with uncertainty; share machine-readable data and code
 - **Integrate modelling:** Use agent-based models to connect exposure routes and predict colony outcomes alongside field trials
 - **Regulatory alignment:** Map studies to OECD GD 332 (homing) and evolving EFSA Bee Guidance (2023) to aid ERA uptake
-

A standardised field protocol for quantifying homing success following oral exposure already exists—the OECD Honey Bee Homing Flight Test (Guidance Document No. 332; [37]). Although not yet mandatory within current EU ERA frameworks, homing-flight data generated under this protocol may contribute to higher-tier risk assessment once the revised EFSA Bee Guidance (2023) is fully implemented. By contrast, automated bee counters and AI/video systems—despite their potential for continuous, minimally biased monitoring of foraging traffic—still require harmonisation in calibration, deployment, and QA/QC procedures before broader regulatory uptake [38, 40], including recent protocols for evaluating counter accuracy [6].

Taken together, broadening chemical and taxonomic scope, improving methodological standardisation, and integrating automated colony-level monitoring are essential steps toward a more comprehensive and ecologically grounded understanding of pesticide impacts on honey bee foraging. Embedding these advancements into ERA frameworks will help ensure that regulatory assessments better reflect the ecological complexity and biological diversity of pollinator systems, thereby supporting more targeted mitigation and sustainable pesticide use in agricultural landscapes.

Supplementary Information

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Additional file 1.

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Author contributions

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Data availability

All data to reproduce our results are provided with this paper's supplementary information and in the "Open Science Framework" under <https://doi.org/10.17605/OSF.IO/H7J4C>.

Declarations

Ethics approval and consent to participate

Not applicable. This article synthesizes previously published studies and involves no new research with human participants, human data or tissue, or experimental work with animals.

Consent for publication

Not applicable. This article contains no individual person's data (including images, videos, or case details).

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During the preparation of this work, the authors used DeepL Write and ChatGPT to improve the structure, phrasing, and clarity of selected text passages originally written by the authors themselves. These tools were employed to enhance language quality and manuscript organization. Following their use, the authors carefully reviewed and edited all content to ensure accuracy, scientific integrity, and consistency with the intended meaning. The authors take full responsibility for the content of the publication.

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The authors declare no competing interests.

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