



## Research

**Cite this article:** Kaakinen K, Loukola OJ, Vaajamo E-M, Helander M. 2026 Volatilized prallethrin impairs the homing ability of bumblebees. *Biol. Lett.* **22**: 20250749. <https://doi.org/10.1098/rsbl.2025.0749>

Received: 26 November 2025

Accepted: 4 March 2026

### Subject Category:

Conservation biology

### Subject Areas:

cognition, ecology

### Keywords:

bumblebee cognition, navigation, pollinator, pollinator decline, pyrethroid, prallethrin, sublethal effects

### Author for correspondence:

Kimmo Kaakinen

e-mails: [kikaak@utu.fi](mailto:kikaak@utu.fi);

[kimmo.kaakinen@gmail.com](mailto:kimmo.kaakinen@gmail.com)

Supplementary material is available online at

<https://doi.org/10.6084/m9.figshare.c.8400178>.

# Volatilized prallethrin impairs the homing ability of bumblebees

Kimmo Kaakinen<sup>1</sup>, Olli Juhana Loukola<sup>1,2</sup>, Eva-Maria Vaajamo<sup>1</sup> and Marjo Helander<sup>1</sup>

<sup>1</sup>Department of Biology, University of Turku, Turku, Finland

<sup>2</sup>Ecology and Genetics Research Unit, University of Oulu, Oulu, Finland

KK, 0009-0009-0498-2666

Pollinator decline is one of the most urgent environmental challenges of our time, and pesticide use is considered a major contributing factor. In this study, we investigated whether exposure to volatilized prallethrin, a widely used insecticide, impairs the homing ability of bumblebees. Using a consumer-grade vaporizing device, we exposed foraging bees to field-realistic doses of prallethrin and then tested their ability to return to their colony in a rural area where they were already familiar with the surroundings. Our results show that longer exposure durations reduced the bees' return rates, indicating disrupted navigational ability. However, among those that did return, homing time was not affected by the treatment. While our study only focuses on one key behavioural trait, the findings provide clear evidence of a sublethal effect of a commonly used household insecticide on an essential pollinator species.

## 1. Introduction

Insecticides are essential tools for controlling pests in agriculture and households. Annually, 20–40% of crop yields are lost globally due to pests and diseases [1,2]. Besides damaging crops, insect pests also spread plant diseases [2]. Additionally, insects, particularly mosquitoes (Culicidae), transmit serious diseases such as malaria, dengue and yellow fever, which pose a threat to nearly half of the world's population [3]. At the household level, pyrethroid-based products are widely used to reduce human contact with mosquitoes and lower the risk of vector-borne diseases.

Insecticides have a negative impact on non-target species, particularly wild and managed pollinators, which are vital for biodiversity and food security [4,5]. The role of insecticides in the decline of pollinator populations is well-documented [6], highlighting the need for safer pest control methods. Most modern insecticides, such as neonicotinoids and pyrethroids, are neuroactive agents that disrupt the nervous systems of insects [7]. Due to their well-established risks to pollinators, the European Union banned the use of neonicotinoids in open-field crops in 2018 [8]. This ban has generated increased interest in alternative insecticides, such as pyrethroids, although their potential sublethal effects on pollinators remain poorly understood [9,10].

Pyrethroids are synthetic insecticides that were introduced in the 1970s and are widely used in households and agriculture to repel or eliminate insects [11]. They act primarily on voltage-gated sodium channels in neuronal membranes, causing delayed channel inactivation and prolonged depolarization, which lead to neuronal hyperexcitation, paralysis and death [7,12–14]. Prallethrin, a type I pyrethroid commonly used in vaporizing repellents such as Thermacell<sup>®</sup>, shares this mode of action.

Certain pyrethroid compounds, such as allethrin (D-allethrin), are prohibited in some European countries [15]. In contrast, others, like

prallethrin, remain widely approved and are actively used in consumer products, including aerosol sprays and vaporizing devices that release airborne chemical plumes to repel pests. In 2024, the European Commission approved prallethrin for biocidal use for a 10-year period, effective from 1 March 2026 to 29 February 2036 [16].

While the adverse effects of pyrethroids on pollinators have been widely studied [17–21], and the toxicity of volatilized pyrethroids has been examined in humans and laboratory animals [22–25], research on volatilized household pyrethroids, particularly prallethrin, and their effects on pollinators remains limited. Couvillon *et al.* [26] reported that volatilized prallethrin did not affect honey bee foraging at a feeder or recruitment dances; however, these behavioural endpoints primarily reflect short-term foraging activity near the repeller and may not capture navigation-related or other subtle sublethal effects, such as impairments in spatial memory or flight performance, which have been shown to be sensitive to neurotoxicants [27].

Volatilized pyrethroids are often viewed as safe for use in gardens and domestic areas, yet they generate airborne chemical plumes in areas frequently visited by pollinators. Their impact may therefore be more widespread than assumed, particularly in urban and suburban areas. Impaired homing means that bees may fail to return with food or perform their in-nest tasks, which can have serious colony-level consequences. In eusocial insects like bumblebees, colony success depends heavily on foraging workers. Therefore, even small decreases in forager return rates can negatively impact the overall colony fitness over time [28,29]. Since foraging workers play a crucial role in provisioning the brood and supporting colony growth, a decline in their effective workforce due to disruptions in orientation may lead to long-term population declines.

We investigated how exposure to volatilized prallethrin affects the homing ability of buff-tailed bumblebees (*Bombus terrestris*), a key pollinator in northern ecosystems [30]. This species is a central place forager, typically foraging up to 2 km from its colony [31,32] and can return from distances up to 9.8 km. The bees primarily rely on landscape cues for navigation [31–33]. Disruption of their navigation due to neuroactive insecticides may lead to colony-level consequences [11,34–37].

We conducted a post-exposure homing ability experiment for bumblebees to study the effects of volatilized prallethrin from a Thermacell MR-300 Portable Mosquito Repeller. Bees were released 1000 m from the colony, and we recorded both their success in returning home and their return times. We hypothesized that increasing the duration of exposure to volatilized prallethrin would impair homing ability. Any observed reductions in homing success or increases in return latency could result from disrupted spatial navigation and memory, compromised flight capacity or a combination of both. This experiment does not allow us to distinguish between these potential mechanisms, but it reveals the sublethal behavioural effects of prallethrin exposure. In addition to the homing experiment, we conducted a complementary laboratory assay to study mortality rates following prallethrin exposure. Understanding both sublethal behavioural effects and potential lethal effects is critical for assessing the ecological risks associated with biocides and for developing safer pest control strategies.

## 2. Methods

We conducted the field experiment in Ruissalo, southwestern Finland (60°26′00″ N, 22°10′23″ E) between June and August 2024, using 11 commercial colonies of *B. terrestris* (Koppert B.V). Two colonies (colony pair) were tested simultaneously over 8-day periods, after which they were replaced by new colonies. One colony showed signs of an unknown disease and was therefore removed immediately before the start of the experiment; consequently, one colony pair consisted of only a single colony.

On the first day of each period (day 1), colonies (queen + 80–120 workers) were placed in two-chamber wooden nest boxes (29 × 30 × 9 cm) inside a greenhouse. A transparent tunnel through the wall allowed free foraging outdoors. Colony entrances were painted either green or silver to help bees distinguish between the two colonies, which were positioned 3.5 m apart. Foraging was permitted for 4 or 5 days to allow bees to familiarize themselves with the local environment. Exposure and displacement experiments were conducted only in calm, rain-free weather.

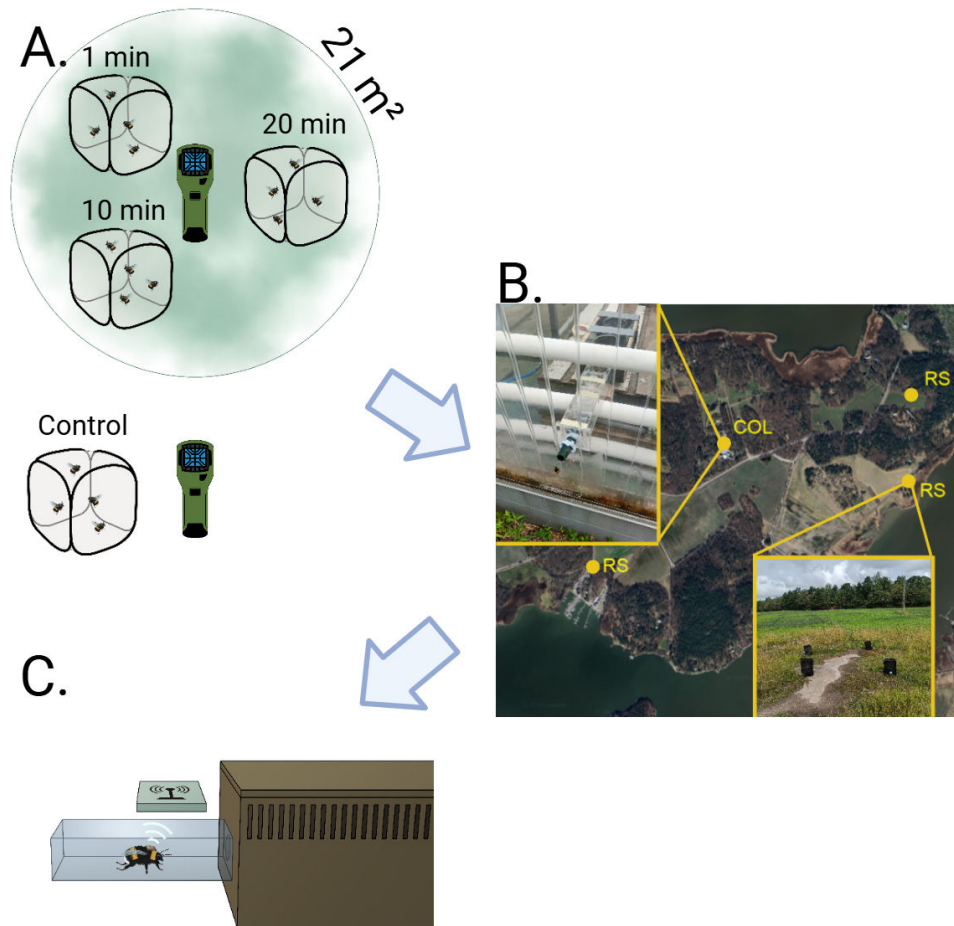
On day 4 or 5, we captured 12–16 returning foragers per colony and tagged them with individual 1.5 mm<sup>3</sup> radio frequency identification (RFID) tags (Microsensys<sup>®</sup> mic3Q1.6). We affixed the RFID tags to the thorax of bumblebees using super glue, i.e. we gently pressed the tag to the thorax of each captured bumblebee while holding it in place. We recorded the bee ID, colony number (1–11) and exposure treatment (1, 10 or 20 min, and control). Tagged bees were sorted into four net cages (35 cm diameter × 45 cm height, mesh 0.5 mm) by treatment. One colony from each colony pair was processed in the morning and the second in the afternoon. All four treatments were applied to each colony, except colonies 1 and 2, which did not include the 10 min exposure group.

Exposure durations (1–20 min) reflected plausible foraging times near insecticide-emitting devices. Site fidelity, e.g. a tendency to revisit previously visited locations, is common among pollinators [38–41], and Couvillon *et al.* [26] showed that honeybees repeatedly encountered pyrethroid vapours. Therefore, bumblebees might also encounter airborne prallethrin multiple times daily in urban or suburban gardens.

Bees were exposed to prallethrin using a Thermacell MR-300 Portable Mosquito Repeller, a consumer-grade device that vaporizes prallethrin (0.19 g per mat) over an area of approximately 21 m<sup>2</sup>. Control bees were housed near an identical device without a prallethrin mat. Devices were pre-heated for 15 min to ensure full vapour release. Net cages were then positioned in the exposure area, within 1 m from the device, beginning with the 20 min group and adding shorter exposure groups sequentially. The control cage was placed approximately 50 m away to avoid contamination (figure 1A).

After exposure, all tagged bees were transported to one of three open release sites, each located 1000 m from the colonies (figure 1B). Sites were selected based on floral availability and accessibility. The release site assignment was randomized by using a random number generator.

At the release site, net cages were opened one by one. To prevent the bees from following each other, we waited until the previous treatment group of bees had left the release site before opening the next net cage. Some bees were reluctant to fly first,



**Figure 1.** (A) Illustration of tagged bumblebees inside net cages corresponding to the 1-, 10- and 20 min exposure groups, placed within the effective range (approx. 21 m<sup>2</sup>) of a Thermacell MR-300 Portable Mosquito Repeller loaded with a Thermacell Anti Mosquito II mat containing 0.19 g of prallethrin. Control group bumblebees were housed in a separate net cage located within the coverage area of another Thermacell device without a prallethrin mat. (B) The map shows the release sites (RS), each located 1000 m from the colony (COL). The small image shows one of the RS with the net cages just before the bees were released. (C) Illustration of a tagged bumblebee (with an RFID tag on its back) returning to the colony through a tunnel, with an RFID reader mounted on the tunnel's roof to record its return.

especially the bees from longer treatment groups, and we gently placed them on the ground to encourage take-off, an essential step based on prior delays in initial trials. All released individuals were seen taking active flight and continuing to fly until they were out of sight. Bees were then allowed 3 days to return to their home colony [33], after which the colonies were removed. Returning bees were automatically registered by RFID readers installed at the nest tunnel entrances (figure 1C).

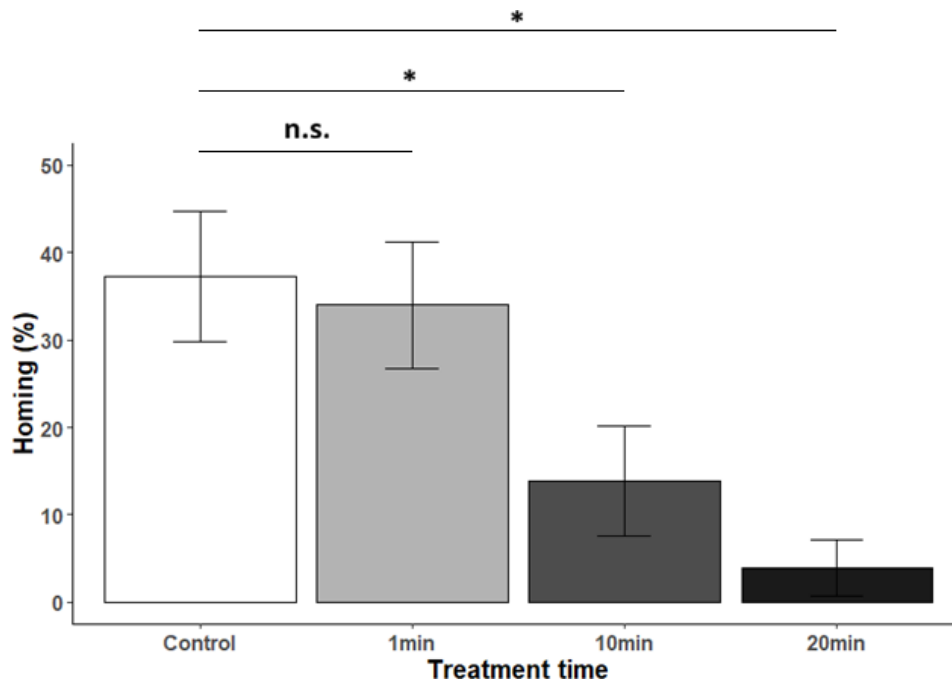
After each 8-day period, old colonies were euthanized using CO<sub>2</sub> and stored in a freezer before being replaced by new colonies for the next trial phase.

In the first colony pair, a 60 min exposure was used instead of the 10 min exposure. Upon further consideration, a 60 min exposure was deemed not field-realistic for freely foraging bumblebees. We therefore removed the 60 min treatment from the experiment and replaced it with a 10 min exposure in subsequent colony pairs and were therefore excluded from further analyses. Bumblebees subjected to the 60 min exposure were also reluctant to fly for an extended period after release.

To evaluate whether prallethrin exposure affected survival, we conducted a complementary laboratory assay using 47 workers from seven colonies between January and March 2025. On day 1, individual foragers were exposed to prallethrin vapour inside an inactive fume hood for either 1 or 10 min using the same Thermacell device and prallethrin mats as in the field experiment. Control bees were handled identically but exposed only to air. Bees were maintained under standard laboratory conditions after exposure, and survival (alive/dead) was recorded on day 4.

### 3. Statistical analyses

We analysed two behavioural outcomes: (i) homing rate (proportion of bees returning), and (ii) homing time (in minutes). Homing rate was modelled using a generalized linear mixed-effects model (GLMM) with a binomial error distribution and logit link function using the *glmmTMB* package [42]. Homing time was log-transformed to meet assumptions of normality and homoscedasticity and analysed using a separate GLMM. In both models, colony pair (replicate pair) was included as a random effect to account for between-pair variation. Model diagnostics indicated acceptable fit and dispersion (homing rate:  $p = 0.848$ ; homing time:  $p = 0.704$ ), as assessed using the *DHARMA* package [43]. In addition, we analysed the laboratory mortality dataset using a GLMM with binomial error structure and logit link function to test whether exposure duration affected survival. Mortality (alive = 1, dead = 0) was included as the response variable and treatment as a fixed effect, while colony was used as a random effect. The model was fitted using the *glmmTMB* package [42].



**Figure 2.** Homing rates (%) of bumblebees after exposure to prallethrin vapour for varying durations using a Thermacell MR-300 Portable Mosquito Repeller. Bars show back-transformed least square means ( $\pm$ s.e.). The asterisk above the bracket indicates a significant difference, and n.s. indicates no significant difference.

**Table 1.** Summary of the post-exposure homing ability experiment for bumblebees after exposure to prallethrin vapour for varying durations using a Thermacell MR-300 Portable Mosquito Repeller. Tot bees indicates the number of bumblebees included in each treatment group and returned indicates the number of individuals that successfully returned to the colony. EMMs represent the estimated marginal means, with corresponding 95% confidence intervals (CI lower, CI upper) derived from the GLMM.

treatment	tot bees	returned	EMMs	CI lower	CI upper
control	43	16	37.21	22.97	53.27
1 min	44	15	34.09	20.49	49.91
10 min	35	6	17.14	6.56	33.65
20 min	44	2	4.55	0.56	15.47

## 4. Results

We tagged 167 bumblebees with RFID chips, of which 39 returned to their colonies. Homing success varied substantially across treatment groups: control bees had the highest return rate (16/43; 37.2%), followed by the 1 min exposure group (15/44; 34.0%). Homing rates dropped markedly in the 10 min (17.1%) and 20 min (4.5%) exposure groups (table 1 and figure 2).

Generalized linear mixed-effects modelling revealed statistically significant negative effects of both 10 min (estimate = -1.31, s.e. = 0.58,  $p = 0.025$ ) and 20 min exposures (estimate = -2.67, s.e. = 0.81,  $p = 0.001$ ) on homing rate. In contrast, no significant differences were found among treatment groups on homing time: 1 min (estimate = 0.53, s.e. = 0.29,  $p = 0.062$ ); 10 min (estimate = 0.22, s.e. = 0.40,  $p = 0.574$ ); 20 min (estimate = 0.62, s.e. = 0.62,  $p = 0.324$ ).

Mortality was low across all laboratory-exposed groups (control: 2/14; 1 min: 0/16; 10 min: 1/17). A binomial GLMM with colony as a random factor detected no effect of treatment on survival (1 min: estimate = 27.34, s.e. = 36093.04,  $p = 0.999$ ; 10 min: estimate = -2.00, s.e. = 3.517,  $p = 0.569$ ).

## 5. Discussion

Our results show that even short-term exposure to volatilized prallethrin significantly impairs the homing ability of bumblebees. While nearly 40% of control bees returned, the return rate dropped to just 13.9 and 3.7% after 10 and 20 min of exposure, respectively. These findings suggest that prallethrin, a widely used pyrethroid insect repellent, can cause acute behavioural disruption in non-target pollinators.

Reduced homing success may arise from multiple, non-mutually exclusive mechanisms, including impaired navigation, reduced flight performance or general physiological stress. However, our experimental design does not allow us to disentangle these mechanisms.

Because homing times did not differ between groups, the effect is unlikely to stem from reduced flight speed or physical stamina. Similar non-lethal effects on navigational performance have been documented with sublethal pyrethroid [36] and

neonicotinoid exposures [35,44], where homing success declined even without increased mortality. By contrast, volatilized prallethrin showed no effects on honey bee foraging or communication behaviours in another context [26], supporting the conclusion that the observed reduction in homing success here reflects navigational impairment rather than lethality.

We acknowledge that homing time estimates are based on a limited number of returning individuals and should be interpreted with caution. Although it remains theoretically possible that some exposed bees died before returning, several observations argue against this explanation. All released individuals were seen taking active flight and continuing to fly until they were out of sight, indicating that they were alive and physically capable of flight immediately after exposure. Bumblebees typically do not initiate flight when severely debilitated or moribund, so this behaviour suggests that acute lethality was unlikely. Moreover, all individuals who successfully returned to the nest were detected by the RFID system and remained alive and active for several days thereafter. Further supporting this interpretation, our complementary laboratory survival assay showed that mortality remained low and statistically indistinguishable between treatment groups, including bees exposed for 10 min, the same exposure duration that caused a pronounced reduction in homing success. Survival was assessed on day 4 after exposure, corresponding to the end of the homing window in the field experiment, indicating that volatilized prallethrin did not cause delayed mortality that could explain the low return rate. Together, these findings indicate that exposure to volatilized prallethrin did not cause immediate or delayed mortality but rather impaired the bees' navigational ability or orientation during the homing flight.

Such effects are consistent with the neurophysiological mode of action of pyrethroids, which can disrupt normal neuronal signalling and lead to transient impairments in sensory processing, motor control and spatial orientation [12–14]. These sublethal disturbances provide a plausible mechanism for the observed navigational deficits, even in the absence of overt toxicity or mortality.

The exposure times in this study (1, 10 and 20 min) were selected to reflect realistic conditions in domestic settings, where foraging bees may encounter vapour plumes from repellents multiple times per day. Previous research by Couvillon *et al.* [26] demonstrated that honey bees regularly foraged within the active range of a Thermacell device. However, honey bees and bumblebees differ in ecology, physiology and pesticide sensitivity, and effects observed in honey bees may not directly translate to bumblebees. Although we did not directly measure avoidance, wild bumblebees were frequently observed around the exposure cages, suggesting that prallethrin vapour may not effectively deter them, increasing the likelihood of repeated exposure.

Our overall homing rates were lower than those reported in earlier studies. For example, Stanley *et al.* [44] observed a 67% return rate for bumblebees released 1 km from their colony, and Goulson & Stout [33] reported a 90% return rate at 1.1 km. One likely explanation for our lower success is the abundance of floral resources in early summer, which can shorten foraging distances and weaken spatial memory for distant areas. Studies have shown that bumblebee foraging ranges often remain below 1 km when resources are locally plentiful [45,46], and our study site, the Botanic Garden in Ruissalo, typically has a high abundance of suitable flowering plants. In a similar experiment conducted in the same environment a year earlier, the homing rate of control bees also remained relatively low [47]. In addition, natural variation in bee behaviour, including foraging experience and familiarity with the surrounding landscape, introduces uncertainty into field experiments. While such variability is difficult to control, it reflects realistic ecological conditions and underscores the relevance of our findings.

While the decline of pollinators is a complex issue involving many factors, small-scale stressors, such as domestic insecticide use, likely interact with broader pressures including habitat loss [6,48,49], climate change [50–52], pollution, invasive species [53,54] and pesticide exposure [55]. Together, these factors may drive vulnerable populations towards collapse, a phenomenon described as 'death by a thousand cuts' [56].

In conclusion, our study tentatively shows that prallethrin, a common ingredient in household insect repellents, can significantly disrupt the homing ability of bumblebees after even brief exposure. Although our study focuses on a single behavioural trait and does not identify the underlying mechanism, these findings highlight the need to reassess the ecological safety of consumer-grade pyrethroid-based products, especially as their use continues to expand in domestic and recreational spaces.

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

**Data accessibility.** All data supporting the findings of this study are provided as Supplementary Files [57].

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

**Authors' contributions.** K.K.: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing—original draft, writing—review and editing; O.J.L.: data curation, formal analysis, funding acquisition, supervision, validation, visualization, writing—original draft, writing—review and editing; E.-M.V.: investigation, methodology, writing—review and editing; M.H.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Conflict of interest statement.** We declare we have no competing interests.

**Funding.** This work was supported by the Novo Nordisk Foundation (grant no. NNF0093951) and the Finnish Cultural Foundation to M.H. and the Kone Foundation (grant no. 202010852) to O.J.L.

**Acknowledgements.** We are grateful to Emma Häkkinen for her assistance with figure preparation.

## References

- Oerke EC. 2007 Crop losses to animal pests, plant pathogens, and weeds. *Encycl. Pest Manag.* **2**, 116–120. (doi:10.1201/9781420068467.ch29)
- Oerke EC. 2006 Crop losses to pests. *J. Agric. Sci.* **144**, 31–43. (doi:10.1017/S0021859605005708)
- Shaw WR, Catteruccia F. 2019 Vector biology meets disease control: using basic research to fight vector-borne diseases. *Nat. Microbiol.* **4**, 20–34. (doi:10.1038/s41564-018-0214-7)
- Klein AM, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T. 2007 Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B* **274**, 303–313. (doi:10.1098/rspb.2006.3721)
- Ollerton J *et al.* 2012 Overplaying the role of honey bees as pollinators: a comment on Aebi and Neumann (2011). *Trends Ecol. Evol.* **27**, 141–142. (doi:10.1016/j.tree.2011.12.001)
- Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE. 2010 Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* **25**, 345–353. (doi:10.1016/j.tree.2010.01.007)
- Casida JE, Durkin KA. 2013 Neuroactive insecticides: targets, selectivity, resistance, and secondary effects. *Annu. Rev. Entomol.* **58**, 99–117. (doi:10.1146/annurev-ento-120811-153645)
- EFSA. 2018 *Neonicotinoids: risks to bees confirmed*. See <https://www.efsa.europa.eu/en/press/news/180228>.
- Blake R. 2018 EU neonicotinoid ban removes vital tools in global fight against pests. *Outlooks Pest Manag.* **29**, 197–200. (doi:10.1564/v29\_oct\_02)
- Klatt BK, Rundlöf M, Smith HG. 2016 Maintaining the restriction on neonicotinoids in the European Union—benefits and risks to bees and pollination services. *Front. Ecol. Evol.* **4**, 1–4. (doi:10.3389/fevo.2016.00004)
- Casida JE, Quistad GB. 1998 Golden age of insecticide research: past, present, or future? *Annu. Rev. Entomol.* **43**, 1–16. (doi:10.1146/annurev.ento.43.1.1)
- Mužinić V, Želježić D. 2018 Non-target toxicity of novel insecticides. *Arch. Ind. Hyg. Toxicol.* **69**, 86–102. (doi:10.2478/aiht-2018-69-3111)
- Narahashi T. 2002 Nerve membrane ion channels as the target site of insecticides. *Mini Rev. Med. Chem.* **2**, 419–432. (doi:10.2174/1389557023405927)
- Soderlund DM. 2012 Molecular mechanisms of pyrethroid insecticide neurotoxicity: recent advances. *Arch. Toxicol.* **86**, 165–181. (doi:10.1007/s00204-011-0726-x)
- EUR-Lex. *Commission Implementing Decision (EU) 2023/470 of 2 March 2023 not approving d-Allethrin as an existing active substance for use in biocidal products of product-type 18 in accordance with Regulation (EU) No 528/2012 of the European Parliament and of the Council (Text with EEA relevance)*. See [https://eur-lex.europa.eu/eli/dec\\_impl/2023/470/oj/eng](https://eur-lex.europa.eu/eli/dec_impl/2023/470/oj/eng) (accessed 9 July 2025).
- EUR-Lex. *Commission Implementing Regulation (EU) 2024/2576 of 2 October 2024 approving 2-methyl-4-oxo-3-(prop-2-ynyl)cyclopent-2-en-1-yl 2,2-dimethyl-3-(2-methylprop-1-enyl)cyclopropanecarboxylate (prallethrin) as an existing active substance for use in biocidal products of product-type 18 in accordance with Regulation (EU) No 528/2012 of the European Parliament and of the Council*. See [https://eur-lex.europa.eu/eli/reg\\_impl/2024/2576/oj/eng](https://eur-lex.europa.eu/eli/reg_impl/2024/2576/oj/eng) (accessed 9 July 2025).
- Decourtye A, Devillers J, Cluzeau S, Charreton M, Pham-Delègue MH. 2004 Effects of imidacloprid and deltamethrin on associative learning in honeybees under semi-field and laboratory conditions. *Ecotoxicol. Environ. Saf.* **57**, 410–419. (doi:10.1016/j.ecoenv.2003.08.001)
- Liao C, He X, Wang Z, Barron AB, Zhang B, Zeng Z, Wu X. 2018 Short-term exposure to lambda-cyhalothrin negatively affects the survival and memory-related characteristics of worker bees *Apis mellifera*. *Arch. Environ. Contam. Toxicol.* **75**, 59–65. (doi:10.1007/s00244-018-0514-1)
- McGregor BL, Giordano BV, Runkel AE, Nigg HN, Nigg HL, Burkett-Cadena ND. 2021 Comparison of the effect of insecticides on bumble bees (*Bombus impatiens*) and mosquitoes (*Aedes aegypti* and *Culex quinquefasciatus*) by standard mosquito research methods. *J. Econ. Entomol.* **114**, 24–32. (doi:10.1093/jee/toaa282)
- Taylor KS, Waller GD, Crowder LA. 1987 Impairment of a classical conditioned response of the honey bee (*Apis mellifera* L.) by sublethal doses of synthetic pyrethroid insecticides. *Apidologie* **18**, 243–252. (doi:10.1051/apido:19870304)
- van dame R, Meled M, Colin ME, Belzunces LP. 1995 Alteration of the homing-flight in the honey bee *Apis mellifera* L. exposed to sublethal dose of deltamethrin. *Environ. Toxicol. Chem.* **14**, 855–860. (doi:10.1002/etc.5620140517)
- Ghanty S, Mandi M, Ganguly A, Das K, Dutta A, Nanda S, Biswas G, Rajak P. 2022 Lung surfactant proteins as potential targets of prallethrin: an *in silico* approach. *Toxicol. Environ. Health Sci.* **14**, 89–100. (doi:10.1007/s13530-021-00119-0)
- Na HG, Kim YD, Choi YS, Bae CH, Song SY. 2018 Allethrin and prallethrin stimulates MUC5AC expression through oxidative stress in human airway epithelial cells. *Biochem. Biophys. Res. Commun.* **503**, 316–322. (doi:10.1016/j.bbrc.2018.06.022)
- Narendra M, Bhattacharyulu NC, Padmavathi P, Varadacharyulu NC. 2007 Prallethrin induced biochemical changes in erythrocyte membrane and red cell osmotic haemolysis in human volunteers. *Chemosphere* **67**, 1065–1071. (doi:10.1016/j.chemosphere.2006.11.064)
- Narendra M, Kavitha G, Helah Kiranmai A, Raghava Rao N, Varadacharyulu NC. 2008 Chronic exposure to pyrethroid-based allethrin and prallethrin mosquito repellents alters plasma biochemical profile. *Chemosphere* **73**, 360–364. (doi:10.1016/j.chemosphere.2008.05.070)
- Couvillon MJ, Ohlinger BD, Bizon C, Johnson LE, McHenry LC, McMillan BE, Schürch R. 2023 A volatilized pyrethroid insecticide from a mosquito repelling device does not impact honey bee foraging and recruitment. *J. Insect Sci.* **23**, 11. (doi:10.1093/jisesa/iead079)
- Ohlinger BD, Schürch R, Durzi S, Kietzman PM, Silliman MR, Couvillon MJ. 2022 Honey bees (Hymenoptera: Apidae) decrease foraging but not recruitment after neonicotinoid exposure. *J. Insect Sci.* **22**, 16. (doi:10.1093/jisesa/ieab095)
- Cartar RV, Dill LM. 1991 Costs of energy shortfall for bumble bee colonies: predation, social parasitism, and brood development. *Can. Entomol.* **123**, 283–293. (doi:10.4039/Ent123283-2)
- Hölldobler B, Wilson EO. 2009 *The superorganism: the beauty elegance and strangeness of insect societies*. New York, NY: W. W. Norton & Company.
- Heinrich B. 1972 Energetics of temperature regulation and foraging in a bumblebee, *Bombus terricola* Kirby. *J. Comp. Physiol.* **77**, 49–64. (doi:10.1007/BF00696519)
- Kreyer D, Oed A, Walther-Hellwig K, Frankl R. 2004 Are forests potential landscape barriers for foraging bumblebees? Landscape scale experiments with *Bombus terrestris* agg. and *Bombus pascuorum* (Hymenoptera, Apidae). *Biol. Conserv.* **116**, 111–118. (doi:10.1016/S0006-3207(03)00182-4)
- Walther-Hellwig K, Frankl R. 2000 Foraging distances of *Bombus muscorum*, *Bombus lapidarius*, and *Bombus terrestris* (Hymenoptera, Apidae). *J. Insect Behav.* **13**, 239–246. (doi:10.1023/A:1007740315207)
- Goulson D, Stout JC. 2001 Homing ability of the bumblebee *Bombus terrestris* (Hymenoptera: Apidae). *Apidologie* **32**, 105–111. (doi:10.1051/apido:2001115)
- Bryden J, Gill RJ, Mitton RAA, Raine NE, Jansen VAA. 2013 Chronic sublethal stress causes bee colony failure. *Ecol. Lett.* **16**, 1463–1469. (doi:10.1111/ele.12188)
- Fischer J, Müller T, Spatz AK, Greggers U, Grünewald B, Menzel R. 2014 Neonicotinoids interfere with specific components of navigation in honeybees. *PLoS One* **9**, e91364. (doi:10.1371/journal.pone.0091364)
- Matsumoto T. 2013 Reduction in homing flights in the honey bee *Apis mellifera* after a sublethal dose of neonicotinoid insecticides. *Bull. Insectol.* **66**, 1–9. <https://archive.bulletinofinsectology.org/pdfarticles/vol66-2013-001-009matsumoto.pdf>

37. Stanley DA, Garratt MPD, Wickens JB, Wickens VJ, Potts SG, Raine NE. 2015 Neonicotinoid pesticide exposure impairs crop pollination services provided by bumblebees. *Nature* **528**, 548–550. (doi:10.1038/nature16167)
38. Fragoso FP, Brunet J. 2023 Honey bees exhibit greater patch fidelity than bumble bees when foraging in a common environment. *Ecosphere* **14**, e4606. (doi:10.1002/ecs2.4606)
39. Moura PA, Corso G, Montgomery SH, Cardoso MZ. 2022 True site fidelity in pollen-feeding butterflies. *Funct. Ecol.* **36**, 572–582. (doi:10.1111/1365-2435.13976)
40. Ogilvie JE, Thomson JD. 2016 Site fidelity by bees drives pollination facilitation in sequentially blooming plant species. *Ecology* **97**, 1442–1451. (doi:10.1890/15-0903.1)
41. Osborne JL, Williams IH. 2001 Site constancy of bumble bees in an experimentally patchy habitat. *Agric. Ecosyst. Environ.* **83**, 129–141. (doi:10.1016/S0167-8809(00)00262-0)
42. Magnusson A *et al.* 2017 Package 'glmmTMB'. R Package Version 0.2. 0, 25. See <https://cran.r-hub.io/web/packages/glmmTMB/glmmTMB.pdf>.
43. Hartig F, Lohsel, de Souza Leite M. 2022 DHARMA: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. See <https://CRAN.R-Project.Org/Package=DHARMA>.
44. Stanley DA, Russell AL, Morrison SJ, Rogers C, Raine NE. 2016 Investigating the impacts of field-realistic exposure to a neonicotinoid pesticide on bumblebee foraging, homing ability and colony growth. *J. Appl. Ecol.* **53**, 1440–1449. (doi:10.1111/1365-2664.12689)
45. Knight ME, Martin AP, Bishop S, Osborne JL, Hale RJ, Sanderson RA, Goulson D. 2005 An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Mol. Ecol.* **14**, 1811–1820. (doi:10.1111/j.1365-294X.2005.02540.x)
46. Wolf S, Moritz RFA. 2008 Foraging distance in *Bombus terrestris* L. (Hymenoptera: Apidae). *Apidologie* **39**, 419–427. (doi:10.1051/apido:2008020)
47. Kaakinen K, Ramula S, Helander M. 2025 Glyphosate-based herbicide increases the number of foraging trips but does not affect the homing of *Bombus terrestris*. *Apidologie* **56**, 54. (doi:10.1007/s13592-025-01180-1)
48. Brown MJF, Paxton RJ. 2009 The conservation of bees: a global perspective. *Apidologie* **40**, 410–416. (doi:10.1051/apido/2009019)
49. Hendrickx F *et al.* 2007 How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *J. Appl. Ecol.* **44**, 340–351. (doi:10.1111/j.1365-2664.2006.01270.x)
50. Dormann CF *et al.* 2008 Prediction uncertainty of environmental change effects on temperate European biodiversity. *Ecol. Lett.* **11**, 235–244. (doi:10.1111/j.1461-0248.2007.01142.x)
51. Soroye P, Newbold T, Kerr J. 2020 Climate change contributes to widespread declines among bumble bees across continents. *Science* **367**, 685–688. (doi:10.1126/science.aax8591)
52. Williams PH, Araújo MB, Rasmont P. 2007 Can vulnerability among British bumblebee (*Bombus*) species be explained by niche position and breadth? *Biol. Conserv.* **138**, 493–505. (doi:10.1016/j.biocon.2007.06.001)
53. Goulson D. 2003 Effects of introduced bees on native ecosystems. *Annu. Rev. Ecol. Evol. Syst.* **34**, 1–26. (doi:10.1146/annurev.ecolsys.34.011802.132355)
54. Stout JC, Morales CL. 2009 Ecological impacts of invasive alien species on bees. *Apidologie* **40**, 388–409. (doi:10.1051/apido/2009023)
55. Dicks LV *et al.* 2021 A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nat. Ecol. Evol.* **5**, 1453–1461. (doi:10.1038/s41559-021-01534-9)
56. Wagner DL, Grames EM, Forister ML, Berenbaum MR, Stopak D. 2021 Insect decline in the Anthropocene: death by a thousand cuts. *Proc. Natl Acad. Sci. USA* **118**, e2023989118. (doi:10.1073/pnas.2023989118)
57. Kaakinen K, Loukola OJ, Vaajamo EM, Helander M. 2026 Supplementary material from: Volatilised prallethrin impairs the homing ability of bumblebees. FigShare. (doi:10.6084/m9.figshare.c.8400178)