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Field-realistic neonicotinoid exposure has sub-lethal effects on non-*Apis* bees: A meta-analysis

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Abstract

Neonicotinoid insecticides can have sub-lethal effects on bees which has led to calls from conservationists for a global ban. In contrast, agrochemical companies argue that neonicotinoids do not harm honeybees at field-realistic levels. However, the focus on honeybees neglects the potential impact on other bee species. We conducted a meta-analysis to assess whether field-realistic neonicotinoid exposure has sub-lethal effects on non-*Apis* bees. We extracted data from 53 papers (212 effects sizes) and found that it largely consisted of two genera: bumblebees (*Bombus*) and mason bees (*Osmia*), highlighting a substantial taxonomic knowledge gap. Neonicotinoid exposure negatively affected reproductive output across all bees and impaired bumblebee colony growth and foraging. Neonicotinoids also reduced *Bombus*, but not *Osmia*, individual development (growth and body size). Our results suggest that restrictions on neonicotinoids should benefit bee populations and highlight that the current regulatory process does not safeguard pollinators from the unwanted consequences of insecticide use.

KEYWORDS
bee health, *Bombus*, bumblebees, insecticide, *Osmia*, wild bees

INTRODUCTION

There are an estimated 20,000 bee species globally, consisting of seven families found in every continent except Antarctica (Ascher & Pickering, 2012). Bees vary across many aspects of their ecology and behaviour, including in their degree of sociality, diet and life-history strategies (Williams et al., 2010). They are key pollinators of wildflowers and also play a critical role in agriculture (Burkle et al., 2013; Mathiasson & Rehan, 2020). While intensive agriculture is often reliant on domesticated honeybees (*Apis mellifera)* for crop pollination, other managed and wild bees also provide important pollination services (Garibaldi et al., 2013; Kremen et al., 2002; Rader et al., 2016). For example bumblebees pollinate crops that require buzz pollination (De Luca & Vallejo-Marín, 2013), squash bees (*Eucera pruinosa*) almost exclusively pollinate cucurbits (pumpkin and squash) (Dorchin et al.,

2018; Petersen et al., 2013) and, even when honeybees are present, other bee species can increase crop yields of apple, almond and coffee (Blitzer et al., 2016; Klein et al., 2003; Koh et al., 2018). While some non-*Apis* bee species (e.g. *Bombus terrestris*, *B. impatiens*, *Osmia lignaria*, *Megachile rotundata*) are managed to provide pollination services, wild bees also provide a free pollination service which acts as a pollination buffer in the face of local honeybee declines or supply issues (Blitzer et al., 2016; Garibaldi et al., 2013; Greenleaf & Kremen, 2006; Mallinger & Gratton, 2015; Winfree et al., 2007). Given the importance of non-*Apis* bees for both wild ecosystems (Burkle et al., 2013; Mathiasson & Rehan, 2020) and sustainable food production (Vanbergen & Insect Pollinators Initiative, 2013), documented global bee declines (Powney et al., 2019; Soroye et al., 2020) will have significant economic and social consequences (Losey & Vaughan, 2006; Rader et al., 2016).

Bee population declines are caused by multiple anthropogenic stressors, including loss of habitat, nutritional stress, climate change and exposure to pathogens and agrochemicals (Goulson et al., 2015; Siviter et al., 2021; Vanbergen & Insect Pollinators Initiative, 2013). In recent years much attention has focused on the potential impact of neonicotinoid insecticides on bees (Pisa et al., 2017). Neonicotinoids are the most commonly used insecticide globally (Simon-Delso et al., 2015). They target insects by acting as agonists of nicotinic acetylcholine receptors (nAChRs) and can be applied as both a seed treatment and as a foliar spray, making them effective on a wide variety of crops (Bonmatin et al., 2015). Being both water-soluble and long-lasting, neonicotinoids can leach into surrounding soil and ground water, persisting in the environment for several months, and in some cases, years (Pisa et al., 2015). As systemic insecticides, neonicotinoids enter the tissue of treated crops, including plants' nectar and pollen, where bees may be exposed (Botías et al., 2016; Hladik et al., 2016; Stewart et al., 2014). In addition, neonicotinoids have been found in wildflowers adjacent to treated crops (Botías et al., 2016; Krupke et al., 2012; Long & Krupke, 2016; Main et al., 2020; Tsvetkov et al., 2017), in non-target trees and foliage (Wood et al., 2019), in agricultural weeds (Wood et al., 2019) and in residential gardens (Lentola et al., 2017; Nicholls et al., 2018). Pesticide regulation relies heavily on toxicity studies to determine the safety of chemicals for agricultural use, but several studies have now demonstrated that exposure to neonicotinoids at field-realistic levels can have negative sub-lethal impacts on both honeybees and other bee species (Godfray et al., 2014; Siviter et al., 2018b; Wood & Goulson, 2017). This evidence has led to restrictions in the EU on the outdoor agricultural use of three neonicotinoids (imidacloprid, thiamethoxam and clothianidin) (EFSA, 2018).

Despite the documented sub-lethal effects on bees, neonicotinoid restrictions remain controversial. In most countries outside of the EU, neonicotinoids are still used extensively in agriculture as well as in residential gardens, and in 2018, a letter published in *Science* signed by 232 international scientists called for a global ban (Goulson, 2018). In contrast, some agrochemical representatives have argued that the restrictions are unjust as they are largely based on laboratory studies where bees were exposed to higher dosages than those that occur in agricultural environments (Campbell, 2013). They also stress that there is no field evidence demonstrating a negative effect of neonicotinoid exposure on honeybees (Campbell, 2013; Cressey, 2017). While some recent field studies contradict this view (Tsvetkov et al., 2017; Woodcock et al., 2017), there are broader issues of using honeybees (*A. mellifera*) as the model species to determine pesticide safety for pollinators (Franklin & Raine, 2019). As a largely domesticated species consisting of colonies of thousands of individuals, honeybees have a unique life history compared to other bee species, most of which are solitary, or live in smaller colonies (Ascher & Pickering, 2012).
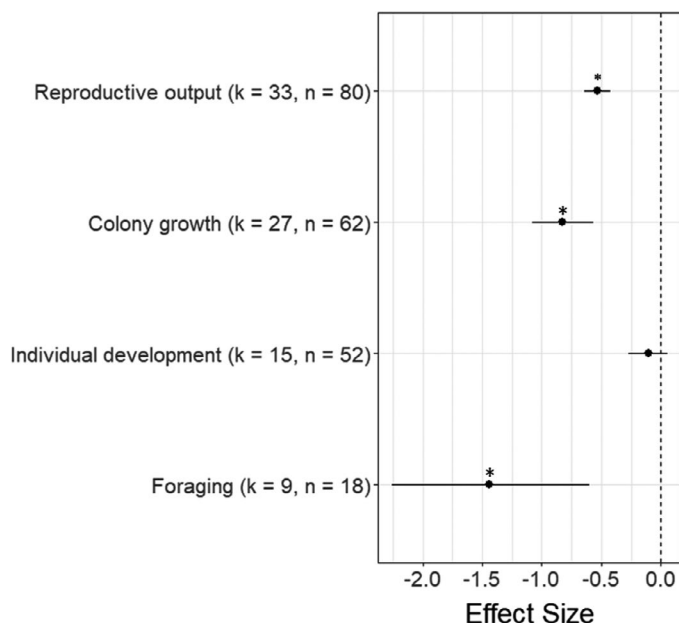
FIGURE 1 Hedges' D (±95% CI) for bees exposed to field-realistic neonicotinoid exposure. Negative values that do not cross zero indicate a significant negative effect of the neonicotinoids on bees, positive values indicate a positive effect. Results that cross zero (e.g. individual development) indicate no difference between control and treatment groups. Asterisks indicate significance at α = 0.05. k = number of papers, n = number of effect sizes. Note that for colony growth *Bombus* is the only genus represented. For a full list of species included within the analysis see Table 1

By focusing the conversation around neonicotinoid restrictions in relation to honeybees, which are more robust to insecticide exposure than other bees (Rundlöf et al., 2015; Woodcock et al., 2017), the potential impact of neonicotinoid exposure on bees more broadly is currently neglected.

Here we conducted a systematic literature search and meta-analysis to assess the potential sub-lethal impact of field-realistic neonicotinoid (imidacloprid, thiamethoxam, clothianidin, acetamiprid) exposure on non-*Apis* bees. Determining field-realism is contentious as regulations and mitigation measures differ between countries (Carreck & Ratnieks, 2014). To standardise field-realism, we based our definition on the maximum estimated concentrations observed in the residue data of nectar and pollen of treated plants from a recent systematic review (Table S1) (Zioga et al., 2020). While this represents what bees can be exposed to, it may not represent what they are typically exposed to. Therefore, we confirmed that results held with a more conservative definition of field realism, using average concentrations found in the nectar and pollen of plants (see methods). In field and semi-field experiments where crops were treated with neonicotinoids, we only included studies where label recommendations were followed. Studies that exposed bees to concentrations higher than this definition of field realism were not included within the analysis. Our analysis focused on four key variables that are known to have important consequences for bee health: (1) reproductive output; (2) colony growth (only relevant for social bees); (3) individual development (e.g. individual growth or body size) and (4) pollen foraging (Gill et al., 2012; Imhoof & Schmid-Hempel, 1999; Kim, 1997). We extracted 212 effect sizes from 53 papers. We first established whether there was an overall negative impact of neonicotinoid exposure on each variable and then tested three additional moderators that we expected could be possible sources of heterogeneity. First, we assessed if the effects of neonicotinoids were consistent across bee genera since there is significant variation across bees in their life-history strategies and ecology. We also considered experiment type (field, semi-field or laboratory) in our analysis, to determine if certain types of experiments were more likely to detect effects than others (N.B. bees in all experiments included were exposed to neonicotinoids at field-realistic levels, even if the experiment was conducted in a laboratory or under semi-field conditions (see Table S1 and (Zioga et al., 2020)). Finally, specific neonicotinoids differ in their toxicity and restrictions (Simon-Delso et al., 2015; Wood & Goulson, 2017), so we also determined whether sub-lethal effects on non-*Apis* bees were consistent across different neonicotinoid types. In summary, we addressed four questions regarding the effects of neonicotinoids on non-*Apis* bees:

1. Does the existing evidence demonstrate significant sub-lethal effects at field-realistic levels?
2. Are these effects consistent across bee genera?
3. Are the effects consistent across field, semi-field and laboratory experiments?
4. Are the effects consistent across different neonicotinoid pesticides?

TABLE 1 Number of effect sizes for bee species across different data categories

	Reproductive output	Colony growth	Individual development	Foraging
Bombus	65	62	16	17
B. impatiens	12	22	2	0
B. lucorum	0	2	2	0
B. occidentalis	1	1	1	0
B. pascuorum	0	2	2	0
B. pratorum	0	2	2	0
B. terrestris	52	33	7	17
Eucera	2	0	0	1
E. pruinosa	2	0	0	1
Megachile	0	0	3	0
M. rotundata	0	0	3	0
Osmia	13	0	31	0
O. bicornis	7	0	12	0
O. cornuta	1	0	1	0
O. lignaria	5	0	18	0
Scaptotrigona	0	0	2	0
S. aff. *depilis*	0	0	2	0
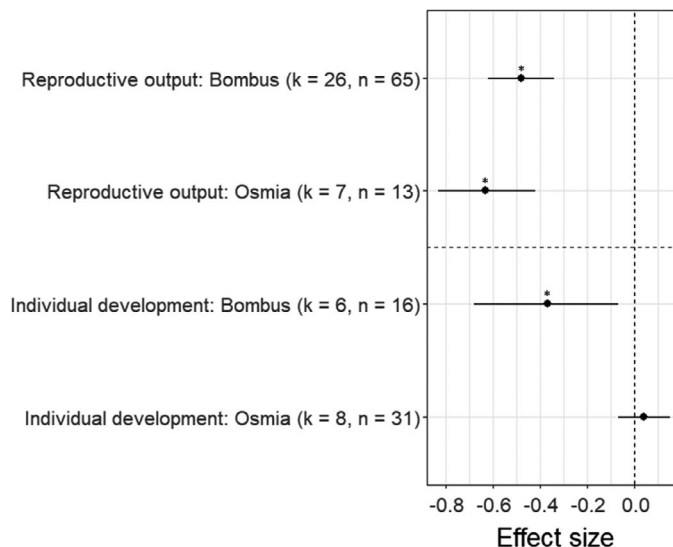
FIGURE 2 Hedges' D (±95% CI) for different bee genera exposed to neonicotinoids at field-realistic levels. Minus values that do not cross zero indicate a significant negative effect of neonicotinoids on bees, positive values indicate a positive effect. Results that cross zero indicate no difference between control and treatment groups. Asterisks indicate significance at α = 0.05. k = number of papers, *n* = number of effect sizes. For a full list of species included within the analysis see Table 1

MATERIALS AND METHODS

Literature search

We used Web of Science as our primary search engine, with the search terms ("pesticide*" OR "insecticide*" OR "neonicotinoid*" OR "neonic*" OR "imidacloprid" OR "thiacloprid" OR "thiamethoxam" OR "clothianidin" OR "acetamiprid" OR "dinotefuran" OR "nitenpyram") AND ("bumblebee*" OR "bumble bee*" OR "*Bombus*" OR "wild bee" OR "native bee" OR "*Osmia*" OR "*Megachile*" OR "wild bees" OR "solitary bee" OR "solitary bees" OR "*Scaptotrigona*" OR "stingless bee" OR "*Melipona*" OR "*Plebeia*" OR "mason" OR "squash bee" OR "squash bees" OR "*Peponapis*" OR "*Lasioglossum*" OR "sweat bee" OR "sweat bees" OR "*Frieseomelitta*" OR "*Tetragonisca*" OR "*Andrena*" OR "*Chelostoma*" OR "*Megachile rotundata*" OR "*Nomia melanderi*" OR "*Nomia*" OR "*Eucera pruinosa*" OR "*Eucera*" OR "*Nannotrigona*" OR "sting less bee*" OR "sting-less bee*" OR "*Trigona*" OR "*Megachilidae*" OR "*Andrenidae*" OR "*Halictidae*" OR "*Colletidae*" OR "*Stenotritidae*" OR "*Melittidae*" OR "*Anthophila*") AND ("health" OR "sub-lethal" OR "sub lethal" OR "reproductive output" OR "reproduction" OR "cost" OR "fitness" OR "brood" OR "ovary development" OR "colony growth" OR "queen survival" OR "foraging" OR "performance" OR "mass" OR "mortality" OR "survival" OR "species richness" OR "monitoring" OR "assessment" OR "behavior" OR "behaviour" OR "foraging" OR "pollen" OR "toxicity" OR "pathogen"). The search was conducted on 20/04/2021 and yielded 604 results. We crosschecked this against reference lists from (1) relevant narrative reviews (Alkassab & Kirchner, 2017; Barbosa et al., 2015; Blacquière et al., 2012; Pisa et al., 2015, 2017) (2) a recent meta-analysis (Arena & Sgolastra, 2014), (3) a systemic review (Lundin et al., 2015) and (4) two evidence restatements (Godfray et al., 2014, 2015). This yielded one additional paper (see Figure S1 for PRISMA flowchart).

Inclusion criteria and data extraction

To be included within our analysis, experiments had to expose non-*Apis* bees to a neonicotinoid insecticide at a field-realistic dosage and compare them to a control (untreated) group (Table S1 (Zioga et al., 2020)). We addressed the effects of neonicotinoids on bees using four dependent variable categories: reproductive output, colony growth (social bees only), individual development and foraging. Reproductive output included measures of unmated females/queens, male and brood production; colony growth included measures of colony weight, size and number of workers in the nest as well as food stores; individual development included data relating to bee size, individual weights or ovary development and foraging performance included data relating to bee pollen foraging (for a full list of all response variables considered see Table S2). We only included pollen foraging (as opposed to nectar foraging) in our analysis as this (1) ensured that bees were true foragers and were not leaving the nest to perform other colony functions such as corpse removal (Munday & Brown, 2018) and (2) pollen is collected primarily to feed developing larvae, which will likely have a direct effect on reproductive output (Pereboom, 2000). In cases where there were multiple dependent variables per category, a random number generator was used to
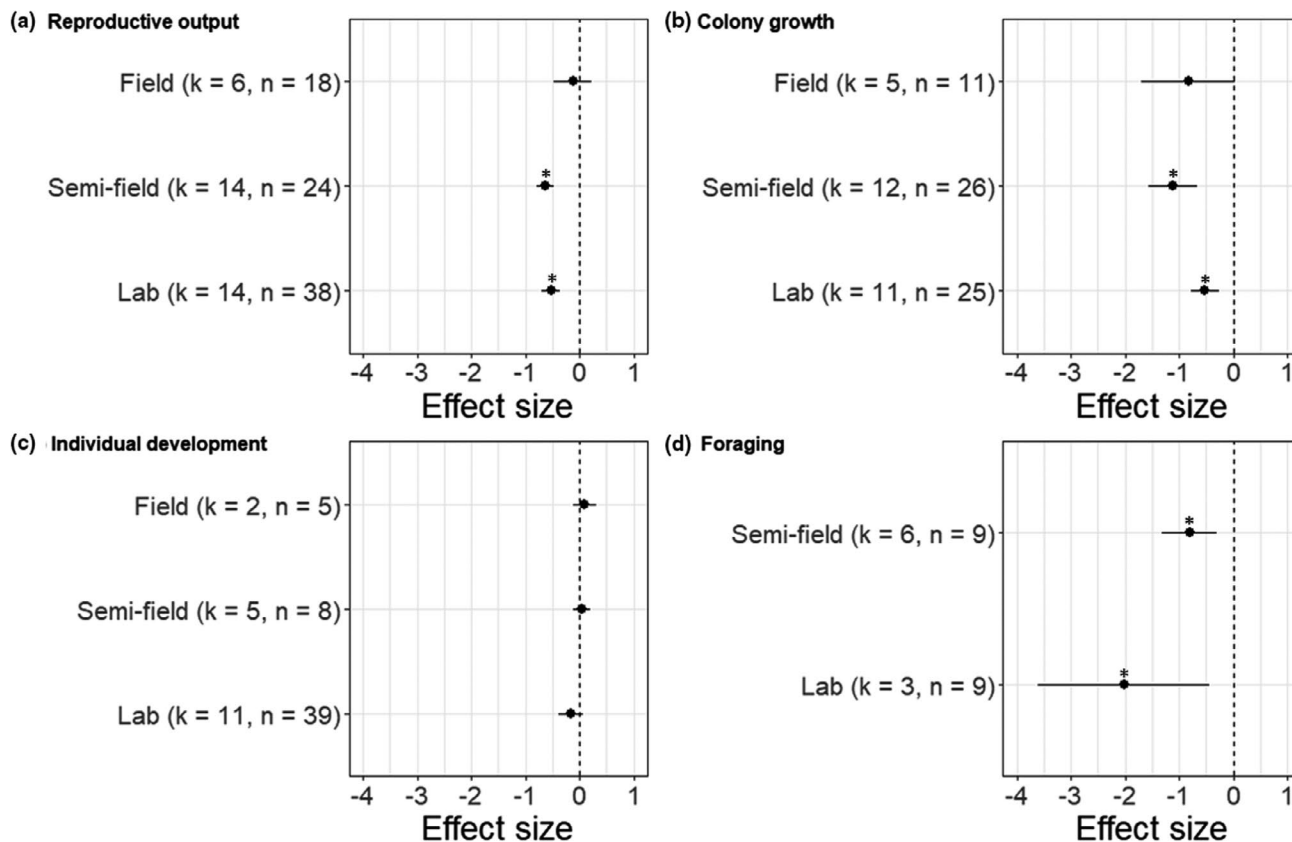
FIGURE 3 Hedges' D (±95% CI) for bees exposed to neonicotinoids at field-realistic levels across different experiment types. Minus values that do not cross zero indicate a significant negative effect of neonicotinoids on bees, positive values indicate a positive effect. Results that cross zero indicate no difference between control and treatment groups. Asterisks indicate significance at α = 0.05. k = number of papers, *n* = number of effect sizes

determine which variable was extracted unless otherwise stated. For data relating to reproductive output, we prioritised data concerning both female and male production. In cases where both female and male data were provided, we combined this data to generate a single value. For data relating to colony growth, we prioritized using the number of workers in the colony as the dependent variable over other variables measured. For all effect sizes generated (see Results) we recorded the bee species, neonicotinoid type, dose and experiment type (field, semi-field or laboratory). Experiments were classified as semi-field experiments when at least one part of the experiment was conducted in a laboratory or a cage (e.g. Chan & Raine, 2021; Ruddle et al., 2018; Whitehorn et al., 2012)). We did not include data regarding toxicity and mortality as this was the topic of a previous meta-analysis (Arena & Sgolastra, 2014).

For all data that met our criteria for inclusion, we aimed to extract the means, SD and n values. In cases when the relevant information was not in the text, or attached as raw data, we extracted data from figures using the website WebPlotDigitizer (https://apps.autom eris.io/wpd/). In cases where this was not available, we contacted authors to request data. We did not include data if there was no obvious control group, if

the dosages used were higher than field-realistic levels (see Table S1) or if the samples size for any treatment group was less than 1 (making it impossible to calculate Hedges' d). When extracting data from field studies, we considered the sample size to be the number of fields (rather than the number of colonies placed around or on treated fields).

We were able to extract data from 53 papers published between 2000 and April 2021, resulting in 212 effect sizes (reproductive output *n* = 80, colony growth =*n* = 62, individual development =n = 52, foraging *n* = 18, see Figure S1 for PRISMA flowchart and Table S3 for a full list of all papers included).

Statistical analysis

The analysis was conducted in R (version 3.5.2) using the *Metafor* package (Viechtbauer, 2010).

All data categories (reproductive output, colony growth, individual development and foraging) were analysed separately. The standardised mean difference between control and treatment groups for each data point was calculated using the 'escalc' function. Fitted-random effect models were used to calculate the
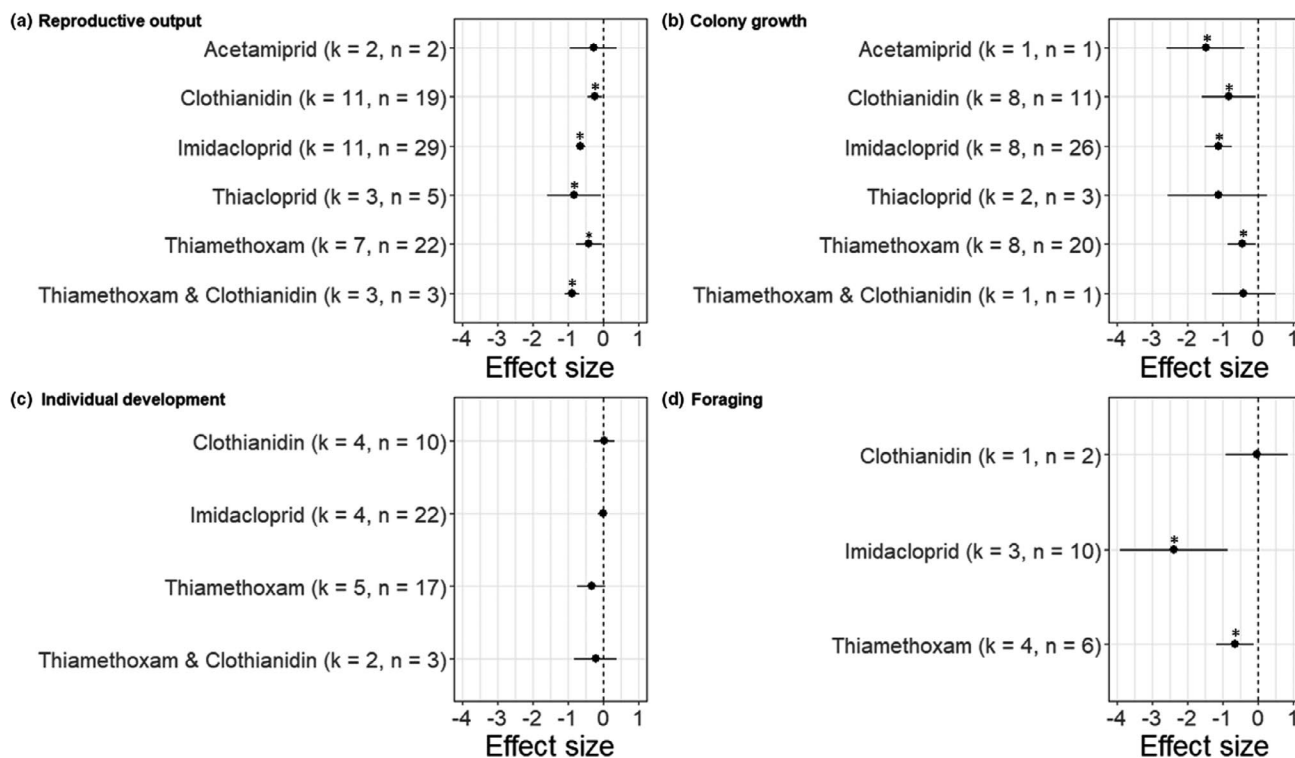
FIGURE 4 Hedges' D (±95% CI) for bees exposed to different neonicotinoids. Negative values that do not cross zero indicate significant a negative effect of neonicotinoids on bees, positive values indicate a positive effect. Results that cross zero indicate no difference between control and treatment groups. Asterisks indicate significance at $\alpha = 0.05$. k = number of papers, *n* = number of effect sizes

overall means and 95% confidence intervals for each data category.

Meta-regression was used to explore sources of heterogeneity (variation) in each data set. Bee genus, neonicotinoid type and experiment type were included as moderators (fixed factors) for the reproductive output, individual development and foraging data sets. Bee species (rather than genus) was included when analysing colony growth (as all data were from *Bombus*). Originally, we had planned to include exposure type within the analysis (chronic vs. acute exposure), but most of data gathered were from chronic exposure experiments (chronic *n* = 209 compared with acute exposure *n* = 3), making formal analysis redundant. As there were often multiple data sets extracted from the same paper, 'paper source' was included in each model as a random factor.

To test for any potential bias in the data sets, we conducted a trim-and-fill analysis to estimate the number of 'missing' studies (Koricheva et al., 2013) in each data category (Figures S2 & S3). We found that for bee reproductive output and individual development data sets, the analysis predicted that there were studies missing showing a negative effect of neonicotinoid exposure on both data categories (Figure S2 and Figure S3). When the means were re-calculated to include the missing studies, we found negative effects on both reproductive output and individual development (See Figures S2 and S3 for funnel plots; reproductive

output, d = −0.58, CI = −0.70 to −0.46; individual development, d = −0.29, CI = −0.46 to −0.13). This suggests that our overall results will underestimate the potential impact of neonicotinoid exposure on reproductive output and individual development (Figure S3, see Results for further comparison). In the current analysis, we used the maximum concentrations of neonicotinoids that have been observed in the residue data of nectar and pollen of treated plants (Table S1) (Zioga et al., 2020). However, since there is substantial variation in the plants that different bee species visit, their level of exposure via foraging will also vary. Therefore, we also repeated our analysis using a more conservative definition of 'field realistic', where the average, rather than the maximum concentration of neonicotinoids in plants was used as the upper limit (see Table S4). This resulted in 55 effects sizes being removed but did not change the results (compare Figure 1 to Figure S4). We also checked for potential outliers within each data set and found that no effect sizes had a Cook's distance of <1; thus potential outliers were not removed. Visual examination of funnel plots (Figure S2) showed three potential outliers in the foraging data. While it is not clear why these data were outliers, to determine whether they were biasing the results, we re-ran the analysis without these data and found the same results (foraging, d = −0.76, CI = −1.12 to −0.39, *n* = 15, see Results section for comparison).

RESULTS

Do neonicotinoids have sub-lethal effects on non-*Apis* bees?

We found that the available data on the sub-lethal effects of neonicotinoids on non-*Apis* bees were taxonomically biased: most of the effect sizes were from studies using bumblebees (*Bombus spp.*; $n = 160$) and mason bees (*Osmia spp.*; $n = 44$). There were two effect sizes from stingless bees (genus *Scaptotrigona*), three from squash bees (*Eucera*) and three leafcutter bees (*Megachile*) (See Table 1 for a full list of all species). *Bombus* was the only genus represented in the colony growth data set.

We found that field-realistic neonicotinoid exposure had a significant negative impact on the reproductive output and foraging of non-*Apis* bees (Figure 1, reproductive output, $d = -0.53$, 95% Confidence intervals (CI) $= -0.64$ to -0.42, $n = 80$; foraging, $d = -1.44$, CI $= -2.26$ to -0.60, $n = 18$), although we found no overall effect on individual development (Figure 1, individual development, $d = -0.10$, CI $= -0.27$ to 0.06, $n = 52$). We also observed significant negative effects on bumblebee colony growth (colony growth, $d = -0.83$, CI $= -1.08$ to -0.57, $n = 62$). Within our analysis, heterogeneity was high for all categories (reproductive output, $I^2 = 27.47\%$; colony growth $I^2 = 82.36\%$; individual development, $I^2 = 79.01\%$; bee foraging, $I^2 = 91.69\%$) and so we used meta-regression to test the effect of potential moderators (see Methods for full details). The moderators (genus or species, pesticide type, experiment type) had a significant influence on heterogeneity for the reproductive output ($p < 0.02$) and individual development ($p < 0.01$) but not the colony growth ($p = 0.59$) or foraging ($p = 0.1$).

Were sub-lethal effects consistent across genera (*Bombus* and *Osmia*)?

While we intended to compare the effects of neonicotinoids across a greater taxonomic breadth, 75% of effect sizes generated were from *Bombus*, 21% from *Osmia*, 1.5% from *Eucera*, 1.5% from *Osmia* and 1% from *Scaptotrigona*. As the sample sizes for genera beyond *Bombus* and *Osmia* were low here, we focus on the comparison between *Bombus* and *Osmia* (see Figure S5 for all genera).

Neonicotinoids had negative effects on *Bombus* and *Osmia* reproductive output (reproductive output, genus, $p = 0.82$), but we found contrasting effects on *Bombus* and *Osmia* individual development (individual development, genus, $p < 0.001$) (Figure 2). Neonicotinoid exposure impaired bumblebee and *Osmia* reproductive output (Figure 2: *Bombus* reproductive output, $d = -0.48$, CI $= -0.62$ to -0.34, $n = 65$; *Osmia* reproductive output,

$d = -0.63$, CI $= -0.83$ to -0.42, $n = 13$) but while neonicotinoid exposure impaired bumblebee individual development ($d = -0.37$, CI $= -0.68$ to -0.07, $n = 16$) there was no detectable effect on *Osmia* individual development (Figure 2; individual development, $d = 0.04$, CI $= -0.07$ to 0.15, $n = 31$).

Were sub-lethal effects consistent across experiment type?

Whether neonicotinoids affected bee reproductive output depended on whether the experiment was conducted in the laboratory, semi-field or in the field (reproductive output, experiment type: $p = 0.03$). Neonicotinoid exposure had an overall negative influence on bee reproductive output in laboratory and semi-field experiments but not in field experiments (Figure 3, field: $d = -0.12$, CI $= -0.47$ to 0.22, $n = 18$; semi-field: $d = 0.63$, CI -0.78 to -0.48 $n = 24$; lab: $d = -0.52$, CI -0.70 to -0.35, $n = 38$). However, a trim-and-fill analysis indicated a bias in the field data published (Figure S6). As with the overall effects (see methods), when 'missing' studies were included after a trim-and-fill analysis was conducted there was an overall negative effect of neonicotinoid exposure in field studies (Figure S6, Field, $d = -0.38$, CI $= -0.72$ to -0.03). This confirms that the currently available data are likely underestimating the potential impact of neonicotinoids on non-*Apis* bees in field trials. The effects of neonicotinoid were similar across experiment type for colony growth (experiment type, $p = 0.02$), bee individual development (experiment type, $p = 0.55$) and bee foraging (experiment type, $p = 0.42$) (Figure 3).

Were sub-lethal effects consistent across neonicotinoid type?

The most commonly tested neonicotinoid was imidacloprid ($n = 87$), followed by thiamethoxam ($n = 65$), clothianidin ($n = 42$), thiamethoxam and clothianidin in combination ($n = 7$), thiacloprid ($n = 8$) and acetamiprid ($n = 3$). We found no available data on the neonicotinoid dinotefuran. The type of neonicotinoid that bees were exposed to significantly affected reproductive output (neonicotinoid type, $p < 0.001$), with exposure to imidacloprid being more detrimental than clothianidin and thiamethoxam (Figure 4, imidacloprid, $d = -0.64$, CI $= -0.77$ to -0.51, $n = 29$; thiamethoxam, $d = -0.4$, CI $= -0.77$ to -0.02, $n = 22$; clothianidin, $d = -0.23$, CI $= -0.43$ to -0.03, n $=19$). The specific neonicotinoid that bees were exposed to did not influence any other variables we addressed (Figure 4; neonicotinoid type, colony growth, $p = 0.32$; bee individual development, $p = 0.55$; bee foraging, $p = 0.11$).

DISCUSSION

Policy makers require synthesised data to inform legislation. Here, we combined data from the last two decades and confirmed that field-realistic neonicotinoid exposure reduces the reproductive output of non-*Apis* bees, which will likely contribute towards wild bees declines (Baron et al., 2017; Woodcock et al., 2016). Neonicotinoid exposure also impaired the colony development and foraging performance of bumblebees, which offers a potential mechanism driving the observed downstream effects on reproductive output. We also found genus-level differences, with neonicotinoids impairing *Bombus*, but not *Osmia* individual development, highlighting the limitations of generalising results across bee genera (Franklin & Raine, 2019; Siviter & Muth, 2020). Our results confirm that policies that restrict and reduce neonicotinoid use will likely benefit bee populations.

Our analysis demonstrated that most of the existing studies with non *Apis*-bees have been conducted with bumblebees (*Bombus*) (Figure S5). Both *Apis* and *Bombus* are highly social, and so are not representative of bees more broadly, most of which are solitary (Ascher & Pickering, 2012). This may have important implications for the impact of pesticides. For example in eusocial or social species, if an individual worker is exposed to an insecticide, the colony may buffer the effects of worker loss. In contrast, the survival of developing larvae from a solitary species is dependent on a single individual. Beyond degree of sociality, many other life-history variables may lead to differences in the potential exposure routes and consequences of pesticide exposure, such as nesting biology (Franklin & Raine, 2019; Gradish et al., 2019; Sgolastra et al., 2019). While in the current meta-analysis we estimated 'field realistic' exposure based on bees' foraging exposure, ground-nesting bees are also likely exposed via soil, where neonicotinoids have been found in substantially higher concentrations than in floral nectar and pollen (Chan et al., 2019). Thus, current estimates may underestimate exposure for native bees with diverse ecologies. The existing data show negative effects on the solitary, ground-nesting bees *Eucera*, critical for squash pollination, yet more data are needed to compare these effects to those seen in *Bombus* and *Osmia*. While neonicotinoid exposure impaired both *Bombus* and *Osmia* reproductive output, only *Bombus* individual development was impaired. Most of the *Osmia* data considered the potential impact of neonicotinoids on bee weight and/or size (30/31 effect sizes). We cannot confirm the mechanism driving these contrasting effects on *Osmia* reproduction and individual development, but *Osmia* may take longer to provision larvae when exposed to neonicotinoids (Jin et al., 2015), meaning fewer provisions overall. As such, it is possible that *Osmia* respond to fewer provisions by investing in fewer offspring overall, rather than providing less per offspring. Regardless of mechanism, our results demonstrate the limitations

of generalising results across genera and highlight the importance of broadening the taxa examined in future research (Figure S5) (Franklin & Raine, 2019). While *Bombus* and *Osmia* have been the focus of research due to their commercial availability, efforts should be made to develop new model species for assessing the impact of pesticides on wild bees more broadly, especially solitary, ground nesting bees which are poorly represented in the current literature (but see Chan et al., 2019; Chan & Raine, 2021)).

One criticism of research on neonicotinoid effects on bees, and in turn, the ban on neonicotinoid use in the EU, is that bees are exposed to concentrations of insecticides in laboratory studies at higher doses than those that would occur under field conditions (Campbell, 2013; Carreck & Ratnieks, 2014; Cressey, 2017). Here, we reclassified studies as field-realistic based on up-to-date residue data (see Table S1 and Zioga et al. (2020)). We found that neonicotinoids had significant, sub-lethal effects on non-*Apis* bees, even when taking a more conservative definition of field-realism (Table S4). These effects were largely consistent across experiment type, with one exception. We found significant negative effects of neonicotinoid exposure on bee reproductive output in laboratory and semi-field experiments, but not in field experiments. This could suggest that laboratory, and semi-field-based studies overestimate the potential impact of insecticides on non-*Apis* bees, possibly because bees are often exclusively feeding on contaminated nectar and pollen. An alternative explanation is that field studies may not have adequate pesticide-free controls to serve as a baseline to which the impacts of pesticides can be compared. One of the difficulties of conducting large-scale field experiments is the contamination of control fields, as bees foraging next to 'untreated' fields are often exposed to various agrochemicals (Campbell et al., 2016; Goulson, 2015; Woodcock et al., 2017). As pesticide residue analysis is expensive, it may: (1) not occur at all; (2) be limited in time; or (3) be limited to just the target insecticide, which reduces costs but means potential contamination of control sites may be missed. Taken together, this means that the control groups do not always function as true controls, thus limiting the interpretation of field studies. Furthermore, field studies are also often poorly replicated, and in some cases only contain one field per treatment group (Goulson, 2015; Sterk et al., 2016). Finally, the results of our trim-and-fill analysis confirmed that the current data from field studies may be underestimating the potential impact of neonicotinoid exposure on non-*Apis* bees which suggests future carefully controlled field studies should be conducted.

In addressing whether the observed effects were consistent across different types of neonicotinoids, we found largely similar effects across the different insecticides but some, such as acetamiprid and dinotefuran, were either absent, or poorly represented within our analysis. Research with honeybees has demonstrated

sub-lethal effects of both acetamiprid and dinotefuran (Liu et al., 2019; Shi et al., 2020), but whether these effects are consistent across other bee species is unclear. Given that acetamiprid is still licenced for use in the EU, and that both insecticides are used globally, more research on their impact on non-*Apis* bees is clearly required. Similarly, our data demonstrated a geographic bias towards North American and European bees. Given that the risk of neonicotinoid exposure in tropical regions is high (Bonmatin et al., 2019, 2021), and the importance of wild bees for pollination of crops such as chillies and coffee (Jha & Dick, 2010; Landaverde-González et al., 2017), future research should focus on understanding the potential impact of neonicotinoid exposure on non-*Apis* bees in tropical regions (Jamieson et al., 2019).

Our results support the view that restrictions on neonicotinoid use will benefit wild bee populations. However, intensive agriculture is still heavily reliant on insecticides for controlling insect pests and bans on neonicotinoid use has increased the demand for replacement insecticides. The development of novel systemic insecticides, such as sulfoxaflor and flupyradifurone, that have a similar mode of action to neonicotinoids, offer a direct replacement for neonicotinoids (Brown et al., 2016). While less is known about these novel insecticides, they can impair bee foraging behaviour (Hesselbach et al., 2020; Tong et al., 2019) (but see (Siviter et al., 2019)), reproductive output (Siviter et al., 2018a, 2020b) and they can also increase bee mortality at field-realistic levels (Siviter et al., 2020a; Tosi & Nieh, 2019) (recently reviewed in (Siviter & Muth, 2020)). Therefore, while our results confirm that bans on neonicotinoid use will likely benefit wild bee populations, they will only be successful if paired with (1) changes to the agrochemical regulatory process, that ensures novel insecticides do not have a similar sub-lethal effects on non-*Apis* bees and (2) a reduction in intensive agriculture, and a move towards an integrated pest management approach that promotes biological control, and reduced insecticide use (Colin et al., 2020; Siviter & Muth, 2020). A failure to radically change food production, and agrochemical regulation, will result in a continued decline in bee populations that we rely on for functioning eco-systems.

COMPETING INTERESTS

The authors declare they have no competing interests.

AUTHORS' CONTRIBUTIONS
H.S and S.K.R conceived the idea independently before collaborating on the manuscript. H.S conducted the literature search, data extraction, analysis and wrote the first version of the manuscript. H.S, S.K.R and F.M contributed to subsequent drafts.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.