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RESEARCH ARTICLE

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Impacts of multiple pollutants on pollinator activity in road verges

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Abstract

1. To tackle pollinator declines, there is a major need to increase the quantity of flower-rich habitats. Road verges offer one such opportunity but are exposed to diverse forms of pollution from roads and road traffic.
2. We carried out a broad initial assessment to establish if and how pollution affects the quality of road verges as pollinator foraging environments. We assessed the spatial distribution of pollution, flowers and pollinators in road verges, then used field experiments to simulate and measure the impacts of four ubiquitous and little studied forms of road pollution (noise, turbulence, dust and metals) on pollinator densities and foraging behaviour.
3. We found that pollinators in road verges were exposed to noise, turbulence, dust and metal pollution, which decreased with distance from the road edge but, with the exception of turbulence, extended more than 8 m into road verges.
4. Pollinator densities were lower closer to the road edge—particularly within first 2 m (55% lower than at 7–9 m)—where pollution is greatest. This was despite a similar density and species richness of flowers.
5. Simulated turbulence deterred pollinators by causing intermittent disturbance (reducing visit duration by up to 54%), and some pollinator taxa preferentially avoided concentrations of metals that were more frequently found in flowers within 2 m of roads (resulting in up to 75% fewer visits), while noise and dust had no apparent effect.
6. *Synthesis and applications*. Pollinators in road verges are exposed to many forms of pollution, and we found impacts of roadside-realistic levels of turbulence and metals on pollinator densities and foraging behaviour. Although the findings suggest that road verges are largely suitable for pollinator conservation, management enhancements should prioritise areas more than 2 m from the road edge, and verges along roads with relatively lower traffic densities.

KEYWORDS

bees, heavy metals, highway, insects, noise, pollution, roadside, traffic

1 | INTRODUCTION

Habitat loss is a major cause of pollinator declines (Potts et al., 2016). Road verges have been proposed as part of the solution (Plantlife, 2020) because they collectively cover a significant area of land (e.g. an estimated 270,000 km^2—0.2% of land—globally; Phillips et al., 2020), can be hotspots of flowers and pollinators, and are managed by relatively few organisations (i.e. governments and associated highways authorities; Phillips, Bullock, et al., 2020; Phillips, Wallace, et al., 2020). However, pollinators in road verges are exposed to diverse forms of pollution from roads and road traffic, including noise, light, exhaust fumes, dust and metals (Forman et al., 2003). The impacts of road pollution on pollinators are poorly understood (Phillips, Wallace, et al., 2020), but will determine if, when and where it is appropriate to use road verges for pollinator conservation.

In the first instance, pollinators might avoid polluted areas—reducing their exposure, but also thereby restricting the quality of such areas as foraging environments. Otherwise, pollinators exposed to pollution might be affected directly due to mortality or sub-lethal effects, or indirectly due to pollution-related changes in the quantity, quality and attractiveness of floral resources. If pollinators are not deterred by road pollution, and (sub-)lethal effects are sufficiently large, road verges may constitute an ecological trap (Hale & Swearer, 2016). In general, road pollution and associated impacts will increase with traffic density and decrease with distance from the road, and some observational studies have reported fewer pollinators closer to roads (Corcos et al., 2019; Phillips et al., 2019) and along roads with greater traffic densities (Martin et al., 2018; Phillips et al., 2019). However, it is difficult to disentangle the impact of pollution from other possible causes. For example, greater traffic densities result in more vehicle-pollinator collisions (e.g. Skórka et al., 2015), and areas further from the road edge are likely to be closer to pollinator source habitats (e.g. hedges; Garratt et al., 2017). Furthermore, different forms of pollution may have very different effects on pollinators, but most studies have focused on single forms of road pollution and single pollinator species (Phillips, Wallace, et al., 2020). Here, we investigate four ubiquitous and little studied forms of road pollution: noise, turbulence, dust and metals, which we describe in turn.

Anthropogenic noise, such as that produced by traffic, results in behavioural and physiological changes in many animal species (Kight & Swaddle, 2011), but few studies have considered insects or pollinators, despite many taxa (including Hymenoptera, Diptera and Lepidoptera) being capable of hearing within the main frequency spectra of much anthropogenic noise (Morley et al., 2013). Noise pollution can affect arthropod abundances (Bunkley et al., 2017), but only one study has considered insect pollinators specifically: Davis et al. (2018) found that a 2-hr exposure of monarch butterfly *Danaus plexippus* larvae to recorded traffic noise increased heart rates, while 7- or 12-day exposure resulted in habituation.

Traffic-generated turbulence at the road edge (gusts of wind equivalent to an average wind speed of approximately 16 km/hr; Bani-Hani et al., 2018) might disturb pollinators and is likely to make foraging more difficult (Hennessy et al., 2020). One study has considered this. Dargas et al. (2016) found that pollinators were more likely to cease foraging when vehicles passed at greater speeds. This was attributed to turbulence, but it is difficult to exclude other possibilities such as noise and vibrations.

Roads and road traffic produce dust, which is roughly the same size as pollen, accumulates on flowers and has been shown to affect plant reproduction (Jaconis et al., 2017; Waser et al., 2016), and so might affect the attractiveness of flowers to pollinators. Few studies have explored the impacts of roadside dust on invertebrates (but see Łukowski et al., 2018), let alone pollinators. Roadside dust also contains metals (e.g. cadmium, copper, lead, antimony and zinc; note that we use the term 'metals' for simplicity to include heavy metals, other metals and metalloids) from the wear and tear on road vehicles and road surfaces, that accumulate in roadside soils and vegetation (Werkenthin et al., 2014). Studies have found that road proximity and density are often positively correlated with elevated concentrations of metals in insects (e.g. Urbini et al., 2006; Zhou et al., 2018). Many metals are toxic to insects at sufficient concentrations (Di et al., 2016; Muñoz et al., 2015; Rothman et al., 2020), and they might affect the attractiveness of floral resources at much lower levels. Moroń et al. (2012) found relationships between higher concentrations of Cd, Pb and Zn and reduced bee diversity and abundance, and studies on *Bombus impatiens* bumblebees found that concentrations of Pb were negatively related to colony growth (Sivakoff et al., 2020) and that flowers containing 100 ppm Al in nectar were visited for shorter durations (though no effect of 100 ppm Zn; Meindl & Ashman, 2013). Few studies have tested impacts of roadside-realistic concentrations of metals on pollinators, although studies on monarch butterflies found that 10–66 ppm Zn found in roadside milkweeds (larval host plants; Mitchell et al., 2020) did not affect caterpillar survival (Shephard et al., 2020). This is a major research gap, given that anthropogenic sources of metal pollution are widespread, yet few studies have explored potential impacts on pollinators at all, let alone using roadside-realistic levels (Phillips, Wallace, et al., 2020).

In reality, pollinators in road verges are exposed to many different forms of pollution at the same time. But, understanding how each form of road pollution affects pollinators can help to identify road verges (or parts of them) where the most detrimental pollutants are lowest, and can influence future research and measures to mitigate these. It can also inform how the quality of road verges for pollinator conservation might change in the future, for example, with the uptake of ultra-low emission vehicles, which inherently produce less noise and exhaust fumes.

In this study, we explore if and how the quality of road verges as pollinator foraging environments is affected by pollution, focusing on observations of pollinator densities and foraging behaviour as a result of exposure to pollution. We fill a major gap in existing research (Phillips, Wallace, et al., 2020) by considering diverse pollinator taxa and four ubiquitous and little studied forms of road pollution: noise, turbulence, dust and metals. We take a broad, pragmatic approach—aiming to provide an initial, rapid assessment of impacts of these multiple pollutants. This approach is appropriate, given a lack of previous research, to inform road verge management decisions that are currently being made, and to identify the most important avenues for more targeted research on specific pollutants. Specifically, we address the following research questions:

1. What is the spatial distribution of pollution, flowers and pollinators in road verges?
2. How do field-realistic pollution levels affect pollinator densities and foraging behaviour?

2 | MATERIALS AND METHODS

The study was carried out in Cornwall, United Kingdom in 2019 and 2020. First, we used roadside surveys to assess the spatial distribution of pollution, flowers and pollinators in road verges. Second, we used field experiments (away from roads) to simulate each form of pollution separately and measure the impacts on pollinator densities and foraging behaviour to explain the spatial distribution of pollinators observed in road verges. We summarise the materials and methods here, and provide a full version in Appendix S1.

2.1 | Spatial distribution of pollution, flowers and pollinators (roadside surveys)

We surveyed nine road verges to compare the spatial distribution of pollution, flowers and pollinators. Sites were all located in rural landscapes dominated by agriculture, but covered a variety of road types (major roads to unclassified rural roads) and traffic densities (110–1,416 vehicles/hr). Verges were all at least 9-m wide to allow measurements over a range of distances, and were adjacent to an arable or pasture field, separated by a hedge. At each site, we set up four 50-m transects parallel to the road at distances of 1, 3, 5 and 8 m from the road edge. We measured the width of each road verge at distances of 5, 15, 25, 35 and 45 m along the transect and calculated a mean. We measured traffic density by counting the number of vehicles passing by the road verge in either direction for 10 min, on three separate days, between 09.00 and 16.30 hr.

2.1.1 | Pollution measurements

We measured noise, turbulence, dust and metals along each transect, and measured background levels for areas away from roads where required, using the methods summarised in Table 1 (full details in Appendix S1).

2.1.2 | Flower and pollinator surveys

We compared flower and pollinator communities along each transect to explore if they changed across expected pollution gradients. We refer to flower-visiting insects here as ‘pollinators’, although actual pollen transfer was not measured. Surveys took place between 29 April and 22 May 2019, because road verges were cut from late May onwards. Surveys were carried out on days with no rain, temperature at least 12°C, and wind speed less than Beaufort scale 4. Temperature (°C) and wind speed (Beaufort scale)

TABLE 1 Summarized methods for measuring pollution in road verges. Full details are provided in Appendix S1

Variable	Method	Measurements	Frequency	Estimated background level
Noise	Digital sound meter (Voltcraft SL-200): held at chest height and arm's length	Max sound level [dB(A)] when a vehicle (selected at random) passed	15 vehicles/transect (5 vehicle/day × 3 days)	40 dB(A) (Gjestland, 2008)
Turbulence	‘Pollinator swingometer’: a 40 cm plastic stake, with a 180° protractor attached to the top, facing downwards, with a dead pollinator (*Platycheirus* sp. hoverfly, 20 mg) suspended	Relative force exerted by passing vehicle = angle of insect swing to nearest 10°	5 vehicles/transect (on days with low wind (<Beaufort 2)	Zero on the relative scale, as this was the only value measured beyond 3 m from the road edge
Dust	Sticky traps: 40-cm plastic stakes with transparent sticky tape attached to the top, facing the road, left out for 4 days	Relative coverage of dust on sticky trap (0–4), scored using a 5-point scale, where 0 = no visible dust and 4 was extensive visible dust (differences between each point on the scale were apparent with the naked eye)	3 sticky traps/transect	Sticky traps at three locations with similar vegetation, but >50 m from roads
Metals	Mass spectrometry (ICP-MS): A representative sample of flowers collected, freeze dried, ground and tested for metals using mass spectrometry (ICP-MS)	Concentrations (ppm) of Cu, Cd, Pb, Sb and Zn	1 sample/transect	Vegetation at three sites collected from the far edge of an adjacent agricultural field, >50 m from roads

were recorded at the start of each survey. We recorded the identity and total number of each species of flower along transects within 1 m either side (Appendix S1). A floral unit was defined as one or multiple flowers that can be visited by an insect without having to fly between them, following Baldock et al. (2015). We walked each transect in both directions at a steady pace over roughly 10 min and recorded all pollinators within 1 m either side of the transect and 2 m ahead. For analyses, we grouped pollinators into flies (non-syrphid Diptera), hoverflies (Syrphidae), moths (Lepidoptera), bumblebees (*Bombus* spp.), solitary bees (non-*Bombus*, non-*Apis* Apoidea) and sawflies (Symphyta). Butterflies (Lepidoptera), beetles (Coleoptera) and honeybees (*Apis mellifera*) were observed too rarely (<10% of surveys) to carry out formal analyses. We surveyed each transect twice per day, on three separate days.

2.1.3 | Sentinel plants

As few bees were observed during the roadside surveys, we conducted an additional experiment (15–23 July 2019) using sentinel plants to assess bee visitation at different distances from roads, in three of the nine road verges (sites 3, 4 and 7) that had been cut (containing few other floral resources; Appendix S1). We grew 20 plants of *Borago officinalis* (a highly attractive bee foraging plant) in pots. Once flowering, we placed plants out in one of the road verges in five blocks (5, 15, 25, 35 and 45 m along transects), with a plant at each of 1, 3, 5 and 7 m from the road within each block. We waited 24 hr, then observed plants during 5-min periods, carried out three times per plant. During observations, we recorded the number of bees visiting the plant, and for individual bees, recorded the number of flowers visited and the time spent foraging on the plant. Once finished, we collected the plants, watered their foliage to remove possible roadside dust and then repeated the experiment at the other two road verges on different days. We rotated the position of plants within blocks, and of blocks along transects, between sites.

2.2 | Effects of pollution on pollinator activity (pollution experiments)

We carried out four experiments across three non-roadside sites separately to test the effects of ‘medium’ and ‘high’ road-realistic levels of noise, turbulence, dust and metals on pollinator densities and foraging behaviour. Experiments are summarised in Table 2, with additional description below and full details in Appendix S1. While different forms of pollution may have interacting and synergistic effects, we chose to do separate experiments because the methodology required for exposing pollinators to the different pollutants in a realistic way differed between pollutants. Experimental exposure to noise and turbulence was done using wild plant communities, while exposure to simulated roadside dust required potted plans and exposure to metals in nectar required feeders. The noise and turbulence experiments both used Before-After-Control-Impact (BACI) designs because treatments affect surrounding areas so could not be ran simultaneously, whereas the dust and metals choice experiments both used Latin Square designs. Thus, comparisons between pollutants are inferred rather than direct.

2.2.1 | Noise experiment

Traffic noise was recorded next to a busy road and a more typical road (Appendix S2). Sound files were edited to produce experimental treatments (Table 2). We used a BACI design in 1-m^2 wildflower patches, and recorded measures of pollinator density and bumblebee foraging behaviour during 5 min observations before and after the treatment had been applied (Table 2; Appendix S1). We used a different flower patch (with similar flower community) between treatments of the same replicate, with a total of 24 replicates per treatment.

2.2.2 | Turbulence experiment

As for the noise experiment, we used a BACI design in 1-m^2 wildflower patches, recording measures of pollinator density and foraging behaviour during 5-min observation before and after the treatment had been applied, for a total of 24 replicates per treatment. Experimental treatments were blowers that produced a form of intermittent disturbance, comparable to that of turbulence from passing vehicles, which provided similar ‘pollinator swingometer’ measurements to those measured in the roadside surveys (Table 2; Appendix S1). We additionally recorded the behaviour of all bees and flies because simulated noise dissipated beyond the 1-m^2 area, whereas simulated turbulence did not. This meant that measures of pollinator visitation to the 1-m^2 area in the noise experiment reflected deterrence effects, while deterrence effects in the turbulence experiment were primarily limited to pollinator behaviour within the 1-m^2 patch.

2.2.3 | Dust experiment

Plants of *Sinapis arvensis* were grown in pots until flowering. Plants were then split between three locations—two bordering the University campus study site and one bordering the University research field site, each consisting of a road verge and a non-roadside grassland area >50 m from the road (Appendix S1). Roads were two major roads (estimated vehicles/hr = 800–1,000) and a minor road (estimated vehicles/hr = 200–400). At each location, plants were arranged at different distances from the road, according to four experimental treatments (Table 2), which were expected to affect accumulation of roadside dust on plants. Plants were left for 4 days,

TABLE 2 Summarized methods for the experiments measuring the impacts of roadside-realistic levels of pollution on pollinator densities and foraging behavior. Full details are provided in Appendix S1

Pollutant	Experimental design	Treatments	Measurements
Noise	17–24 June 2019 Before-After-Control-Impact • 1-m^2 flower patches • Setup, 1-min wait, 5-min observation (before), experimental treatment applied, 1-min wait, 5-min observation (after) • 24 replicates/treatment	A speaker (Foxpro Fury 2), raised 30 cm from the ground on a table, with the following treatments: • Control 1: speaker turned off • Noise (medium): playback of typical road (6 vehicles/min) • Noise (high): playback of busy road (24 vehicles/min) • Control 2: playback of typical road, with vehicle sounds edited out (0 vehicles/min) The volume was set at a constant level, based on field measurements, so that the sound level reached 85 dB(A) 1 m from the speaker when a vehicle passed on the Noise (high) sound file	For the 1-m^2 area: • Flower species • Number of floral units • Pollinator visits/5 min For individual bumblebees: • Number of flowers visited • Time spent in the 1-m^2 area (s)
Turbulence	24–28 July 2019 Before-After-Control-Impact • 1-m^2 flower patches • Setup, 1-min wait, 5-min observation (before), experimental treatment applied, 1-min wait, 5-min observation (after) • 24 replicates/treatment	A row of three in-line blower fans, arranged at the height of the majority of flowers, with the following treatments: • Control 1: blower turned off • Turbulence (medium): 1 m from typical road (3 vehicles/min: 1 s on, 19 s off cycle) • Turbulence (high): 1 m from busy road (12 vehicles/min: 1 s on, 4 s off cycle) • Control 2: blower turned on, as for Turbulence (high), but facing away from the observation area, controlling for noise, because blowers generated 75 dB(A) of noise 1 m away, and other possible effects of the blower	For the 1-m^2 area: • Flower species • Number of floral units • Pollinator visits/5 min For individual pollinators: • Number of flowers visited • Time spent in the 1-m^2 area (s)
Dust	28 June to 4 July 2019 Latin square • 48 potted plants split across three 5 × 5 m arrays, plants 1 m apart, arrays > 20 m apart • 12 plants/treatment, with 8 × 5 min observations/plant	Potted plants of *Sinapis arvensis*, left for 4 days across three sites, at different distances from the road based on the following treatments: • Control (−): positioned > 50 m from the road • Road 4 m: positioned 4 m from road • Road 1 m: positioned 1 m from road • Control (+): positioned > 50 m from road, but prior to data collection, dusted extensively with roadside dust (collected with a dust pan and brush from edges of the respective road, sieved to exclude particles over 1 mm, then 20 g slowly sieved over the top of the plant over 10 s)	For each plant: • Pollinator visits/5 min For individual pollinators: • Number of flowers visited • Time spent visiting plant (s)
Metals	29–31 July 2020 Latin square • 16 feeders, arranged in a single 12 × 12 m array, feeders 2 m apart • 4 feeders/treatment/day, with 5 × 5 min observations/feeder, and the entire array reset and rearranged each day for 3 days (three array replicates)	Feeders containing a 50% (w/v) aqueous sucrose solution and different concentrations of metals (Cd, Cu, Pb, Sb and Zn), which were determined based on field measurements: • Control: 0 ppm Cd, 0 ppm Cu, 0 ppm Pb, 0 ppm Sb and 0 ppm Zn • HMx1: 0.20 ppm Cd, 17 ppm Cu, 0.46 ppm Pb, 0.15 ppm Sb and 59 ppm Zn. Median values from the field measurements, which are typical for flowers in road verges 3–8 m from the road edge and mostly within background concentrations (Figure 1d–h) • HMx2: HMx1 concentrations × 2 (mean difference between the median and 75% quartile across metals was 1.86). Concentrations are typical for flowers in road verges 1 m from the road edge (Figure 1d–h) • HMx10: HMx1 concentrations × 10 (mean difference between the median and maximum across metals was 9.96). Concentrations are extreme, but still field-realistic and similar to the maximum values measured for flowers in road verges (Figure 1d–h)	For each plant: • Pollinator visits/5 min For individual pollinators: • Time spent visiting feeder (s)

then retrieved and arranged in three Latin square arrays (cut to remove wildflowers). Over the following 2 days, we carried out eight 5 min observations of each plant, observing one quarter of an array at a time (four plants), and measuring pollinator densities and foraging behaviour (Table 2; Appendix S1).

2.2.4 | Metals experiment

As for the dust experiment, we used a choice experiment with Latin Square design. We used experimental feeders arranged in a single experimental array replicated across decay 3 days (Table 2;

Appendix S1). Experimental treatments were 50% (w/v) aqueous sugar solutions containing different concentrations of metals typical of those found on roads and emitted by vehicles (Cd, Cu, Pb, Sb and Zn; Werkenthin et al., 2014), based on field measurements (Table 2). Preparation of experimental solutions is described in Appendix S1. Before the experiment, we put out training feeders containing aqueous sugar solution with a drop of anise oil (a chemical cue)—one in the middle of each of the four quadrants of the array—to attract pollinators to the feeders. After 24 hr, we swapped the feeders for the 16 experimental feeders. We then carried out 5-min observations of feeders, observing four feeders at a time (one of each treatment). This was repeated for a total of five observation rounds per day, with 10 min between rounds. At the end of each day, we retrieved and washed all feeders, and alternated their position and treatment between days, for a total of 3 days.

2.3 | Statistical analyses

All statistical analyses were carried out in R 3.6.1 (R Core Team, 2019) using generalised linear mixed effects models (GLMM; LME4 package; Bates et al., 2015). In all cases, models were initially fitted using Poisson error structure. Fixed effects were scaled (divided by 10 or 1,000) where necessary to allow model convergence. We used the link function that provided the lowest AIC. Residuals were checked to meet model assumptions, and models were tested for dispersion, and for multicollinearity using variance inflation factors, which were <10 in all cases. The significance of the main effects was assessed using Wald χ^2 and the significance of pairwise contrasts was assessed using least-square means (LSMEANS package; Lenth, 2016) and Tukey's adjustment for multiple comparisons. Further details are provided in Appendix S1, and descriptions of each statistical model are provided in Appendix S3.

3 | RESULTS

3.1 | Spatial distribution of pollution, flowers and pollinators (roadside surveys)

Levels of noise, turbulence, dust and metals generally decreased with increasing distance from the road (Figure 1; Appendix S3). Noise was far above background levels at 8 m from the road edge (Figure 1a). Turbulence decreased rapidly, primarily only affecting areas up to 1 m from the road, and was undetectable by 5 m (Figure 1b). Dust decreased with distance from the road but was above background levels at 8 m from the road. Change in metal concentration differed between metals (Figure 1d–i). Pb and Sb were much greater than background concentrations at 1 m. Pb concentrations rapidly decreased beyond 1 m towards background levels, while Sb declined but remained far above background levels at 8 m. Cu and Zn showed a similar but less extreme pattern, and Cd showed no clear trend with distance, although measurements were often greater than background levels, at all distances. Overall, high traffic sites generally had the greatest measurements for all forms of pollution, while low and medium traffic sites were more similar (Figure 1).

During transect surveys, we recorded a total of 121,348 flowers belonging to 46 plant species, and 4,502 pollinators including 23 hoverfly, 18 bee and 7 butterfly species (Appendix S4). Flower density, but not flower species richness, differed with distance from the road edge (Figure 2a,b; Appendix S3), although showed no clear trend and rather reflected differences in flower communities, whereby *Anthriscus sylvestris* (the most abundant flower species) was more common at 0–2 m and 7–9 m than at intermediate distances (Appendix S4). Pollinator densities decreased with increasing proximity to the road edge, with mean pollinator density 11% lower at 4–6 m, 32% lower at 2–4 m, and 55% lower at 0–2 m, compared to densities at 7–9 m (pollinator density $M \pm SE$: 0–2 m 9.34 ± 1.81, 2–4 m 14.33 ± 2.76, 4–6 m 18.63 ± 3.57, 7–9 m 20.96 ± 4.03; Figure 2c; Appendix S3). The number of flower visits showed a similar trend, as did each pollinator taxon, although trends for bumblebees and moths were not significant (Figure 2d–j; Appendix S3). The number of bumblebees visiting sentinel plants of *B. officinalis* also did not differ significantly with distance from the road edge, although the number of flower visits and visit duration per bee were significantly greater at 7 m than nearer to the road (Appendices S3–S4). There was no significant effect of traffic density on the density of any pollinator taxa, although a marginally significant negative effect on solitary bee ($p = 0.093$) and hoverfly densities ($p = 0.073$; Appendix S3). There was a significant positive effect of verge width on hoverfly density, but not on the density of any other pollinator taxa (Appendix S3). Further details of the flower and pollinator communities are provided in Appendix S4.

3.2 | Effects of pollution on pollinator foraging (field experiments)

For the noise experiment, we observed a total of 1,024 pollinators and recorded the foraging behaviour of 233 bumblebees. Simulated traffic noise did not negatively affect pollinator density in the 1-m^2 observation area (Figure 3a). In fact, fly density was significantly greater after exposure to the noise (high) treatment (Appendix S4). However, bee density was also significantly greater after exposure to the Control 2 treatment (Appendix S4) and a non-significant increase was observed in almost all cases in the 'after' period (Appendix S3), so these differences likely result from pollinator densities increasing following initial disturbance while setting up the equipment. There was no effect of noise treatment on bumblebee foraging behaviour (Figure 3b,c; Appendix S3).

For the turbulence experiment, we observed a total of 669 pollinators and recorded the foraging behaviour of 507 individual pollinators (129 bumblebees, 72 honeybees, 51 solitary bees, 172 hoverflies and 83 other flies). Turbulence had no effect on pollinator visitation (Figure 3d; Appendix S4), but significantly reduced the number of flowers visited and the time spent in the 1-m^2 observation

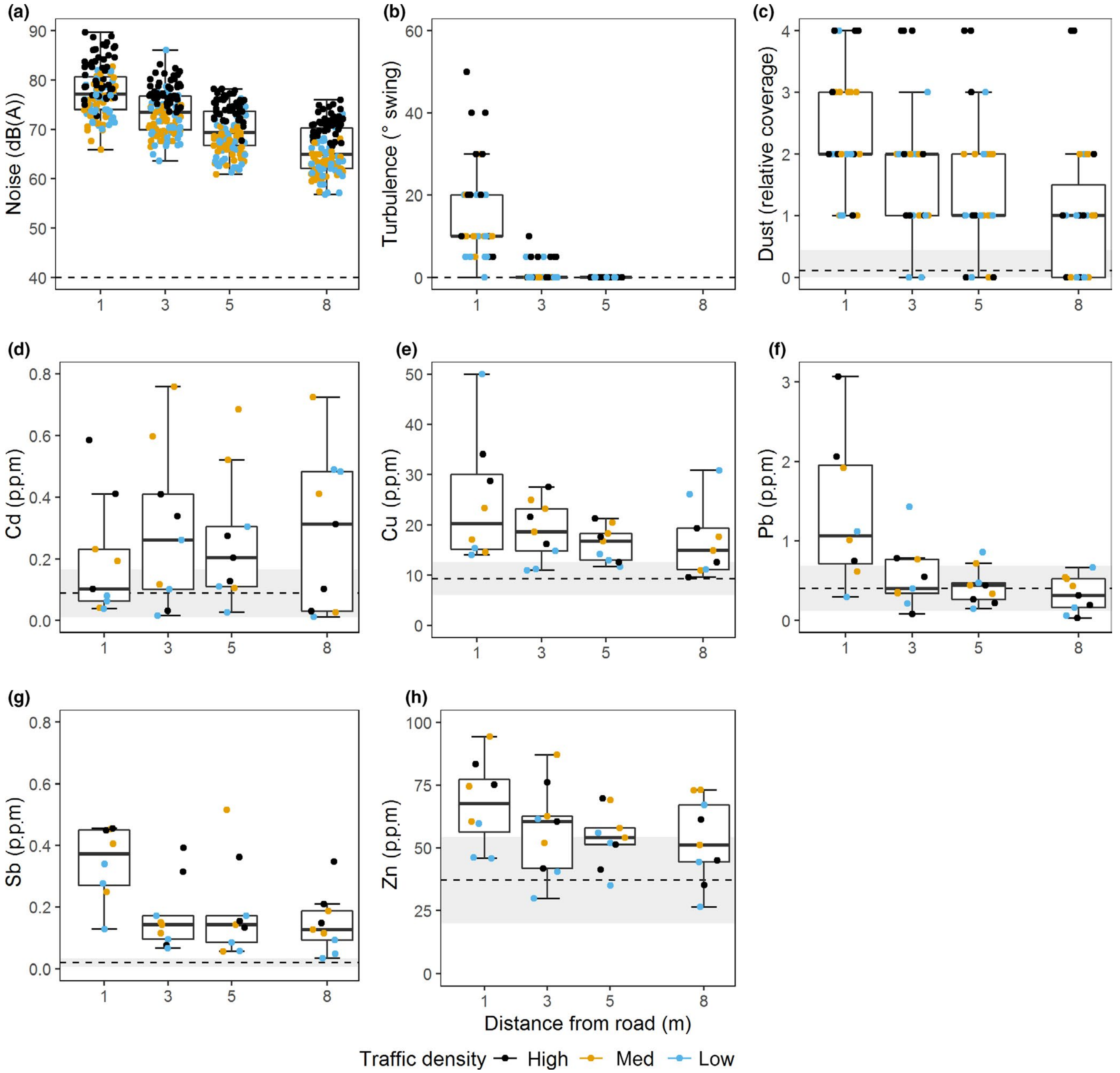


FIGURE 1 The spatial distribution of pollution in road verges: (a) noise (maximum dB(A) when a vehicle passed), (b) turbulence (the maximum angle (°) swing, from vertical, of a suspended pollinator when a vehicle passed), (c) dust (the relative coverage of dust on a piece of sticky tape after 4 days), and (d–h) metals (cadmium, copper, lead, antimony and zinc). Dashed lines in a-b are background levels, while dashed lines with grey areas in c–h are the $M \pm SD$ at control sites (>50 m from roads). See Table 1 for descriptions of methods for measuring each form of pollution. Traffic density (vehicles/hr) categories are: low 100–250, medium 300–400 and high 900–1,500. Data points are jittered for clarity of presentation. Samples sizes (*n*) per boxplot are (a: 135, b: 45, c: 27, d–h: 9). Four metal outliers have been cropped for clarity of presentation (all for distance from the road = 1 m): 192.983 ppm Cu at site 2 (high traffic), 1.456 ppm Sb at site 1 (high traffic), 622.200 ppm Zn at site 2 (high traffic), and 7.959 ppm Pb at site 8 (low traffic). Statistical analyses are provided in Appendix S3

area (Figure 3e,f; Appendix S3). Pollinators visited 21% fewer flowers in the medium turbulence treatment ($M \pm SE$ flowers visited: before 4.00 ± 0.979, after 3.15 ± 0.849) and 47% fewer flowers in the high turbulence treatment (before 5.63 ± 1.209, after 5.63 ± 1.209), and spent an average of 38% less time in the 1-m^2 observation area in the medium turbulence treatment [$M \pm SE$ visit duration (s): before 26.0 ± 6.47, after 16.1 ± 3.71] and 54% less time in the high turbulence treatment (before 34.9 ± 8.09, after 16.2 ± 3.87; Figure 3e,f; Appendix S3).

For the dust experiment, we observed 176 pollinators and recorded the foraging behaviour of 64 pollinators (12 bumblebees, 1 honeybee, 18 solitary bees, 32 hoverflies and 1 other fly). There were no significant effects of dust treatments on pollinator visitation to *S. arvensis* plants (Appendices S3–S4).

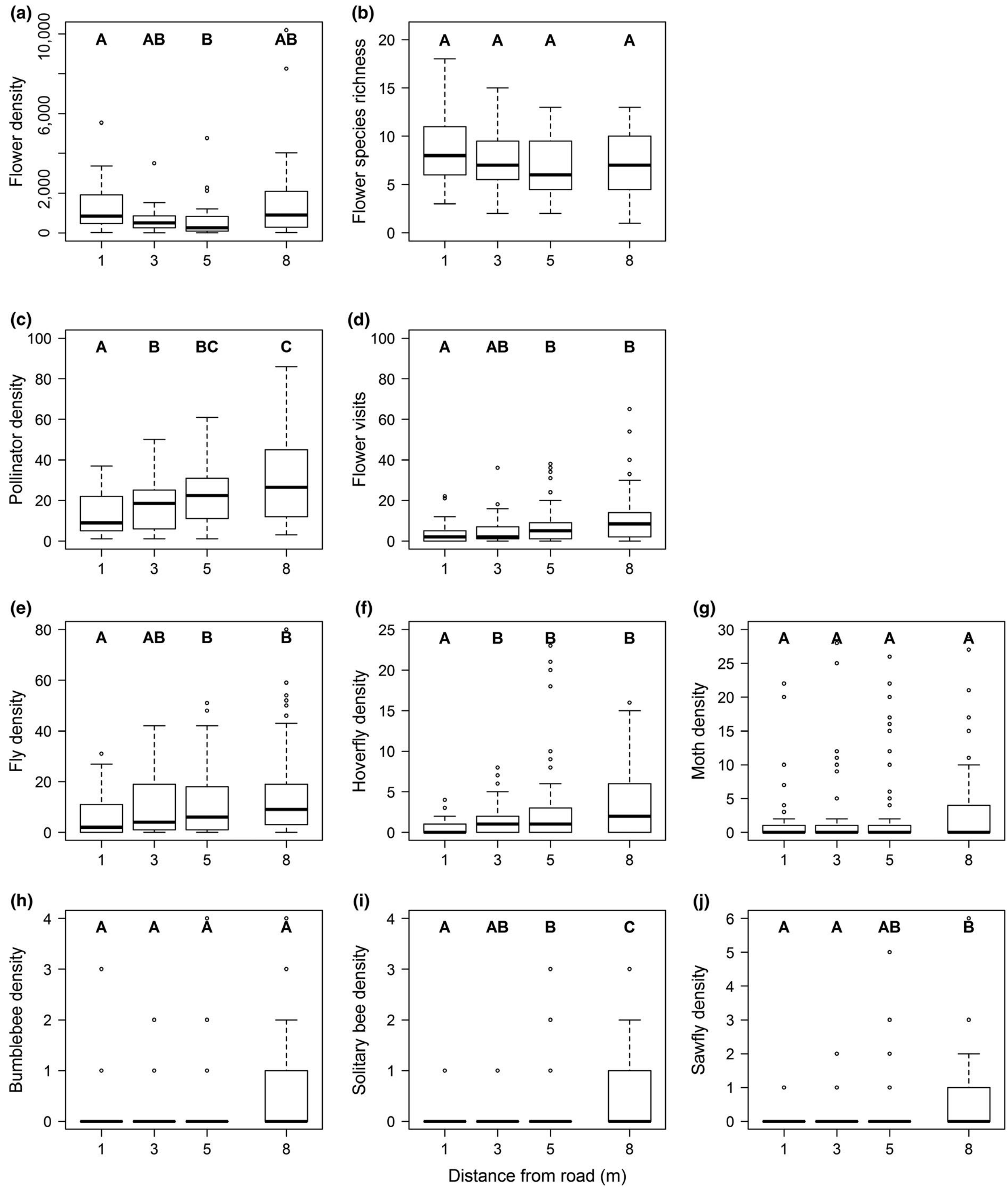


FIGURE 2 The relationship between the distance from the road and (a) flower density, (b) flower species richness, and the density of pollinators for (c) all pollinators, (d) flower visits by all pollinators, and (e–j) different pollinator taxa, along each 50 × 2 m transect in road verges at the nine study sites. Each data point represents a single transect survey, with two pollinator surveys per day at each transect, and three survey days at each of the nine road verge study sites [*n* per boxplot = 27 for (a, b), 54 for (c–j)]. Boxplot columns that do not share the same letter are significantly different pairwise contrasts ($p < 0.05$). Full model details are provided in Appendix S3

For the metals experiment, we observed 6,578 pollinators and recorded the foraging behaviour of 268 pollinators (208 honeybees and 60 wasps). Compared to the control, the HMx10 treatment received 41% fewer visits by honeybees ($M \pm SE$ visits: control 20.3 ± 8.54, HMx10 12.0 ± 5.08), which spent 61% less time at HMx10 treatment feeders during a visit ($M \pm SE$ visit duration (secs): control 42.9 ± 5.59, HMx10 16.6 ± 1.57), and 75% fewer visits by wasps (control 3.4 ± 1.23, HMx10 0.85 ± 0.322), which spent 56% less time at HMx10 treatment feeders during a visit (control 20.5 ± 2.42, HMx10 9.1 ± 1.88; Figure 4; Appendix S3). The HMx1 and HMx2 treatments had 35% and 37% fewer visits by wasps, respectively (control 3.4 ± 1.24,

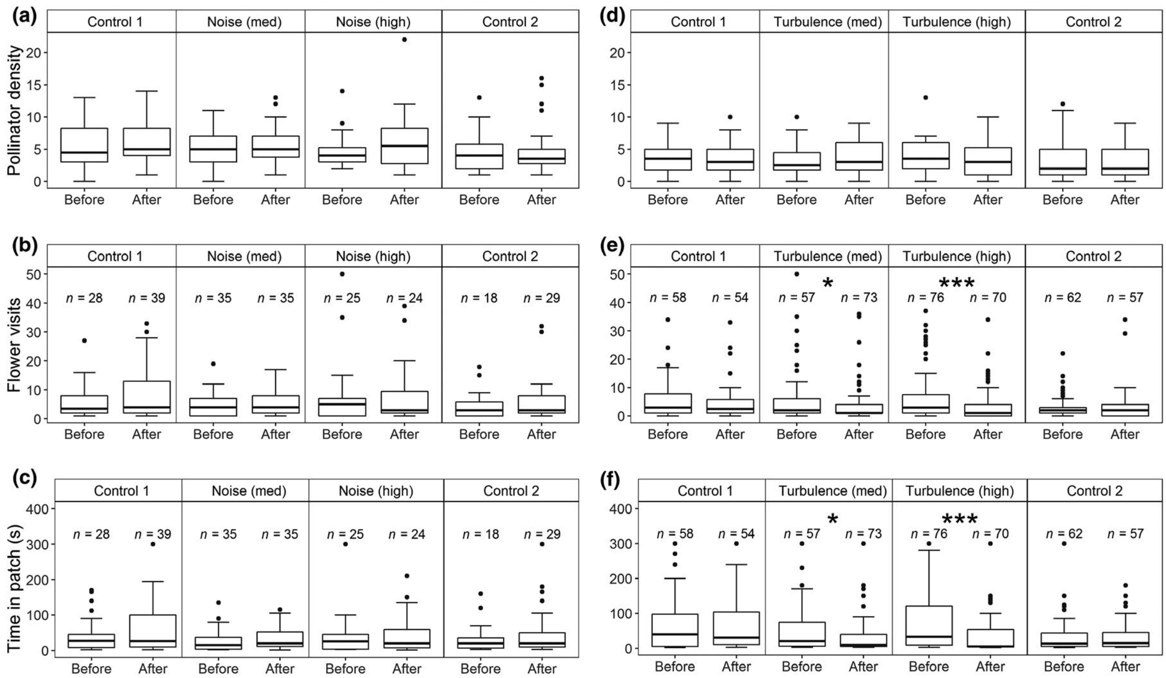
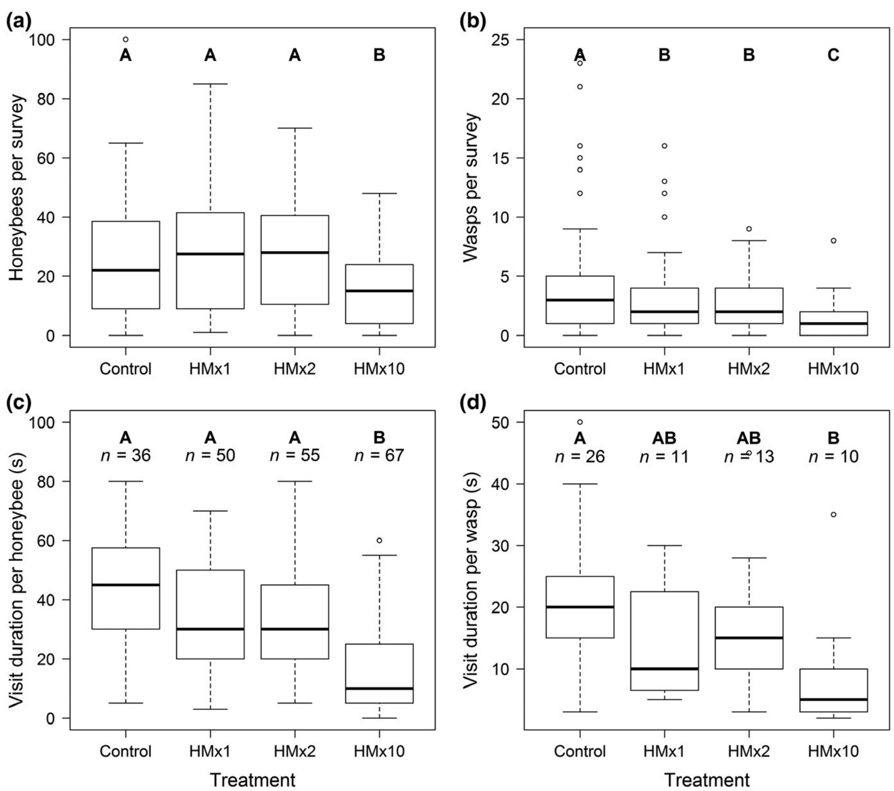


FIGURE 3 The effects of simulated traffic noise (a–c) and turbulence (d–f) on pollinator density (a, d), flower visits per pollinator (b, e) and time in patch per pollinator (c, f) for wild pollinators within 1-m² patches of wildflowers. See Table 2 for descriptions of experimental treatments. *n* per boxplot = 24 for (a) and (d) and is otherwise indicated for (d–e; f–j). Levels of significance between pairs of boxplots are indicated by symbols (**p* < 0.05, ***p* < 0.01, ****p* < 0.001). Full model details are provided in Appendix S3

FIGURE 4 The effects of different roadside-realistic concentrations of metals in 50% (w/v) aqueous sugar solutions on pollinator visitation (a, b) and visit duration (c, d) to feeders. See Table 2 for descriptions of experimental treatments. *n* per boxplot = 60 for (a, b) and is otherwise indicated for (c, d). Boxplot columns that do not share the same letter are significantly different pairwise contrasts (*p* < 0.05). Full model details are provided in Appendix S3. One outlier has been cropped from graph (c) for clarity of presentation: a 180-s visit duration by a honeybee to a control feeder



HMx1 2.2 ± 0.82, HMx2 2.2 ± 0.79), but did not significantly differ in their number of visits by honeybees, although showed a non-significant trend for slightly lower visit duration (Figure 4; Appendix S3).

4 | DISCUSSION

Pollinators in road verges are exposed to many forms of pollution. However, we found that pollinators actively reduced their exposure to some forms of pollution (namely turbulence and metals), which explains why fewer pollinators were observed in areas of road verges closer to the road edge. Specifically, we found that:

1. Pollinators in road verges were exposed to noise, turbulence, dust and metal pollution, which decreased with distance from the road edge but, with the exception of turbulence, extended more than 8 m into verges.
2. Pollinator densities were lower closer to the road edge, where pollution is greatest, especially within the first 2 m, despite a similar density and species richness of flowers.
3. Simulated turbulence deterred pollinators, and some pollinator taxa preferentially avoided concentrations of metals that were more frequently found in flowers within 2 m of the road edge, while noise and dust had no apparent effect.

4.1 | Spatial distribution of pollution, flowers and pollinators in road verges

Levels of noise, turbulence, dust and metals decreased with distance from the road but, with the exception of turbulence, extended more than 8 m into road verges. Of the metals studied, Pb and Sb showed the clearest decline, with particularly high levels 1 m from the road edge and maximum concentrations of 8 ppm Pb and 1.5 ppm Sb. Pb in road verges comes from multiple sources including tyre and vehicle wear and fluids, and the historic use of leaded fuels, while Sb is primarily found in vehicle brake linings (Werkenthin et al., 2014). However, concentrations are likely to be much greater in some flowers because measurements were for aggregated samples of multiple flowers from multiple plant species to meet weight requirements for the acid digestion and ICP-MS analysis.

Flower communities differed with distance from the road (though showed no clear trend in terms of flower density or species richness), which could partly be due to differences in metal pollution, or other factors that we did not measure, such as nitrogen, salt spray or soil depth. We observed many fewer pollinators closer to the road edge, especially within the first 2 m. This trend supports previous studies (Corcos et al., 2019; Phillips et al., 2019) and was consistent among taxa, though weaker and non-significant for bumblebees and moths. While some previous studies have also found no effect of distance from the road on butterfly densities in adjacent verges (e.g. Skórka et al., 2018), bumblebees and butterflies are probably less affected because they are larger (so less affected by turbulence) and more mobile than other pollinator taxa. Our experiments suggest that pollution is a major contributing factor to there being fewer pollinators closer to road edges, as they are being disturbed by turbulence and avoiding metals. However, mortality due to pollinator-vehicle collisions is an another possible contributor to these patterns. Areas of verges closer to the road edge were also inherently further from the hedge bordering the exterior of the road verge, which could be a source of pollinators (Garratt et al., 2017). Yet, this is unlikely to be a major driver of the observed patterns because we found that wider verges (in which transects were further from the bordering hedge) had similar or greater densities of pollinators, not fewer.

4.2 | Effects of pollution on pollinator activity

We found clear impacts of both turbulence and metals on pollinators, with pollinator visit duration up to 54% lower when exposed to simulated turbulence, and up to 61% lower to feeders containing roadside-realistic concentrations of metals. The scale of these impacts was similar to the scale of the reduction in pollinator densities within 0–2 m from the road edge (55% lower compared to 7–9 m).

Turbulence is fairly specific to roads so unsurprisingly its impacts on pollinators have only been considered in one previous study. Similar to our findings, Dargas et al. (2016) found that pollinators were more likely to stop foraging when vehicles passed at greater speeds, and attributed this to turbulence. Although it is difficult to exclude other possibilities in their study (e.g. differences in noise or vibrations), we have been able to do so. Although our simulated turbulence was a somewhat crude imitation, it provided a similar intermittent disturbance.

Previous studies have shown that concentrations of metals in the environment are often related to those found in insects (e.g. honeybees Zarić et al., 2016; Zhou et al., 2018). The concentrations of metals that we measured in road verge flowers were within the range of those measured previously within honeybees (Zhou et al., 2018) and bumblebees (Lindqvist, 1993). However, it is unclear how the concentrations of metals that are measured in dried samples of flowers and pollinators relate to those that are experienced directly by pollinators (e.g. in nectar and pollen)—an unfortunate limitation of current methods for measuring metal concentrations. The concentrations that we measured were relatively low compared to in highly polluted areas, for example far lower than those measured in pollen collected by *Osmia rufa* bees in areas containing industrial smelters, even many kilometres away, where Pb was consistently measured above 40 ppm (Moroń et al., 2012)—10 times the maximum that we measured in road verge flowers. Our findings suggest a need for much greater consideration of the impacts of even relatively low levels of metal pollution on pollinators.

To our knowledge, only a single previous study has assessed pollinator choices among different concentrations of metals. Meindl and Ashman (2013) found no effect of 100 ppm Zn in nectar (comparable to the 112 ppm in our HMx2 treatment) on the foraging behaviour of *Bombus impatiens* bumblebees. Our feeders were predominantly visited by honeybees and wasps, so future research should explore whether other taxa have similar responses. Although visitation was reduced, pollinators did frequently consume even the greatest experimental concentrations of metals. Further research is needed to understand if and how this might affect them, though concentrations of Pb have been negatively related to bumblebee colony growth in urban areas (Sivakoff et al., 2020), concentrations of Cd, Pb and Zn have been linked to wild bee abundance, diversity and forewing structure (Moroń et al., 2012; Szentgyörgyi et al., 2017) and concentrations of Zn between 55 and 1,158 ppm (a similar range to that measured in road verge flowers) have been found to affect caterpillar survival and development (Shephard et al., 2020). A recent study estimated that the LC50 after 7 days for bumblebees feeding on contaminated sugar water was 0.83 ppm for Cd and 66.55 ppm for Cu (Rothman et al., 2020). These are comparable to some of the highest concentrations that we measured, though a study on honeybees found that the LC50 was far greater than roadside-realistic concentrations for Cd and Pb (Di et al., 2016). Encouragingly, our study suggests that some pollinators actively avoid lethal concentrations of metals in the field.

While we found no impacts of noise or dust, we cannot rule out the possibility of effects. Many pollinator taxa (including Hymenoptera, Diptera and Lepidoptera) are capable of hearing within the main frequency spectra of much anthropogenic noise (Morley et al., 2013) and research has found that longer term exposure can affect arthropod abundances (Bunkley et al., 2017) and monarch butterfly heart rate (Davis et al., 2018). While ours is the first study to test whether exposure to noise pollution affects pollinator communities, there are other aspects of noise that might be important besides noise intensity (as measured by decibels; Morley et al., 2013) that were not captured with our recording and playback equipment. On the other hand, our experimental dust treatments, whereby potted plants were left alongside roads for 4 days, likely incorporated additional effects on plants that were unrelated to dust, such as increased physical disturbance from turbulence and changes in herbivore exposure. Although we detected no short-term impacts of these possible effects on pollinators visiting *Sinapis arvensis* plants, they may be important over longer time periods, or for different plant species or contexts.

4.3 | Other potential impacts of road pollution on pollinators

Our study has provided a broad initial assessment of possible impacts of pollution on pollinators in road verges, presenting avenues for future research. First, the roadside surveys and pollution experiments were each carried out at relatively small scales, and differing methods resulted in a focus on different pollinator taxa, making comparison between them somewhat difficult. However, our findings suggest that turbulence and metals are important targets for further, more detailed research—metal pollution in particular because our experimental feeders only attracted wasps and honeybees (a limited subset of the pollinator community), yet it is a widespread environmental pollutant. Experiments that consider the intensity of noise and turbulence, as well as the frequency, would also be beneficial. A larger-scale study of roadside surveys would also reveal the full distribution of pollution levels across road verges (including maximum values), and allow for exploration of whether effects of distance from the road on pollinator density are mediated by traffic volume. Second, our simulations of pollution do not fully capture real life conditions. For example, dust may differentially affect pollinators visiting plant species with different flower structures and shapes, airborne dust may affect pollinators in addition to that on the surface of flowers, and metals in feeders (an extremely large food source of singular quality) may elicit very different responses than metals in flowers (a much smaller food source with various sugar concentrations and chemical cues). Third, there are several other forms of road pollution that we did not consider such as light, exhaust fumes and vibrations. Fourth, our experiments assessed each form of pollution in isolation, whereas there may be synergistic effects. Finally, we focused on pollinator densities and foraging behaviour, which essentially measure the extent to which pollinators are avoiding road pollution and their resulting exposure. From this, future research should further assess possible short- and long-term physiological and behavioural lethal and sub-lethal impacts on pollinators. Most pollinators are temporary visitors to road verges, so are subjected to road pollution for relatively short and infrequent periods. However, less mobile pollinator taxa, and life stages using road verges for reproduction, nesting or overwintering, will be exposed for much longer periods, so are more vulnerable.

5 | CONCLUSIONS

Given current and growing interest in enhancing road verges for pollinator conservation, our study provided a broad initial assessment of the impacts of road pollution on pollinator densities and foraging behaviour. The study fills an important research gap by assessing the collective impact of road pollution on diverse pollinator taxa, and experimentally assessing the impacts of four ubiquitous but little studied forms of road pollution: noise, turbulence, dust and metals (Phillips, Wallace, et al., 2020). Furthermore, despite extensive study into pollinators and their declines (Potts et al., 2016), this is one of few studies to assess the impacts of most of these forms of pollution on pollinators, not just in the context of roads. Overall, the findings suggest that road verges are largely suitable for pollinator conservation, and that road pollution is unlikely to make verges an ecological trap because pollinators apparently avoid areas where pollution is greatest. However, further research is needed to ascertain if and when the net population-level benefits of verges as habitats for pollinators are outweighed by the collective negative impacts of road pollution and vehicle-pollinator collisions (Phillips, Wallace, et al., 2020). In the meantime, our study suggests that management enhancements should prioritise verges alongside roads with relatively lower traffic densities and areas more than 2 m from the road edge.

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AUTHORS' CONTRIBUTIONS

B.B.P. conceived the ideas, collected and analysed the data, and led the writing of the manuscript; J.M.B., K.J.G., K.A.H.-E., C.W. and J.L.O. contributed to the ideas, methodology and interpretation of the results; C.F. and D.C. developed experimental methods; M.B. assisted with data collection. All authors contributed to manuscript drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the University of Exeter's institutional repository https://doi.org/10.24378/exe.3003 (Phillips et al., 2021).

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SUPPORTING INFORMATION

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

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