



Diesel exhaust and ozone adversely affect pollinators and parasitoids within flying insect communities

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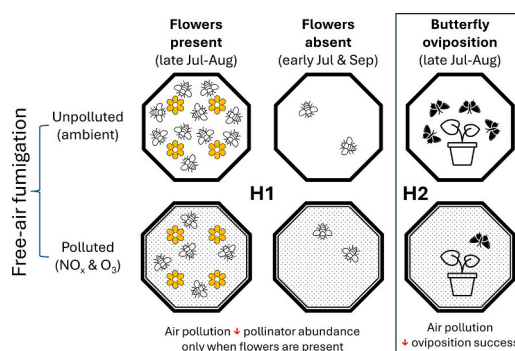
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HIGHLIGHTS

- Air pollution reduces activity of beneficial insect pollinators and parasitoids.
- Diesel exhaust and O₃ alter floral cues that beneficial insects use to forage.
- Pollinator and parasitoid activity is lowest in O₃-polluted atmospheres.
- Air pollution has either a positive or no effect on insect herbivores.
- Both air pollutants significantly reduce butterfly oviposition success.

GRAPHICAL ABSTRACT



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ABSTRACT

The effects of air pollution on human and animal health, and on the functioning of terrestrial ecosystems, are wide-ranging. This potentially includes the disruption of valuable services provided by flying insects (e.g. pollination and biological control). However, quantifying the extent of this disruption requires a clearer understanding of insect community responses at field-scale.

By elevating diesel exhaust and ozone (O₃) pollutants, individually and in combination, over two summers, we investigated the field-scale effects of air pollution on the abundance and diversity of flying insects from pan traps. We quantified which groups of insects were more at risk of air pollution-mediated decline and whether responses to air pollution were influenced by the presence of flowering plants. In addition, a common pest of Brassicaceae, the large cabbage white butterfly (*Pieris brassicae* L.) was used to investigate the effects on oviposition success of the two interacting air pollutants.

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Air pollution had the most detrimental effects on pollinators and parasitoids, compared with other insect groups, lowering their abundance by up to 48 % and 32 %, respectively. The adverse effects of O₃ and diesel exhaust on pollinators occurred only when flowers were available, indicating the relative importance of floral odors compared with visual cues. Air pollutants resulted in either increased insect herbivore abundance or had no effect, potentially increasing the threat air pollution poses to food security. However, both pollutants resulted in decreased oviposition by cabbage white butterflies, which, if demonstrated to be a more ubiquitous phenomenon, may result in reduced larval pest damage.

Quantifying the relative changes in composition and abundance among feeding guilds is valuable for predicting the effects of air pollution on insect communities. Of the groups identified, pollinators are likely to be at the greatest risk of air pollution-mediated decline due to their use of floral odour cues for foraging.

1. Introduction

Air pollution is a growing global concern, posing a threat to both human health and the environment (Chen et al., 2024; Sigmund et al., 2023). In 2019, outdoor air pollution contributed to 4.2 million deaths worldwide, and the projected annual agricultural yield losses linked to air pollution are estimated to range from USD\$14 to \$26 billion by 2023 (Avnery et al., 2011; Rao et al., 2017). Compounding this challenge is the growing evidence that commonly occurring tropospheric pollutants like ozone (O₃) and nitrogen oxides (NO_x) can adversely affect vital ecosystem services upon which humans rely (Burkey et al., 2020; Chan et al., 2024; Dubuisson et al., 2024; Pinto et al., 2010).

Nitrogen oxides, generated during the combustion of fossil fuels, particularly from road transport, plays a pivotal role in the formation of tropospheric O₃ (Jonson et al., 2017; Sillman, 1999). These pollutants exist in a quasi-equilibrium, whereby elevated O₃ episodes depend on atmospheric NO_x levels. Moreover, in high NO_x-polluted areas next to busy roads or in urban areas, O₃ levels are quenched by NO_x, and therefore O₃ levels tend to be higher in rural areas compared with urban or high-traffic areas (Bae et al., 2020; Jhun et al., 2015).

Compared with other air pollutants, O₃ and NO_x pose the greatest threat to economically important insects, particularly pollinators and natural pest regulators (Ryalls et al., 2024). Both pollutants can indirectly impair plant and insect fitness by reacting with and chemically altering volatile organic compounds (VOCs), which are crucial for communication between plants and insects (Blande, 2021). Both insects and plants heavily rely on olfactory cues and VOC detection to perceive and interact with their surroundings (Bouwmeester et al., 2019; Renou and Anton, 2020). While vision also plays a role, insects primarily use VOCs to locate mates, identify oviposition sites, and forage for food (Cardé and Millar, 2004). The disruption of these VOC-mediated interactions may therefore interfere with the ecologically- and economically-significant ecosystem services insects provide (Knaden et al., 2022; Mondor et al., 2004; Rollin et al., 2022).

Considering the complex atmospheric interplay between NO_x and O₃ mixing ratios (Liu and Shi, 2021), and their phytotoxic and VOC-degradation properties (Girling et al., 2013; Ramya et al., 2023), the number of studies evaluating the effects of O₃ on plants and insects far outweighs those that have considered the effects of NO_x and/or the combined effects of O₃ and NO_x on plant-insect ecology (Chan et al., 2024; Ryalls et al., 2024). In addition, the majority of studies on individual pollutants have been undertaken at laboratory-scale or with simulation models. Field-based assessments with O₃ and/or NO_x (e.g. Khaling et al., 2020; Mofikoya et al., 2017; Percy et al., 2002; Ryalls et al., 2022b) are relatively rare because, in open air conditions, it is practically challenging to elevate pollutants in a controlled manner. We used a Free-Air Diesel and Ozone Enrichment (FADOE) facility to explore how air pollution impacts critical ecological processes in the field. Experimental studies using this facility suggested that the negative effects of air pollution on pollination and natural pest control may be significantly greater than predicted by laboratory studies and simulation models (Ryalls et al., 2022a; Ryalls et al., 2022b).

Here, we tested the hypothesis (H1) that the presence of common air pollutants would alter the abundance and diversity of flying insects identified from pan traps (i.e. brightly coloured bowls that visually-resemble flowers). By categorizing these airborne insects based on their feeding guild, a classification level found to best predict air pollution's impact on terrestrial invertebrates (Ryalls et al., 2024), we identified the insect groups most susceptible to decline. Concurrently investigating the effects of air pollution and flower availability (i.e. by including or excluding flowering plants), we mechanistically determined whether the presence of flowers and odour cues – distinguishing floral-mediated effects from the direct effects of air pollution – could be driving these changes in the composition or foraging activity of the flying insect community.

While insects can have multiple roles in a community, air pollution studies rarely consider insect community-level effects and interactions that may influence pest dynamics and crop production (Ryalls et al., 2024). For example, enhancing pollinator performance may unintentionally increase pest populations because some pollinator larvae, such as those of moths and butterflies, are herbivorous pests. Therefore, in addition to investigating the impacts of air pollution and floral cues on flying insect abundance and diversity, we also determined whether air pollution affects another key behaviour in the lifecycle of foraging insects, their oviposition success (H2). Butterflies are considered to be highly dependent on visual stimuli when foraging for suitable host resources (Barragán-Fonseca et al., 2020). However, when searching for suitable oviposition sites, female butterflies can use olfactory cues to seek out young plants, which are more beneficial for larval development (Hasan and Ansari, 2011), therefore there is the potential for olfactory disruption of this process by air pollution. We tested the hypothesis that air pollution (diesel exhaust, O₃ and their interaction) would alter the oviposition preferences of butterflies, using a model system consisting of the common butterfly (the cabbage white, *Pieris brassicae*) and one of its host plants, oilseed rape (*Brassica napus*). To achieve this, oilseed rape plants were placed in the FADOE rings and the oviposition rate of cabbage white butterflies recorded.

2. Material and methods

2.1. Free-Air Diesel and Ozone Enrichment (FADOE) system and mixing ratios

In April 2018, eight 8-m-diameter FADOE rings were constructed and distributed evenly in an octagonal formation (50 m from the centre of the field, each separated by a distance of at least 30 m) within a field of winter wheat (*Triticum aestivum* cv. Skyfall) at the University of Reading's Sonning farm, UK (51.482853° N 0.897749° W). Two rings were assigned to each of four pollution treatments, comprising diesel exhaust (D), ozone (O₃), diesel exhaust and ozone combined (D + O₃) and an ambient air control (CON). Rings of the same treatment were positioned opposite each other in the field to minimise spatial effects. Diesel exhaust and O₃ were generated between 4.30 a.m. and 9.30 p.m. each day, pumped to the rings and then dispersed in a diffuse plume

towards the centre of the rings via corrugated conduit, resulting in elevated pollutant concentrations within the rings. Full details of the FADOE system configuration, including data for wind speed and direction, are described and visualised in Ryalls et al. (2022b). Temperature changes (recorded using DS1922L iButtons placed within one CON and one D ring for 23 days; Table A2) were consistent between rings (i.e. diesel exhaust pollutants had no significant effect on air temperature relative to control rings). Mixing ratios of NO_x (NO + NO₂) and O₃ at the centre of each ring were monitored sequentially (from ring 1 to 8) using NO_x and O₃ analysers. The entire FADOE facility was moved to an adjacent field of winter wheat in April 2019; therefore, the FADOE rings were fumigated during two summer seasons (May–September 2018 and 2019). The wheat fields (c. 85 cm in height when mature) in which the rings were located provided a non-insect pollinated (i.e. non-flowering) buffer, limited plant diversity and maximised weed control. Air pollutant mixing ratios, in ppb, recorded every second and averaged over 120 s for each ring throughout the summer season, for the treatments CON (NO_x: 9.2 ± 0.1, O₃: 20.9 ± 0.2), D (NO_x: 59.6 ± 1.0, O₃: 18.0 ± 0.2), D + O₃ (NO_x: 42.5 ± 0.7, O₃: 20.9 ± 1.1) and O₃ (NO_x: 8.6 ± 0.2, O₃: 35.2 ± 0.6) are visualised in Ryalls et al. (2022b). Fumigation levels were maintained below 90 ppb O₃ (based on peak concentrations recorded in rural European sites in 1990–2012; Colette et al. (2016)) and 120 ppb NO_x (based on average mixing ratios reported next to major UK roadways; Ares and Smith (2017)). If mixing ratios exceeded these values, valves and UV light controllers (for controlling diesel exhaust and O₃, respectively) would automatically adjust to lower the levels of air pollutants released into the rings.

2.2. Flying insect community assessment

Triple pan traps (i.e. blue (Pantone 801C), white (Pantone white with optical brightener) and yellow (Pantone 803C) visual traps that superficially resemble patches of flowers) were placed within each FADOE ring and filled with 20 % propylene glycol and washing-up liquid (to break water surface tension). Traps were left in the rings for 72 h before insects were sieved from the solution and collected in 60 mL tubes. Eight pan trap collection runs were undertaken over two years (2018 and 2019), four runs per year. Within each year, two runs were undertaken when the FADOE rings contained 24 flowering *Brassica nigra* plants (10–13 July 2018, 16–19 July 2018, 2–5 September 2019 and 16–19 September 2019) and two runs were undertaken when no *B. nigra* plants, and therefore no flowers, were present within the rings (24–27 July 2018, 27–30 August 2018, 28 September to 30 August 2019 and 5–8 August 2019; Table A1). This allowed field-scale changes between pollutant treatments to be determined when floral odour cues were both present and absent. *Brassica nigra* was selected based on its fast growth, long flowering period and evidence from previous studies that O₃ degrades its floral signal and affects flying insect pollinators (Farré-Armengol et al., 2016; Saunier and Blande, 2019). Five-week old potted *B. nigra* plants containing 2.7 kg of vegetable topsoil were distributed evenly within each ring and dug into the ground within the wheat crop, such that the lip of each pot was flush with the surface of the soil (Ryalls et al., 2022b). Their average height was 105 cm, which was consistent between treatments (CON: 104 ± 11, D: 105 ± 9, D + O₃: 108 ± 11, O₃: 102 ± 9). For those runs containing flowering *B. nigra* plants, a random set of 12 plants within each ring were counted upon each pan trap collection event to determine the relative abundance of flowers between rings. From pan traps, 18,191 winged insects were identified to Genus or the most precise taxonomic resolution possible, which included 120 taxa from 106 Families and 11 Orders (Table A1). Insect taxa were classified by feeding guild, which has previously been found to be a fundamental predictor of the effects of air pollution on insects and other terrestrial invertebrates (Ryalls et al., 2024). The different feedings guilds included detritivore, fungivore, scavenger, pollen and/or nectar feeder, parasitic wasp (parasitoid), predator, cell-feeding herbivore (cell-feeder) and foliar-chewing herbivore (chewer). The feeding strategies of many insect

taxa encompass multiple feeding guilds, which is reflected in the nine feeding groups included in analyses (Table 1). There was inconsistency in the literature of whether certain taxa were classified as detritivores, fungivores or scavengers. Therefore, these three groups were pooled and defined as DFS. Pollen and/or nectar feeders were classified as pollinators, and cell-feeding insects included phloem or sap-sucking insects.

2.3. Oviposition assessment

Six young (3-week old) *Brassica napus* plants were positioned in the centre of each FADOE ring for one week. At the end of the week, the number of cabbage white butterfly (*P. brassicae*) eggs were recorded from each plant and the proportion of plants with eggs were calculated. This experiment was repeated three times in July–August of each year when flowering *B. nigra* plants were also present in the FADOE rings and *P. brassicae* butterflies were abundant. Young *B. napus* plants were used to assess oviposition success because *P. brassicae* tend to select young plants to oviposit on, the foliage of which provides a more suitable food resource for their herbivorous larvae compared with older plants (Hasan and Ansari, 2011). It is possible that adult butterflies oviposited on older *B. nigra* plants that were also present in the rings, which may have influenced their attraction to the young *B. napus* plants. As such, flower numbers were counted prior to each sampling event to determine whether changes in the abundance of *B. nigra* flowers influenced the oviposition success of *P. brassicae* on young *B. napus* plants. We note that each ring contained an average of 164 flowers across sampling events, which did not vary between rings or treatments (see results section for further details).

2.4. Statistical analysis

All statistical analyses were conducted in R version 4.3.2. We used the *vegan* package (Oksanen et al., 2017) to calculate taxonomic richness and Shannon diversity, based on the most precise resolution available in the dataset, which included specimens identified to higher taxonomic levels (e.g. Family), as described in Staton et al. (2021). To evaluate the interactive effects of air pollution and flower availability on Shannon diversity and taxonomic richness for all insects and pollinators, we applied linear mixed-effects models (LMMs) with a normal error distribution. We used generalised linear mixed-effects models (GLMMs) with a negative binomial distribution to determine the interactive effects of air pollution and flower availability on insect abundances for the different insect groups, as these data did not fit a Poisson distribution. All models were analysed using the package *lme4* (Bates et al., 2015) and post-hoc testing (for pairwise comparisons of means) was carried out using the *emmeans* package (Lenth, 2021) with Bonferroni correction for multiple comparisons. Models included the nested random effects of Year, Run and Ring location to account for repeated measures and spatial differences between rings and years. Prior to analysis, the response variable ‘Shannon diversity’ was exp-transformed (Table 1). GLMMs with a negative binomial distribution were also used to assess the effects of air pollution on *B. nigra* flower abundance and butterfly oviposition success (number of eggs and number of plants with eggs).

3. Results

3.1. The effects of air pollution and flower availability on insect abundance and diversity

Flower availability significantly increased the abundance of all but two feeding guilds (‘pollinator or predator’ and ‘cell-feeder’). When all insects were grouped together, including those that could not be classified into feeding guilds, they were more abundant when flowers were available but did not vary in abundance between rings (i.e. air pollution did not have a significant effect on total insect abundance). In contrast, when all pollinators, including those with other feeding strategies, were

Table 1

The effects of air pollution and flower availability on insect abundance and diversity metrics from mixed-effect models. DFS refers to detritivores, fungivores or scavengers. *P*-values highlighted in bold indicate significance ($P < 0.05$). Where appropriate, response variables were transformed (^aexp) before analysis. Insect abundance negative binomial models are reported as a likelihood ratio χ^2 test statistic. All other parameters are reported as *F*-values. $N = 64$ pan traps. Statistically significant effects of flower availability on the abundance of feeding groups or guilds indicate an increase when flowers were present. Significant decreases and increases in the abundance of insects under one or more air pollution treatments (relative to the ambient air control treatment) are indicated by red (down) and blue (up) arrows, respectively, from *emmeans* post-hoc tests.

Response variable	Fig.	Pollutant		Flowers		Pollutant × Flowers	
		χ^2_3	<i>P</i>	χ^2_1	<i>P</i>	χ^2_3	<i>P</i>
INSECT ABUNDANCE	1						
All insects	-	0.51	0.916	8.13	0.004	1.18	0.773
All pollinators	↓	12.13	0.007	6.91	0.009	20.02	< 0.001
<u>Feeding guilds:</u>							
DFS	-	2.56	0.465	3.72	0.054	8.57	0.036
Pollinator or DFS	↓	9.05	0.029	3.77	0.052	8.58	0.035
Pollinator	↓	11.98	0.007	10.67	0.001	12.49	0.006
Pollinator or Parasitoid	↓	12.84	0.005	8.60	0.003	6.74	0.081
Pollinator or Predator	-	1.31	0.727	2.17	0.141	2.24	0.525
Parasitoid	↓	8.49	0.037	5.76	0.016	1.48	0.687
Predator	-	1.07	0.784	4.63	0.031	4.10	0.251
Cell-feeding herbivore	↑	9.00	0.029	1.28	0.258	0.34	0.953
Chewing herbivore	-	1.40	0.706	7.88	0.005	5.19	0.158
INSECT DIVERSITY	2						
<u>All insects</u>							
Taxonomic Richness	-	2.13	0.546	9.27	0.002	2.32	0.509
Shannon's Diversity ^a	-	1.93	0.587	0.20	0.652	0.52	0.915
<u>All pollinators</u>	-						
Taxonomic Richness	-	2.85	0.415	8.29	0.004	3.28	0.350
Shannon's Diversity ^a	-	4.88	0.181	2.66	0.103	2.36	0.501

considered, which made up 30 % of all insects caught, their abundance was significantly lower under individual and combined air pollutants compared to ambient controls, but only when flowers were present (Table 1; Fig. 1).

When flowers were present in the rings (Fig. 1; highlighted grey), five feeding guilds, including three of the four nectar/pollen-feeding (i. e. pollinator) groups, were less abundant under air pollution (Table 1). In particular, there were fewer pollinators, which included pollinators

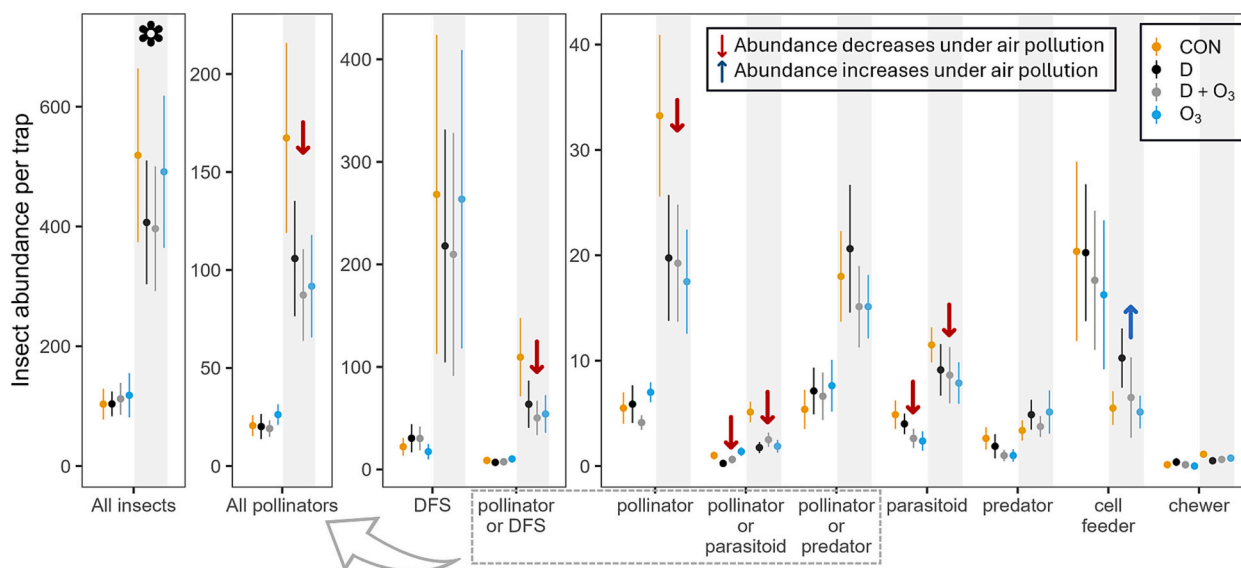


Fig. 1. The effects of air pollution and flower availability on insect abundance. Grey highlighted regions represent pan trap catches when *Brassica* flowers were present in the FADOE rings. ‘All insects’ include those that could not be classified into feeding guilds. DFS = detritivores, fungivores or scavengers. All pollinators include feeding guilds classified as ‘pollinator or DFS’, ‘pollinator only’, ‘pollinator or parasitoid’ and ‘pollinator or predator’. Significant ($P < 0.05$) decreases and increases in the abundance of insects under one or more air pollution treatments (relative to the ambient air control treatment) are indicated by red (down) and blue (up) arrows, respectively, from *emmeans* post-hoc tests.

only (i.e. pollinator) and those that could also be parasitoids, detritivores, fungivores or scavengers (i.e. ‘pollinator or parasitoid’ and ‘pollinator or DFS’ groups), in diesel exhaust, O₃ and combined rings compared with ambient air control rings. Abundances of all three of these pollinator groups were lowest in O₃-polluted rings.

Air pollution had a significant effect on only two groups when flowers were absent; compared with ambient air control rings, abundances of the two parasitoid groups (i.e. ‘parasitoid’ and ‘pollinator or parasitoid’) were lower in rings polluted with O₃, including those with both pollutants combined, regardless of whether flowers were present in the rings. Abundances of predators, herbivore chewers, and the group ‘DFS’, did not vary between rings, whereas cell-feeding herbivores were significantly more abundant when they were exposed to diesel exhaust without O₃.

Neither air pollution nor flower availability had a significant effect on insect or pollinator diversity. However, species richness of all insects and pollinators increased when flowers were present within the FADOE rings (Table 1; Fig. 2). We note that insect abundances were not scaled according to the number of *B. nigra* flowers within each ring because flower abundances were equivalent between rings/treatments; the abundance of *B. nigra* flowers in four of the eight pan trap runs (i.e. when flowers were present) did not vary significantly between rings ($\chi^2_7 = 9.05$, $P = 0.249$, $N = 32$) or air pollution treatments ($\chi^2_3 = 3.29$, $P = 0.35$, $N = 32$). Control rings contained an average of 79 ± 20 flowers compared with D (90 ± 21 flowers), D + O₃ (72 ± 16 flowers) and O₃ (87 ± 18 flowers) rings. These numbers represent a subset (approximately 50 %) of the flowers counted in each ring.

3.2. The effects of air pollution on butterfly oviposition

Air pollution reduced the oviposition success of *P. brassicae*, whereby

both pollutants, individually and in combination significantly reduced the number of oviposited eggs per plant ($\chi^2_3 = 15.00$, $P = 0.002$, $N = 288$) and the proportion of plants with eggs ($\chi^2_3 = 24.84$, $P < 0.001$, $N = 288$). Compared with the control treatment, D, D + O₃ and O₃ reduced the abundance of eggs oviposited by 83 %, 87 % and 90 %, respectively (Fig. 3).

4. Discussion

Our results demonstrate how the impacts of air pollution on insects can vary according to the feeding strategies that they employ. The effects of air pollution on pollen and/or nectar feeders (defined here as pollinators), in particular, has been a focus of recent research (Chan et al., 2024; Dubuisson et al., 2024; Langford et al., 2023; Ryalls et al., 2024; Saunier et al., 2023). Our results suggest that pollinators, compared with other insects, are at the greatest risk of air pollution-mediated decline, especially when they are exposed to elevated levels of O₃. Their significant 37–48 % decrease in total abundance under the individual and combined effects of O₃ and diesel exhaust occurred only when *B. nigra* flowers were present in the FADOE rings. Therefore, the oxidizing effect of O₃ and NO_x on floral VOCs is the most likely explanation for the reduced attractiveness of floral patches (i.e. lower abundance in polluted relative to ambient air), as demonstrated in previous modelling-, lab- and field-based studies (Farré-Armengol et al., 2016; Fuentes et al., 2016; Khaling et al., 2020; Ryalls et al., 2022b). Pollinating insect species often rely on floral scent plumes, composed of VOCs, as crucial cues to locate flowers. However, the effectiveness of these scent plumes can be compromised or obscured by oxidizing air pollutants (Atkinson and Arey, 2003; Saunier et al., 2023). These pollutants can exhibit a dual impact, reacting directly with floral VOCs in the atmosphere and concurrently altering the biosynthetic pathways of

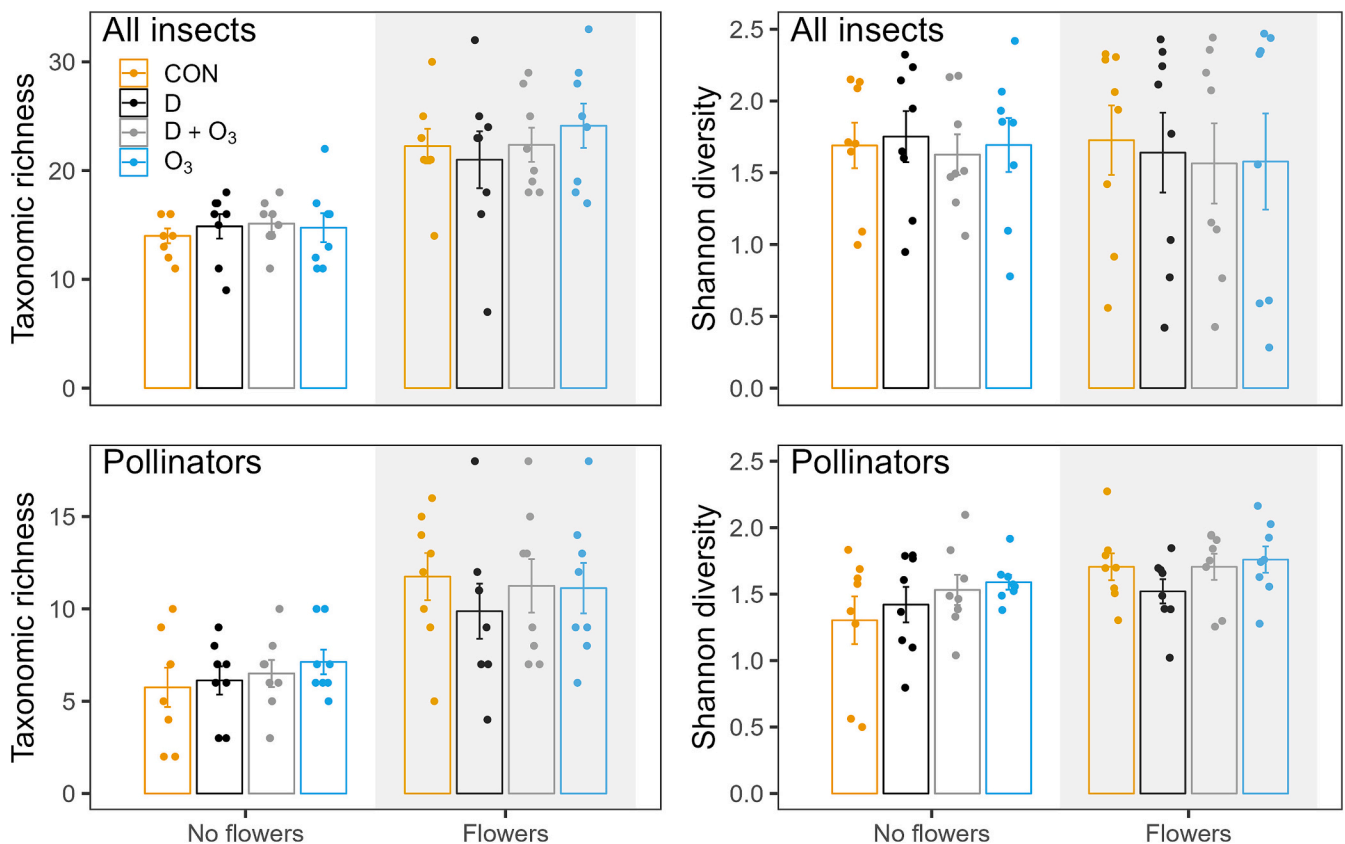


Fig. 2. The effects of air pollution and flower availability on insect taxonomic richness and diversity. Values are means (\pm SE) of taxonomic richness (left) and Shannon diversity (right) for all insects (top) and all pollinators (bottom). All pollinators include feeding guilds classified as ‘pollinator or DFS’, ‘pollinator only’, ‘pollinator or parasitoid’ and ‘pollinator or predator’.

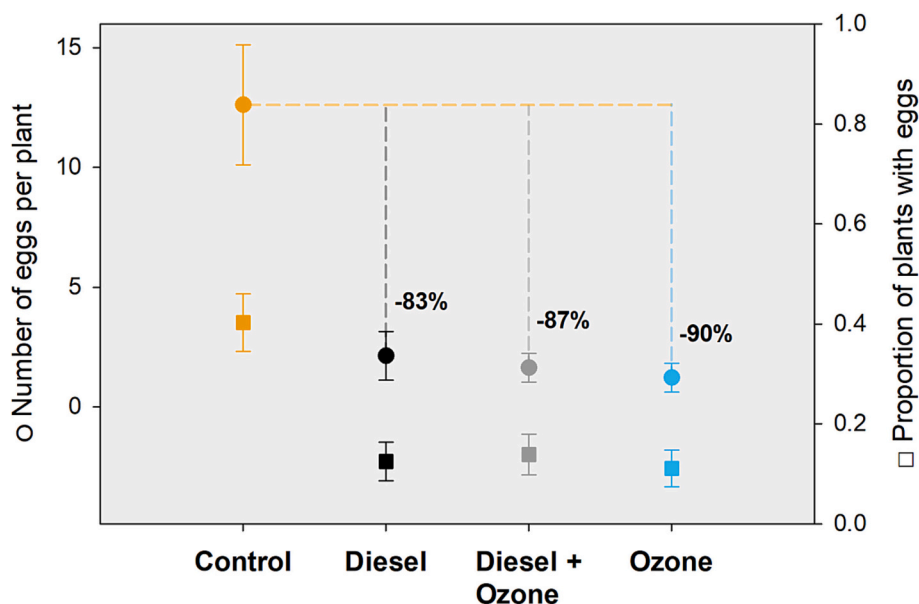


Fig. 3. The effects of air pollution on butterfly (*Pieris brassicae*) oviposition. Values are means (\pm SE) of the number of eggs oviposited per plant (left axis, circles) and the proportion of plants ($N = 6$ per ring per run, 288 in total) that were oviposited on (right axis, squares).

plant secondary metabolites (but see Dubuisson et al., 2024). This modification may result in changes to the profile of floral VOCs released by plants (Pinto et al., 2010). Whether O_3 and NO_x have a direct or indirect effect on the floral VOC profile, it is evident that many VOC-based cues are particularly susceptible to the influence of oxidizing air pollutants (Ryalls et al., 2024). Apart from the impacts on VOCs in the atmosphere and direct plant emissions, exposure to air pollutants also pose direct negative consequences for pollinator health (Thimmegowda et al., 2020) and motility (Vanderplanck et al., 2021), as well as impairing their ability to perceive, learn, and memorize floral scent plumes (Démarets et al., 2022; Leonard et al., 2019; Reitmayer et al., 2019; Wang et al., 2023). Therefore, these mechanisms may also contribute to the overall impact of air pollution on pollinators.

Some studies, in contrast, have shown that pollinators have the capacity to adapt to polluted environments. UK bumblebees, for example, have been shown to exploit floral resources more effectively in high-pollution urban areas compared with agricultural areas (Samuelson et al., 2018); this may be because urban environments typically have a higher density of flowers, allowing bumblebees to forage successfully without relying on visual or olfactory cues. Nighttime chemistry and the formation of nitrate radicals (NO_3) can play a significant role in reducing VOC concentrations and reducing floral visitation by nocturnal pollinators (Chan et al., 2024), although one study has also suggested that a nocturnal pollinator (*Manduca sexta* L.) may be able to adapt to air pollution-altered VOCs by learning to associate them with their floral nectar resource (Cook et al., 2020). Further research into this phenomenon would therefore be helpful to determine where, and in what contexts, air pollution has less of an effect on insect performance.

Our results suggest that the abundance and/or mobility of other beneficial ecosystem service providers, for example parasitic wasps (parasitoids), which can be important natural enemies of agricultural pests, similarly tend to decrease under air pollution, especially O_3 (Gate et al., 1995; Ryalls et al., 2022a). Parasitoids use plant odors (VOCs) emitted by herbivore-damaged vegetation to pin-point the location of their host and, once again, it is these VOCs that are degraded by air pollutants making it harder for them to locate their hosts (Boullis et al., 2015; Dicke, 2000). However, the decrease in parasitoid abundance occurred regardless of whether flowers were present in the FADOE rings, suggesting that they may rely on vegetative cues or VOCs emitted from both/either of the plants (wheat or Brassica) or the insect themselves,

which would remain attractive even in the absence of flowering plants. Parasitoids of pests tend to specialize on fewer hosts and rely more directly on atmospheric VOC-based communication than predators, which likely explains why parasitoids were more negatively affected by air pollution than predators (Boullis et al., 2015).

In contrast, the performance and population abundance of cell-feeding herbivore pests increased in NO_x -polluted atmospheres. These changes may be associated with stress-related increases of plant nutritional (e.g. nitrogen-containing) compounds, decreases in plant defensive compounds (Holopainen, 2002; NECR199, 2016; Port and Thompson, 1980; Pringle et al., 2014; Whittaker, 2001) and/or a reduction of their natural enemies (Bell and Marshall, 2000; Brändle et al., 2001; Gate et al., 1995). In contrast to the diesel exhaust treatment, O_3 , individually and when combined with diesel exhaust, had no effect on the abundance of cell-feeding insects, demonstrating the importance of considering how multiple air pollutants, which occur simultaneously in the natural environment, interact to affect insects (Ryalls et al., 2022b; Valkama et al., 2007). Studies incorporating more realistic pollutant mixing ratios would facilitate predictions of ecosystem-level responses of insects to air pollution (Dohmen, 1988; Holopainen and Kössi, 1998). The positive responses of cell-feeding herbivores to NO_x differed from tissue-chewing herbivores, which showed no clear responses to air pollution. However, the results for this group are inconclusive given the relatively low abundance of tissue-chewing herbivores identified from pan traps. The majority of insects identified in pan traps were classified as detritivores, fungivores or scavengers (Diptera: Phoridae $N = 7995$; Table A1), but there was no clear effect of air pollution on this group, with or without flowers present.

Community-level interactions and tri-trophic effects must also be considered in ecosystem management plans because the larvae of some pollinators are predators (e.g. hoverflies) or pests (e.g. moths and butterflies), therefore improving the performance of pollinators may naturally alter the pest status of the community. Moreover, improving the performance of other natural enemies (e.g. parasitoids) will generally reduce pest communities so it will likely depend on the distribution of different feeding guilds in a community as to whether crop production and/or biodiversity will increase. In air-polluted atmospheres, we demonstrated a severe 83–90 % decrease in the oviposition success of cabbage white butterflies. These butterflies are beneficial pollinators in

their adult form but their herbivorous chewing larvae can kill or inhibit the growth of young *B. napus* plants and other *Brassica* species, therefore reducing crop yields (Mpumi et al., 2020). This demonstrates the importance of considering the relative abundance of economically-important feeding guilds, which can vary with the life stage of the insect and their feeding domain (Staton et al., 2021). We previously demonstrated negative impacts of air pollution on ground-dwelling invertebrates (Ryalls et al., 2022c), suggesting that the deleterious impacts of air pollution is not only limited to active-flying insects. A combination of trapping methods, including whole plant/aerial sampling and/or camera trapping for automated biodiversity monitoring (van Klink et al., 2022; Wägele et al., 2022) would provide a more holistic picture of how community structure and composition is impacted by air pollution. Moreover, quantifying community structure based on the relative performance between feeding guilds may provide a useful general approach to determine the effects of air pollution or other abiotic factors on ecosystem function and crop security.

5. Conclusion

Both O₃ and diesel exhaust, individually and in combination, exhibited the most detrimental effects on pollinators and parasitoids, compared with other feeding guilds, therefore exemplifying what we observed globally (Ryalls et al., 2024). These organisms provide ecologically and economically valuable ecosystem services in the form of pollination and natural pest control, respectively. Pollination, contributing to approximately 5 to 8 % (US\$235–577 billion in 2015) of the total global value of agricultural food production (Murphy et al., 2022; Potts et al., 2016a), is particularly vital, with over 70 % of all crop species relying on insect pollination (Klein et al., 2007). Historically, declines in pollinating insects have not been attributed significantly to air pollution, compared with other environmental stressors such as agricultural intensification, climate change, and the introduction of invasive species (Potts et al., 2016b; Powney et al., 2019). However, these findings provide further evidence to suggest that air pollution is a substantial and previously underestimated factor contributing to these declines. Furthermore, the observed increase in cell-feeding insects (encompassing sap-sucking or phloem-feeding insects) intensifies the potential risk to global food security.

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CRedit authorship contribution statement

James M.W. Ryalls: Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Lisa M. Bromfield:** Writing – review & editing, Methodology, Data curation. **Neil J. Mullinger:** Writing – review & editing, Resources, Methodology, Funding acquisition, Conceptualization. **Ben Langford:** Writing – review & editing, Resources, Methodology, Funding acquisition, Conceptualization. **Adedayo O. Mofikoya:** Writing – original draft. **Christian Pfrang:** Writing – review & editing, Funding acquisition, Conceptualization. **Eiko Nemitz:** Writing – review & editing, Funding acquisition, Conceptualization. **James D. Blande:** Writing – review & editing, Funding acquisition, Conceptualization. **Robbie D. Girling:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data for nitrogen oxide and ozone mixing ratios are available at the EIDC repository doi: <https://doi.org/10.5285/d2e0cf65-010c-4206-8302-195449d0acba>. Data for taxonomic composition and abundance of insects, and butterfly oviposition data are available at the University of Reading Research Data Archive (doi: to follow upon acceptance for publication). Feeding guild classifications for each taxon are shown in Table A1.

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