Lethal and sub-lethal impacts of air pollution on terrestrial invertebrates

Literature review

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Natural England Evidence Review NEER158

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Foreword

Excess atmospheric nitrogen (N) is a major pressure on biodiversity in the UK and globally. There is a wealth of evidence showing that nitrogen deposition is changing sensitive ecosystems, ranging from direct damage to plants to changes to the species composition and richness of entire ecosystems. In England, 95.1% of sensitive habitats had background nitrogen deposition loading above the level considered to cause significant harmful effects[i]. Excess nitrogen results from human activity from both long distance and local sources such as agricultural activities (creating ammonia emissions) and road traffic. The mechanisms of impact are well recognised for higher and lower plants.

Over two thirds of wildflowers in England require low to medium levels of nitrogen, whilst less sensitive species such as Urtica dioica (nettles) thrives in enriched soils. Such effects of nitrogen on plant communities in turn affects dependent wildlife species. For example, negative impacts on butterfly species and other pollinators that are very sensitive to changes in their habitat are already being recorded. There is evidence that nitrogen pollution has driven local extinctions of plant and lichen species across the UK, and increasing evidence of impacts to fungi, insects, birds, and other animals. All of these are important components of biodiversity and contribute to ecosystem functions such as soil formation, carbon sequestration and nutrient cycling.

Less is known regarding the sub-lethal and lethal impacts of gaseous air pollutants present in the air. Negative effects on vegetation occur via direct toxicity. For example, ammonia can be taken up through the leaves via stomata. Impacts include damage to the leaves and increased detrimental interactions with other abiotic and biotic stressors. Of the plant species, we know that mosses and lichens are most at risk from direct toxicity as they have limited detoxification capacity relative to their uptake potential and a large surface area relative to mass. The impact of Persistent, Bioaccumulative and Toxic substances (PBTs) and Volatile Organic Compounds (VOCs) in the environment is a growing area of research, particularly in soils and human health respectively, however, much less is understood regarding the direct interaction with flora or fauna.

In 2022, Natural England hosted two PhD student placements from the ACCE (Adapting to the Challenges of a Changing Environment) Doctoral Training Partnership culminating in two in-depth evidence reviews of the existing and most up to date published research regarding the lethal, sub-lethal and habitat-mediated impacts of air pollutants (concentrations in the air and deposition to the ground) to higher trophic species. This focussed particularly on invertebrates. The reviews identify core evidence gaps and

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[i] This statistic is correct as of 2022 however the report is updated on a yearly basis. Search Trends Report at http://uk-air.defra.gov.uk for the latest statistics.

understudied research areas. These reviews will act as a critical first step in influencing wider future conservation policy and have significant impact on NE advice, raising public awareness of air quality as an environmental issue and engagement with NGOs.

Natural England commission a range of reports from external contractors to provide evidence and advice to assist us in delivering our duties. The views in this report are those of the authors and do not necessarily represent those of Natural England.

Executive summary

Report Purpose

The purpose of this Literature review was to collect and summarise the existing key and most relevant research available on the lethal and sub-lethal effects of air pollution on terrestrial invertebrates. The review is organised into six sections focussing on the primary pollutant groups that have current ambient air quality standards in the UK: 1) Ammonia; 2) Nitrogen Oxides; 3) Volatile Organic Compounds; 4) Ozone; 5) Dust/particulate matter and 6) Heavy metals.

Key Points

Ammonia

Anthropogenic ammonia emissions constitute a major class of air pollutant with significant impacts to health and the environment. Despite the potential for terrestrial invertebrates to be directly exposed to high concentrations of ammonia in the environment, research examining the direct effects of ammonia to terrestrial invertebrates remains largely non-existent. Terrestrial invertebrates living in contaminated wet soils may be particularly sensitive to ammonia toxicity, in much the same way that aquatic invertebrates are, yet evidence is currently lacking and warrants further research. There is a growing body of work exploring the indirect effects of ammonia pollution on land invertebrates, however evidence is still very sparse and remains largely descriptive or correlational. Given the substantial quantities of gaseous ammonia emitted by human activity annually, and the degree to which we rely on invertebrates for essential ecosystem functioning, a greater effort to explore the impacts of ammonia on terrestrial invertebrates is required.

Nitrogen Oxides

Nitrogen oxide (NOx) is considered a major pollutant with direct acute and chronic impacts to human and animal health. NOx further impacts on air quality via its action as a precursor for particulate matter and ozone formation. Research on the effects of NOx on invertebrates has focussed primarily on the indirect impacts. These can occur either via nitrogen deposition, or through its interaction with other pollutants (e.g., ozone and VOCs). Recent research has found that NOx emissions have the potential for significant impacts to pollination services. Specifically, NOx may degrade pollinator floral odour cues (BVOCs), but also directly affect pollinator cognition and behaviour, making it harder for pollinators to locate and memorise floral resources. There is generally very little research on the direct effects of NOx on invertebrates, and our knowledge is also limited by a lack of research on a wider variety of invertebrate species and groups. Future work would also benefit from a greater understanding of the combined effects of NOx with co-emitted pollutants.

Volatile Organic Compounds

Non-methane volatile organic compounds (NMVOCs) can be directly harmful for human health, but their wider impacts on air quality also pose significant concern. These concerns largely revolve around their reactivity in the atmosphere to produce tropospheric ozone and secondary organic aerosols. Emissions of NMVOCs can occur from both anthropogenic sources (AVOCs) and biogenic sources (BVOCs). The direct impacts of AVOCs to invertebrates are not well known, but studies on model lab insects such as the fruit fly (*Drosophila melanogaster*) suggest that varied sub-lethal and lethal impacts can occur. Little is known for other species and groups, and for wild populations. The impacts of BVOCs on invertebrates are more well studied. BVOCs can act as deterrents with numerous pesticidal properties, but they can also act as attractants and play a vital role for herbivory and pollination services. The interaction between VOCs, nitrogen oxides (NOx) and ozone is complex, but has the potential for significant disruption to the relationship between BVOCs and invertebrate health and behaviour. Future work should focus on disentangling these complex interactions, to better understand the impacts to invertebrate communities and particularly insect pollinators.

Ozone

Tropospheric ozone is an important secondary air pollutant, produced as a by-product of reactions between volatile organic compounds (VOCs) and nitrogen oxides (NOx) in the presence of sunlight. impacts to pollinating species have received increasing research attention, and reduced counts of pollinators and a reduction in pollination services have been attributed to ozone exposure. Direct impacts of ozone to invertebrates include potentially toxic impacts, but also changes to insect olfactory learning and memory, reducing their ability to detect plant odour signals (known as biogenic volatile organic compounds – BVOCs). Indirect impacts of ozone to invertebrates include the alteration of plant BVOC composition, concentration, duration of time and distance at which they are detectable by insects. Host-plant quality may also be affected by ozone, with impacts for herbivorous insect community composition – though responses are highly variable among groups. The ability of insects to adapt to ozone modified scentscapes by utilising visual cues, or by learning new odour profiles, may be hindered because: many insects have poor visual acuity; ozone can also modify floral visual traits; ozone can impact timing of floral development; and insect cognition (ability to learn and memorise new floral odours) may also be impacted by ozone exposure. The effects of ozone on plant-invertebrate interactions vary greatly depending on plant species, insect species, individual genotypes, and specific ecological conditions. Effects cannot be generalised across groups without considering the specific life-history and ecology of individual populations. While the impacts of ozone are likely to be particularly significant for invertebrates that rely on plant BVOCs (e.g., arthropods), there is limited knowledge for other invertebrate groups, indicating a need to broaden research to include a greater diversity of invertebrate species.

Particulate Matter

Particulate matter (PM) refers to a broad category of pollutants, encompassing everything in the air that isn't a gas. The impacts to fauna, including invertebrates, are far less well studied than the impacts for humans. Most research on the effects of PM for invertebrates originate from lab-based studies on the model nematode *Caenrhabditis elegans*. The most important impacts of PM for this species appear to be oxidative stress and intestinal dysfunction. Pollinators and other foraging invertebrates can be exposed to PM directly through inhalation, but also through cuticle contact and oral ingestion of contaminated food sources. Initial correlational field studies indicate that bees exposed to pollution experience significant negative behavioural, genetic and physiological impacts from PM, including both lethal and sublethal effects. Other indirect impacts may include physical damage from consuming abrasive particles, reduced host-plant quality due to photosynthetic obstruction, and altered feeding behaviour. Future work should focus on exploring the direct and indirect impacts of PM on a wider range of invertebrates.

Heavy Metals

Atmospheric heavy metal pollution is a significant concern for human and ecosystem health. Once emitted, heavy metals are unable to degrade and so persist in the environment, creating legacy pollution with long-term impacts. Non-essential metals tend to accumulate at higher levels in invertebrates than vertebrates, and invertebrates may be more sensitive to their damaging effects. Certain species accumulate heavy metals to a greater degree than others and make useful bioindicators of heavy metal pollution in the environment. These species include snails, ants, and honeybees and their products (honey and wax). Effects are difficult to generalise across species, because the mode of action and extent of damage caused by exposure to heavy metals will vary by a number of factors including: the specific metal, the combination of pollutants, their bioavailability and concentration, invertebrate species, their ability to accumulate and/or detoxify metals, the developmental stage during exposure, and other ecological impacts.

Conclusions and Recommendations

Terrestrial invertebrates perform vital functions for numerous ecosystem services, but they are currently experiencing global declines. Pollution is now considered a global threat to invertebrates, and air pollution has received increasing attention as a significant risk factor, especially for pollinators. It has been repeatedly acknowledged across studies, that the impacts of air pollution on invertebrates are understudied. In particular, research has focussed primarily on only a narrow set of indirect impacts (e.g., on habitat or resource loss), or on impacts from a limited number/type of pollutants (e.g., heavy focus on agrochemicals such as pesticides). Comparatively little attention has been paid to more direct effects, with a particular lack of knowledge on the impacts of air quality on invertebrate physiology and behaviour.

Contents

Introduction

Terrestrial invertebrates are incredibly diverse, making up ~97% of known species on land. They are often extremely specialised, and provide essential ecosystem services with significant value to global and national economies, food supply and medicine [1]. For example, in Europe 84% of crop species benefit from insect pollination [2]. Despite this, terrestrial invertebrate extinctions are likely to be overlooked and under-recorded [1]. Recent analyses estimate that terrestrial insect abundance is declining at a rate of ~9% per decade [3], however estimates of insect declines vary greatly across species and geographic locations, and are often disputed [4]. The magnitude and global extent of other terrestrial invertebrate declines is largely unknown [3], but according to the latest IUCN Red List, ~23% of all invertebrates assessed are threatened with extinction [5].

Many factors are likely to contribute to these declines, including climate change, habitat loss/fragmentation, and the introduction of invasive species [1]. Air pollution is also considered a major global threat and cause of mortality in humans and animals [6], [7]. Air pollution has increased significantly since pre-industrial times, and is predicted to further increase in some areas of the world [6], [8]. Pollution is now also considered a global threat to terrestrial invertebrates; although research is reportedly still lacking for many species and pollutant types [9]–[11]

The purpose of this literature review was to collect and summarise the existing key and most relevant research available on the lethal and sub-lethal effects of air pollution on terrestrial invertebrates. Gaps in research have been highlighted throughout, and suggestions for future research have been made where possible. The evidence collected during this review will act as a critical step in informing and influencing policymakers, NGOs, and the public. A greater understanding of air quality impacts to higher trophic species and wider impacts to ecosystem services will aid in developing a stronger narrative regarding the significance of air quality impacts to the environment. The evidence collated may also inform how impacts from emissions of pollutants to air are accounted for in air quality risk assessment and decision making.

This review begins with a summary of the methods, followed by a discussion of the general vulnerability of terrestrial invertebrates to air pollution. The review is organised into six sections focussing on the primary pollutant groups that have current ambient air quality standards in the UK: 1) Ammonia; 2) Nitrogen Oxides; 3) Volatile Organic Compounds; 4) Ozone; 5) Dust/particulate matter and 6) Heavy metals. The review concludes with a summary of key messages and a series of recommendations. It should be noted that because atmospheric pollutants do not exist in isolation, but rather interact constantly with one another in the atmosphere, there are considerable overlaps in effects between different pollutant types. These overlaps have been highlighted throughout. This review does not discuss in detail the impacts of indirect effects on terrestrial invertebrates from nitrogen deposition as this is covered in a parallel literature review.

Methods

This review was conducted over a 3-month period between February and May 2022, and all searches were conducted within that timeframe. Given time constraints, these methods were chosen to ensure that the most key and relevant scientific papers for each pollutant type were reviewed. The methods for obtaining literature consisted of 5 steps (Figure 1):

Define search terms: The search engine used was Web of Science. Separate searches were performed for each pollutant type to ensure broad and even coverage of the literature. A steering group was formed (including experts across relevant fields from both academia and government) to ensure search terms were well-defined, and the methods appropriate. A summary of the final search terms used can be found in Table 1 (see Appendix 1 for complete strings including Boolean operators and wild cards).

Define search restrictions: Searches were restricted to 'articles' and 'review articles' only. All years were included, but searches were restricted to the Web of Science Core Collection. Searches were sorted by 'Relevance' (a Web of Science algorithm that sorts papers based on the number of search terms found in each record). The top 100 papers from each search were exported into the reference manager software Mendeley.

Combine results: External sources were added, and these included: additional important citations obtained during the review process; web sources e.g., from the Defra and APIS web pages; and additional citations that were identified to support background knowledge.

Assess relevance: References were then further manually sorted, with irrelevant papers removed if they satisfied any of the following criteria:

No connection to terrestrial invertebrates

No connection to the pollutant type being investigated

Pollutant not airborne

Paper unavailable or retracted

Identify any biases:

The restrictions associated with a review are likely to result in some relevant sources not being identified.

There may be limitations of the Web of Science 'relevance' algorithm. For example, some papers may be highly relevant but only linked with a few of the search terms. This method risks excluding those papers. However, if a paper is highly relevant but appears cited in other relevant papers, it was likely to be picked up during the review process.

There is potential for relevant studies to be missed if they are not retrieved by Web of Science. Time constraints prevented the inclusion of multiple databases; however, the

Web of Science Core Collection is one of the world's leading citation databases and should include the majority of relevant research.

The search-terms used could have failed to capture relevant studies. The presence of an expert steering group to aid with the building of search-terms helped to mitigate this, but there is always a risk with reviews that some relevant research will be excluded.

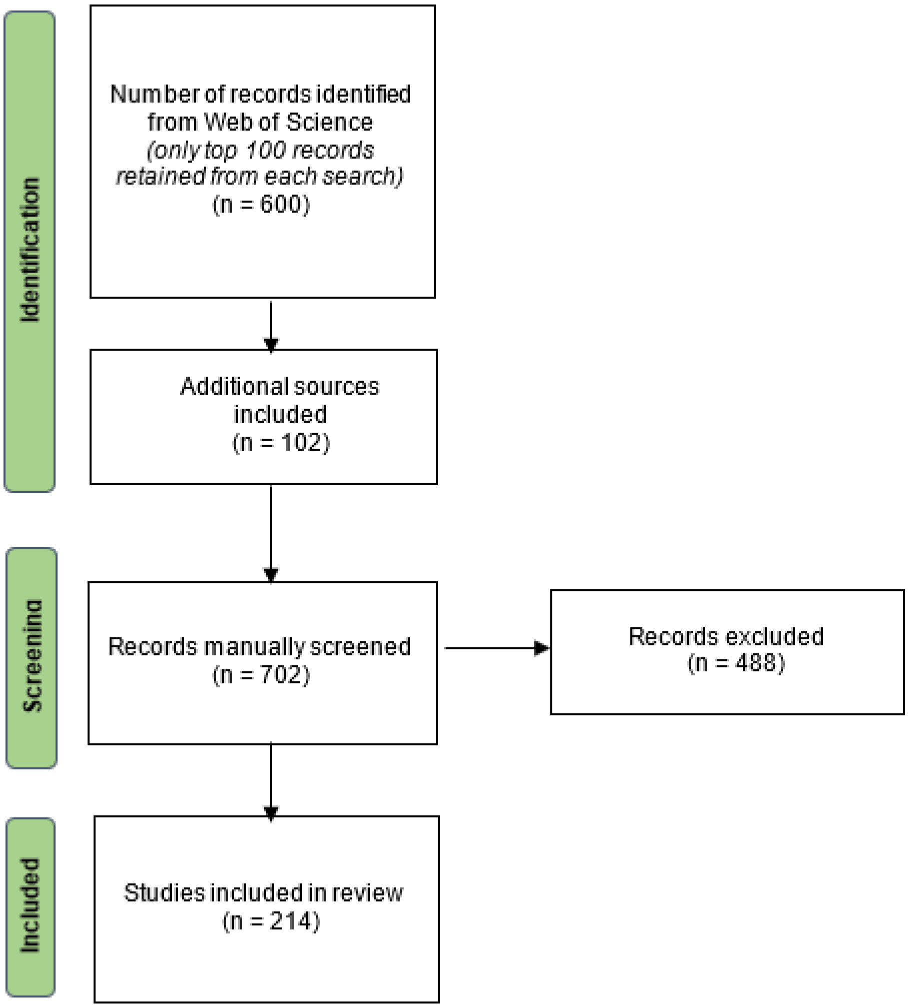

Figure 1. PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) style flowchart of the review process.

Table 1. Search terms used. See Appendix 1 for Boolean operators and wild cards that were used to streamline the search and capture all search term variants.

Pollutant	Action	Species	Excluded Terms
Air pollution; air quality; atmospheric pollutant; airborne pollutant; aerial pollutant; gaseous pollutant; aerosol; emission; smog; smoke; dust; fumes; diesel; petrol; vehicle; particulate; PM2.5; PM10; volatile organic compound; VOC; non-methane volatile organic compound; NMVOC; benzene; 1,3-butadiene; nitrogen oxide; NOx; NO; nitrogen dioxide; NO2; ammonia; NH3; ozone; O3; heavy metal; trace metal	Exposure; dose; concentration; toxic; lethal; sub-lethal; mode of action; impact; uptake; effect; affect; physiology; life-history; behaviour; development; foraging; reproduction; fertility; fecundity; survival; stress; lifespan; mortality; respiration; learning; memory; olfactory	Invertebrate; terrestrial; insect; arthropod; hexapod; pollinator; wasp; bee; honeybee; butterfly; moth; fly; hymenoptera; homoptera; parasitoid; chilopod; myriapod; centipede; millipede; annelid; worm; nematode; gastropod; mollusc; snail; slug; arachnid; spider; beetle	Marine; freshwater; seawater; sea; ocean; benthic; aquatic; swim; mussel; fish; pesticide; fungicide; insecticide; noise; light

Vulnerability of terrestrial invertebrates

The vulnerability of any species to air pollution is generally determined by a combination of factors including: specific sensitivity to the pollutant type, potential exposure to the pollutant, and capacity for recovery from exposure [12]. Such ecological risk assessments are lacking for the majority of terrestrial invertebrates, although considerable progress has been made for aquatic invertebrates, many of which are considered to be highly sensitive to pollution [12]. Some initial general assertions as to the vulnerability of terrestrial invertebrates to air pollution have been made [13], although it is important to note that risk assessments that incorporate both species specific sensitives and ecological vulnerability are still required [12].

Terrestrial animals (both vertebrates and invertebrates) are exposed to air pollution primarily through respiration (although skin is also an underappreciated target organ), with wide ranging acute and chronic impacts to health [14]. Insects are predicted to be especially sensitive to the direct effects of air pollution, due to their greatly increased metabolism and unique respiratory physiology associated with high gas exchange requirements [11], [14]. Unlike vertebrates, that have sophisticated and well-developed respiratory tracts, arthropods[ii] utilise an extensive but far more simplified and primitive system [14]. They intake air via a set of valve-like openings known as spiracles that are connected to a set of highly branching tracheal tubes and air sacs [15]. These eventually lead to an extensive system of tracheoles that lie adjacent to all tissues and serve as the site of gas exchange for the entire body [11]. Some species can actively respire by rapidly compressing and expanding trachea and tracheoles to create air flow [15]. The aeration system within the arthropod body is therefore well adapted for transporting oxygen directly to all internal organs, but this also makes them vulnerable to external airborne toxins that are also distributed throughout the body [11], [14]. This fact is well known and utilised within the pest control industry, where insect pests can be rapidly and effectively exterminated using fumigation techniques. Inhalation of insecticides may be even more effective than topical application, since injecting insecticide directly into spiracles has been shown to result in far more rapid and severe paralysis than application to the cuticle [11].

Invertebrates with a spiracle system may be able to utilise spiracle valves to exert some control over the degree of pollution that enters the body [15], [16]. However, there is very limited observational evidence that arthropods are able to facultatively close spiracles in response to external stressors, for example in response to mechanical disturbance, or elevated CO_2 [11]. Furthermore, if such mechanisms were employed it would come at the cost of reduced oxygen availability for other metabolic function [16]. Such discontinuous gas exchange is thought to only be possible during periods of inactivity [15]. Spiracle closure in response to pollution could therefore restrict other essential physical functions such as flight and foraging duration [16]. Invertebrate respiratory systems are also incredibly diverse. For example, some arthropods lack the ability to close their spiracles, while other invertebrates utilise different respiratory systems altogether, e.g., integumentary surfaces, lungs, or gills. Initial surveys have suggested that terrestrial invertebrates may also be exposed to higher levels of certain pollutants than large mammals in the field (e.g., heavy metals) [13]. In the case of heavy metal pollution, they may also accumulate higher levels of non-essential metals, and may be more sensitive to the damaging effects of metals than vertebrates [13]. Invertebrates are often in prolonged close contact with contaminated soils and vegetation, and due to their specific niches and small size they often have a limited capacity for dispersal and escaping contaminated habitats/food sources [13].

[ii] Arthropods: A diverse phylum of invertebrates including insects, arachnids, crustaceans, millipedes, and centipedes

Ammonia

Atmospheric nitrogen (N_2) naturally makes up 78% of the dry troposphere [17]. However, additional anthropogenic sources of nitrogen constitute a major class of air pollutants that disrupt nitrogen cycling, and have significant impacts to health and the environment [17], [18]. Ammonia (NH_3) is a highly reactive atmospheric nitrogen species accounting for 55% of total anthropogenic nitrogen emissions [17], [19]. Agricultural practices constitute the largest source of ammonia pollution [20], emitting an average of 32Tg of ammonia annually, with the vast majority of emissions originating from animal waste and fertiliser use [21], [22]. Other inputs of anthropogenic ammonia include fossil fuel combustion and biomass burning [17].

Gaseous ammonia has a short lifespan in the atmosphere because it reacts readily with other pollutants such as sulphur dioxide and nitrogen oxides [20]. These reactions result in the formation of fine ammonium (NH_4^+) containing aerosols that contribute to particulate pollution [19]. Particulate matter can then be transferred over large distances, and constitutes a major health concern for humans and other animals [19], [20]. Ammonia can interact directly with plants and can also be deposited directly onto plants and soils as nitrogen. In both cases, it can cause significant disruption to environmental health [19].

Impacts to invertebrates

Research on the harmful effects of ammonia on ecosystem function has primarily focussed on the impacts to sensitive flora, particularly lichen and bryophytes [6], [18], [23]. In terms of higher organisms, research effort has focused largely on freshwater and marine wildlife, where there is strong evidence that aquatic invertebrates can be highly sensitive to both the direct and indirect effects of ammonia pollution [23]–[25]. Far less is known about the impacts to terrestrial animals including invertebrates [23], [25]. Within the cohort of papers examined for this review, none explored the direct toxicity of ammonia (e.g., via contact or inhalation) to terrestrial invertebrates, indicating a lack of research in this area.

Upon direct exposure, ammonia reacts readily with moisture in organismal tissue [26]. Consequently, exposure to high concentrations of gaseous ammonia is known to cause severe acute and chronic injury to humans and other mammals [27]. Ammonia is considered particularly damaging for aquatic invertebrates because it easily diffuses through cell membranes, causing damage to skin and gill tissue as well as disrupting endocrine function [23]–[25]. The degree to which terrestrial invertebrates are impacted by direct contact with ammonia is currently unclear [25], [28]. However, invertebrates are likely to be directly exposed to relatively high concentrations of ammonia under certain conditions, for example: in areas immediately surrounding decaying manure; following gas leaks from industrial ammonia production/transport; and following the direct application of ammonia-containing fertiliser into top soil [21], [26], [27]. Terrestrial invertebrates that come into regular direct contact with ambient surface water or pore water, such as those that live in wet soils, have been suggested to be especially sensitive to the toxic effects of ammonia [25]. While evidence to support this is currently lacking, it stands to reason that many of the mechanisms influencing the sensitivity of aquatic invertebrates to ammonia pollution will also affect terrestrial invertebrates that live in polluted wet soils [25]. It would be beneficial for future work to examine the impacts of direct ammonia exposure on terrestrial invertebrates, and particularly those inhabiting wet soils.

Vegetation composition provides an essential role for invertebrate ecology. Given the well-known impacts of ammonia on terrestrial plant-life, we can infer that there are also likely to be significant knock-on indirect effects on terrestrial invertebrates [23]. For example, an increase in soil nitrogen also generally results in an increase in plant biomass (for vegetation that prefers nitrogen-rich soil) [23], [25], [29]. This has significant impacts on the microclimate of the soil-surface, with a denser layer of vegetation resulting in a reduction in light availability and local temperature changes [23]. This is likely to result in changes to invertebrate community composition - while some invertebrates are well adapted to cold, damp habitats (e.g., ground beetles), others are highly intolerant of such environments (e.g., butterflies and ants) [23], [25]. For some invertebrates, these conditions can result in slower development and longer lifecycles. For species where life cycles are already long (e.g., in large insects), this may mean they are unable to complete a full life cycle within a season [23]. Furthermore, for invertebrate species whose host plants favour nitrogen-poor conditions, the changes in vegetation composition associated with higher nitrogen levels has been associated with population declines and local extinctions [29]. Increased aerial deposition of ammonia may also increase soil acidity and the concentration of trace metals in the soil [25].

Other indirect effects of aerial ammonia deposition could include changes to host plant quality for herbivorous invertebrates [28]. Increased nitrogen availability in plants as a result of ammonia deposition can increase invertebrate herbivory, but ingestion of nitrogen loaded leaves has also been shown to increase the mortality of moths and silkworms under lab conditions [30]. For some invertebrate species, impacts of increased nitrogen in host plants could be beneficial (e.g. in aphid pests [31]), but increases in the abundance of these species can also have wider ecosystem impacts (e.g., defoliation) [23], [32]–[34]. This will also indirectly impact other invertebrates through competition and reduced availability of resources. Increased leaf herbivory has also been shown to impact duration of floral visits by pollinators (possibly as a result of changes to floral odours and nectar sugar concentration) [33]. Some species (such as butterflies, moths and bee’s) are particularly sensitive to changes in host plant quality [23], and negative impacts can include increased mortality and decreased growth rates [25]. This has been suggested to result from the accumulation of nondigestible or toxic compounds, nitrate or nitrogen-based secondary metabolites [25], [28]. Such indirect effects may also accumulate up the food chain to impact predatory invertebrates.

Ammonia emissions could also cause cascading interactive effects between vegetation and air quality, with potential indirect impacts on terrestrial invertebrates [30]. For example, an increase in nitrogen availability in plants can cause increased herbivory by invertebrates [30], which in turn may promote the up-regulation of plant volatile organic compound (VOC) production [35], [36] (see section 6). Biogenic VOCs play an important role in tropospheric chemistry, contributing to the production of other pollutants such as ozone [37] - a major class of air pollutant with potentially harmful effects for invertebrates (Vanderplanck et al., 2021) (see section 7). Increased aerial deposition of ammonia may also increase soil acidity and the concentration of trace metals in the soil [25] which are likely to be harmful to soil invertebrates (see section 9). Pathways of interactive effects between atmospheric and soil chemistry, vegetation and invertebrate communities are likely to be very complex and currently lack evidence. Further research in this area will be important for uncovering the full impacts of ammonia (and other air pollutants) on terrestrial invertebrates.

Nitrogen Oxides

Nitrogen oxides (NOx) are a group of gases primarily produced during the combustion of fossil fuels [39]. The main constituent of NOx is nitric oxide (NO) which, once emitted, is rapidly oxidised by atmospheric ozone to produce nitrogen dioxide (NO_2). This reaction is also reversible under UV light, resulting in NO and NO_2 inter-converting during the day. Consequently, NO and NO_2 are collectively referred to as NOx [40]. Emissions from road transport constitute the largest source of anthropogenic NOx, with other sources including power stations and industrial and domestic combustion [40]. Although NOx emissions have fallen by 76% since 1970 [39], emission declines are gradual, largely because reductions are offset by an increase in the number of road vehicles [40]. Emissions limits for NO_2 in particular are regularly exceeded, especially in urban areas [41].

The impacts of NOx on invertebrates have been most well studied for pollinating species, but the direct effects of NOx on invertebrate health and behaviour is generally poorly understood [2]. Instead, most recent research has focussed on the effects of the interactions between NOx and other atmospheric pollutants on invertebrates.

Impacts to invertebrates

By far the most well studied effects of NO_x relate to its contribution to nitrogen deposition, with associated effects on vegetation and sensitive habitats. The impacts of nitrogen deposition to invertebrates via oxidised nitrogen (NOx) are likely similar to those of reduced nitrogen (ammonia), which have been explored in the ammonia section above (and in more detail in a separate parallel review). Briefly, impacts of nitrogen deposition to invertebrates can occur via changes to vegetation composition and host plant quality, with cascading impacts to higher trophic levels.

In addition to its contribution to nitrogen deposition, NOx is also highly reactive and acts as a precursor emission for the formation of other harmful pollutants - ozone, and particulate matter, both of which have significant implications for health and the environment (see section 7 and 8)[39]. The direct effects of NOx exposure are also known to be important for human health, particularly in areas close to sources (e.g. urban settings, especially roadside verges) [40]. Exposure to NO_2 can cause airway inflammation, exacerbate the symptoms of heart and lung conditions, and increase susceptibility to respiratory infections in humans [39]. There is also evidence to suggest that, when in the presence of equivalent concentrations of sulphur dioxide (SO_2), the effects of NO_2 are far more likely to be negative [40]. While much less Is known for invertebrates, recent work has provided evidence that NOx (and ozone) can have detrimental effects on invertebrate community composition [42]. Effects were found to be particularly negative for specialist and winged species [42], possibly due to greater exposure risks, and their increased reliance on their olfactory environment - though the mechanisms underlying these impacts are unclear. There is also some limited evidence that exposure to NO can delay spermatogenesis and result in increased harmful mutations in the fruit fly (*Drosophila*) [43], although one study found conflicting evidence that NO exposure did not increase mutation rate [44].

Emissions of NOx are partly considered harmful because they interact with atmospheric volatile organic compounds (VOCs) to produce tropospheric ozone (VOCs are also important pollutants in their own right - see section 6). Ozone is known to have both lethal and sub-lethal impacts on invertebrates - although the effects of ozone likely vary with species, and in the presence of other pollutants [42] (see section 7). NOx, VOCs and ozone are anthropogenic pollutants, but plants also naturally release VOCs (termed biogenic VOCs, or BVOCs). The primary function of BVOCs is to enable plants to communicate with other organisms in their environment, including other plants, herbivores, and also invertebrate pollinators [10]. Pollinators have evolved an exceptional ability to detect and memorise new odours [41]. Floral BVOCs are therefore essential for locating new and already known food patches [41], and pollinators prefer to visit food patches of known odour [45]. It is becoming increasingly clear that NOx emissions can disturb the relationship between pollinators and BVOCs. Impacts may occur indirectly when NOx interacts with (and degrades) BVOCs - making them harder to detect. For example, Girling et al., (2013) found that diesel exhaust fumes degraded BVOCs, and NOx was identified as the primary emission responsible. Consequently, the ability of honeybee’s to detect floral VOCs and locate flowering plants was significantly reduced [41]. These findings were later corroborated by Lusebrink et al., (2015) who found that diesel exhaust fumes altered the BVOCs emitted from oilseed rape flowers, even rendering some completely undetectable by honeybees [46], [47]. More recently, Leonard et al., (2019) found that when BVOCs were degraded by petrol exhaust pollution (a primary constituent also being NOx), the ability of honeybee’s to learn and memorise floral odours was significantly reduced [10].

There is also recent evidence to suggest that NOx can affect pollinator cognition and behaviour directly. Reitmayer et al., (2019) provide evidence that honeybees exposed to diesel exhaust fumes[iii] had significantly impaired long-term memory, which reduced their ability to learn and recall odour profiles. Such cognitive impairments were suggested to result from altered protein expression in the brain. Concerningly, bees exposed to diesel exhaust fumes were also found to have reduced tolerance to further stressors, with bee’s

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[iii] 150 minutes of exposure to fumes containing 19.8 and 17.5 ppm (≈34 $\mu g/m^3$) of NO and NO_2 respectively.

experiencing increased mortality following additional exposure to heat stress. This implies that exhaust pollution not only impairs the cognitive function of pollinators, but can interact with other stressors to threaten survival [2].

The combined effects of degraded VOCs and impaired pollinator cognition has the potential to significantly disrupt pollination services. Particularly for species that rely very heavily on odour cues, such as bumblebees [2]. However, whilst NOx is the primary constituent of exhaust fumes, in reality these emissions also contain a complex concoction of other pollutants (e.g., particulate matter, sulphur dioxide, VOCs and heavy metals) albeit at lower concentrations [41], [42], but all with known impacts to air quality. It cannot be ruled out that the observed effects of exhaust fumes on pollinators were not (at least partly) influenced by these (or combinations of these) other pollutants.

Ozone is also known to degrade and impair pollinator detection of BVOCs [48] (see section 7). Increased ozone production in the presence of NOx may therefore exacerbate the impacts to pollination services. Indeed, Ryalls, et al., (2022) found that ozone, both on its own and in combination with NOx[iv], (both at levels below current air quality standards) reduced flower visits by insect pollinators by 83-90% in the field [49]. It is worth noting, that the atmospheric chemistry underlying these reactions is very complex [50], and the causal relationships between individual pollution emissions and pollinator health and behaviour is difficult to tease apart [2]. Nevertheless, risks to pollination services have significant implications for wider ecosystem functioning, as well as food security - with 84% of Europe's food crops relying on insect pollination [2], [41]. Further work on the direct effects of NOx on pollination services, including the effects of interactions between NOx and other atmospheric pollutants (particularly BVOCs, ozone, and co-emitted exhaust pollutants) are essential.

There has been a recent increase in initiatives to support and restore pollinator communities in urban ecosystems [51]. Given that cities constitute a major source of NOx emissions (particularly at roadside verges), a need to increase our understanding of the direct and indirect impacts of NOx on pollinators is needed to ensure these efforts are not hindered. Current research is largely focussed on a very limited number of invertebrate species (primarily insect pollinators) [49]. Given the variety of invertebrate form and function, the effects of NOx are also likely to vary across invertebrate species and groups. Future work should therefore focus on exploring the effects of NOx on a greater diversity of invertebrates.

[iv] NOx = 59.6± 1 ppb (≈116 μg/m^3); O_3 = 35.2± 0.6 ppb relative to control plots

Volatile Organic Compounds

Volatile organic compounds (VOCs) are a broad class of reactive carbon-based chemicals that are readily released as gasses into the atmosphere. Methane is often excluded from VOC monitoring, which allows for easier detection and analysis of non-methane VOCs (NMVOCs) that are usually present in much smaller concentrations in the atmosphere [52], [53]. While some NMVOCs are not a significant risk to health, others - such as benzene and 1,3-butadiene - are carcinogenic [54]. VOCs also vary in their reactivity in the atmosphere [54], with some being relatively inert while others are highly volatile with significant impacts on air quality [55]. In particular, NMVOCs can undergo photochemical reactions in the presence of nitrogen oxides (NOx) to produce secondary organic aerosols, and either form or destroy tropospheric ozone (depending on the concentration of NOx) [54], [56], [57]. The relationship between NOx, NMVOCs and ozone is highly complex and dependent on a variety of factors, such as temperature, humidity, wind-speed and light[50], [58], [59]. Generally, in areas with elevated NOx concentrations (such as urban areas, particularly roadsides), the formation of ozone is increased in the presence of reactive NMVOCs (and sunlight) [56].

Emissions of NMVOCs occur from both anthropogenic and biogenic sources [52]. The largest sources of anthropogenic NMVOCs (AVOCs) come from industrial processes and solvent use [52]. Other sources include agriculture and fossil fuel extraction and distribution [54]. However, the vast majority of global NMVOC emissions into the atmosphere originate from vegetation [56], [57], [60], [61]. Plants emit a wide array of NMVOCs - known as biogenic VOCs (BVOCs) – in order to communicate with their environment. BVOCs are incredibly functionally diverse, acting as signalling compounds both within and between plants, and between plants and other organisms. For example, they can act as both deterrents of herbivorous invertebrates, and attractants of predators (of invertebrates). Importantly, BVOCs also act as odour cues, signalling the location of floral sources for pollinators (primarily insects) [62], [63]. BVOCs are not currently considered substantial contributors to total UK VOC emissions [52], [64]. However, they are rarely monitored in the UK, making it difficult to quantify emissions [64], [65].

Impacts to invertebrates

While very few NMVOCs have been investigated for their direct impacts to invertebrates, some are known to have varying sublethal and lethal impacts on model lab organisms such as the fruit fly (*Drosophila melanogaster*). For example, AVOC exposure can induce a variety of effects (depending on the pollutant) including sedation and inhibition of movement, respiratory disturbances, and reproductive senescence [66]–[68]. Relative to mammals, insects have evolved efficient detoxification mechanisms for certain toxins, suggesting there may be differences between the response of insects and mammals to VOC exposure [68]. However, the sedative effects of the VOC toluene observed in fruit flies are consistent with those seen in rodents [66]. This suggests there may be a degree of transferability between the effects of NMVOCs on mammals and invertebrates [66]. The direct effects of AVOCs on other invertebrate groups are unknown, with most research having focussed on the more indirect interactions between invertebrates, BVOCs and other atmospheric pollutants.

Since many BVOCs function as defensive compounds, they often naturally exhibit pesticidal properties with highly variable impacts for invertebrates. BVOCs can further indirectly harm herbivores by attracting their natural enemies (e.g. parasitoids or predators) [60], and impact on their general behaviour and performance [69]. For example, when exposed to fungal VOCs, flies experience respiratory dysfunction, decreased motility and reduced survival in the lab [70]. Some fungal VOCs also have highly repellent and toxic effects on terrestrial molluscs [71], and other BVOCs can interfere with herbivore oviposition rates [60].

Plants utilise BVOCs to compete for pollinator attention, and function as a vital cue for pollinators to locate and assess the abundance and quality of floral resources [72]. While some BVOCs function as 'generalist attractants' that appeal to a wide diversity of pollinators, others are incredibly species specific, sometimes attracting just one or two highly specialist pollinators[72]. For example, some species of UK *Colletes* are specialist bees that pollinate just one - or very few - plant species [73], [74]. The importance of BVOC composition for pollination services is significant. The direct effects of ozone on pollination services have received increasing recent attention and is discussed in more detail in section 7. Briefly, ozone can interfere with pollinator detection of BVOCs through physiological and behavioural changes [2], [8], or by degrading BVOCs themselves [10], [75]. Increasing our understanding of the relationship between VOCs, other air pollutants (i.e., NOx and ozone) and pollinator health and behaviour is vital to addressing the current global threat to pollination services [8].

Herbivory is a well-known stress factor that generates an upregulation of BVOC emissions, including changes to the blend of volatiles emitted [35], [60], [76]–[82]. Given their substantial global emission rate and high reactivity, BVOCs have significant impacts for atmospheric chemistry [55], [57], [83]. Invertebrate herbivory therefore plays an important (but often over-looked) role in the relationship between the biosphere and the atmosphere, with the potential for cascading ecological impacts [35], [55], [57], [60], [76].

It is likely that changes to invertebrate community composition impacts air quality. For example, increased nitrogen deposition (which can result from ammonia and NOx emissions) [19], [40] can increase the abundance of nitrogen-favouring invertebrates, such as aphids [31], which can then upregulate plant BVOC emissions [34], [63], [84]. The emission rate of BVOCs is also known to increase under other abiotic stressors such as high temperatures [55], [58], [76], increasing carbon dioxide [85], flooding [86], and drought [77], [87]. This may be exacerbated if high temperatures increase the abundance and range of heat tolerant herbivorous pest species [61], [76]. The impacts of invertebrate herbivory on BVOC emissions and atmospheric chemistry in general are likely to be significant, but are complex, difficult to monitor, and are not usually incorporated into emissions models [61], [88]. Furthermore, studies of the ecological interactions between invertebrate herbivores, plant stressors and BVOC emissions rarely use consistent combinations of stressors [61]. Results are also often inconsistent between studies, making it difficult to characterise the complete impacts of BVOC emissions for fauna and air quality in general [61], [85].

Whilst the relationship between herbivorous insects and BVOC emissions have received increasing attention, far fewer studies have explored the relationship between VOCs and non-herbivorous invertebrates [89]. For example, coprophagous and necrophagous invertebrates (e.g., dung and carrion feeding insects) have also been shown to utilise VOCs emitted from decomposing organic matter [89], [90]. Insect decomposers play a vital role in ecosystem functioning and may also contribute to reductions in VOC emissions emitted from manure [91]. The degree to which air quality (i.e., NOx and ozone) interferes with decomposer detection of VOCs is unknown.

Ozone

Ozone (O_3) is a gas present at two different layers of the atmosphere. Stratospheric ozone (15-50km above the Earth's surface) is crucial for filtering incoming ultraviolet radiation from the sun. Tropospheric ozone (0-15km above the Earth's surface) on the other hand, is a toxic secondary air pollutant and greenhouse gas [92]. Rather than being directly emitted by anthropogenic sources, tropospheric (or 'ground-level') ozone is formed by a series of complex chemical reactions involving nitrogen oxides (NOx) and volatile organic compounds (VOCs) in the presence of sunlight (see sections 5 and 6) [92], [93]. Emissions of NOx and VOCs, in combination with warm weather and low wind conditions, can cause transient episodes of concentrated ozone (smog) which is toxic to humans and wildlife [92]. However, the balance of production and removal of ozone from the atmosphere is incredibly complex, and it does not always follow that ozone concentration decreases when air pollution (i.e., NOx and VOCs) in general decreases [94]. In reality, ground-level ozone concentrations vary depending on both pollutant emissions and climate and meteorological factors, making it complex to measure and predict [94].

The direct effects of ozone exposure to human health include cognitive dysfunction, inflammation, and respiratory difficulties (including asthma attacks) [8], [93]. Ground-level ozone is also known to cause widespread damage to vegetation because of its strong oxidative potential at high concentrations, which inhibits photosynthesis, growth and development, and enhances susceptibility to disease [75]. Tropospheric ozone is therefore considered a key threat to food security. Despite the clear impacts to vegetation, the effects of ozone for fauna, and on biotic interactions and other aspects of ecosystem functioning are not fully understood [8], [95].

Impacts to invertebrates

Pure ozone is highly toxic, and is commonly used as a fumigant for insect pest extermination [96], [97]. Even at relatively low concentrations, ozone fumigation is very effective: fumigant containing 5 ppb of ozone was adequate to ensure 100% mortality of eggs and pupae of the potato tuber moth (*Phthorimaea* operculella) [98]; and > 2 ppb of ozone was enough to kill 100% of Indian meal moth (*Plodia interpunctella)* and sawtooth grain beetle (*Oryzaephilus surinamensis*) larvae and adults [99]. The fruit fly (*Drosophila sp.)* is increasingly being utilised as a model lab organism for the study of ozone toxicity, and exposure to ozone has been shown to cause damage to spiracles and decreased survival in Drosophila [14]. Outside of pest control and *Drosophila* lab studies, the direct effects of ozone for invertebrates are rarely explored [14]. Though, increasing attention has focussed on the impacts resulting from the high reactivity of ozone with biogenic volatile organic compounds (BVOCs). BVOCs are chemical odour compounds emitted by plants as a form of communication with other organisms (see section 6). Herbivorous invertebrates and pollinators utilise BVOCs to locate plant and floral resources, and parasitic and predatory invertebrates use BVOCs to locate invertebrate hosts and prey. Ozone can interfere with insect detection of BVOCs, with important consequences for multiple groups of foraging arthropods [47][75].

Evidence for the direct effects of ozone on invertebrate-BVOC interactions largely come from a series of recent experimental studies across several pollinating species. In the fig wasp (*Blastophaga* psenes) – a specialist pollinator of fig trees (*Ficus carica*), environmentally relevant concentrations of ozone[v] were found to induce abnormal motility and distress behaviours (even at low concentrations), with a reduced ability to recover [38]. Further experimentation revealed that ozone[vi] also affects antennal perception of BVOCs in both fig wasps and bumblebees (*Bombus terrestris*) [8]. This effect was dependent on VOC type, concentration and exposure duration, and patterns of antennal response varied between species – with fig wasps appearing to be more sensitive than bumblebees. Although the mechanisms underlying this require further investigation, it was most likely caused by oxidative damage [8]. Dötterl et al., (2016) found that antennal responses to BVOCs in honeybees were reduced for some VOCs but not for others [100]. However, the concentrations of ozone used in this study (1000 ppb) far exceeded what would be considered field relevant. More recently, Démares et al., (2022) exposed honeybees to more environmentally relevant concentrations of ozone[V], finding that they had significantly decreased antennal activity, associated with reduced detection of BVOCs. They also found evidence for impaired olfactory learning and recall of BVOCs, that was associated with reduced ability to memorise the location of floral resources [101].

Tropospheric ozone can also indirectly impact insect-BVOC interactions in two main ways. First, ozone can modify plant physiology resulting in altered BVOC emission profiles, which consequently may be less attractive or unrecognisable to insects [48], [102]. Second, ozone interacts with BVOCs once they are emitted into the atmosphere, which can degrade BVOCs, reduce the distances at which they are detectable, or create novel and unfamiliar odour blends (including other secondary compounds such as

[v] 40, 80, 120 and 200 ppb of O_3.
[vi] 80, 120 and 200 ppb of O_3.

formaldehyde, acetone and carbon monoxide) [48], [102], [103]. For example, under elevated ozone (50 ppb), several important BVOCs involved in host plant detection by the diamondback moth (*Plutella xylostella*) were degraded, altering the overall BVOC blend and reducing the ability of moths to orient towards their host plant. Several novel components of the ozone altered BVOC blend also appeared to have repellent effects, contributing to the overall reduction in searching efficiency [104]. Fuentes (2013) also show that the cucumber beetle (*Acalymma vittatum*), while being neither attracted nor deterred by ozone directly, was unable to detect the location of its host plant in an ozone polluted lab environment[vii] – suggesting the impacts were a result of altered BVOCs[105]. Similar results were found for the alder leaf beetle (*Agelastic coerulea*), that was not directly affected by ozone, but grazed less frequently on their host plant when BVOCs were emitted into an ozone polluted atmosphere[VI] [75]. For some species, the effects appear to be more subtle, for example the parasitoid wasp *Cotesia plutellae* is still able to detect some host BVOCs in ozone polluted environments, but shows a strong preference for intact signals over ozone degraded signals [106].

It has been suggested that some species may be able to mitigate against the effects of ozone by utilising alternative host-finding mechanisms such as visual cues, or by learning ozone-altered odour profiles [103]. However, most pollinators have limited vision beyond very short distances [103], and ozone has also been shown to alter the size and colour of flowers - making them less attractive for pollinators [107]. Skylight – another important visual navigational cue, may also be obstructed if concentrations of other pollutants (i.e. particulate matter) are high [108] (see section 8). The development and timing of flowering can also be disrupted when plants are exposed to ozone, which is especially problematic when pollinators are closely synchronised with the timing of flowering [95], [107]. Additionally, the ability to learn novel odour blends will likely be limited in species where exposure to ozone also affects their capacity for olfactory learning. A recent experimental study found that, while ozone-altered BVOCs were less attractive to hawkmoths *(Manduca sexta*), they were able to learn the new odour blend and associate it with a nectar reward [103]. However, hawkmoths were not directly exposed to ozone themselves. Given the increasing evidence that ozone can affect olfactory learning and recall in pollinators [8], [101], it would be beneficial for future work to explore whether hawkmoths are still able to learn new odour blends when also exposed to ozone.

The degree of vulnerability of plant-insect interactions to VOC degradation will largely depend on several factors. These may include the reactivity of individual BVOCs with ozone (highly reactive VOCs will degrade more quickly), and the spatial-scale at which these interactions take place (long-range signals will spend more time in contact with polluted atmospheres and be more vulnerable to degradation) [109]. Based on these factors, McFrederick et al., (2009) identified the key scent-mediated interactions that are likely to be most vulnerable to pollution: diurnal long-distance pollinator and herbivore

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[vii] At mixing ratios above 80 ppb

attraction (i.e., interactions that occur during the day when pollution is higher); natural enemy of pest attraction; mate attraction; and aggregation pheromones [109]. This suggests that ozone exposure could influence multiple aspects of insect ecology and life-history. Recently, Ryalls et al., (2022) conducted a novel field experiment using a Free-Air Diesel and Ozone Enrichment (FADOE) facility. This enabled them to investigate the effects of regulated and field realistic emissions of diesel exhaust (i.e., NOx) and ozone on insect visitation and pollination of a model flowering plant (*Brassica nigra*). They found that diesel exhaust fumes and ozone – both individually and in combination, and at levels below what is considered safe under current international air quality standards[viii], reduced counts of local wild and managed pollinators (including bees, butterflies and moths) by 62-70%. This was associated with an 83-90% reduction in flower visits, and an overall 14-31% reduction in pollination at these sites (compared to control plots). While the causal factors involved were not investigated, they suggest that interactions between BVOCs and ozone (and other pollutants) are the likely cause of these reductions to pollination. This study indicates that greater research on the complex interactive effects between ozone and insect-mediated ecosystem services is urgently required. It would also be useful for future work to incorporate a greater diversity of flowering plant species into FADOE experimental designs.

In addition to the effects of altered BVOCs, ozone can also indirectly affect invertebrates via changes to host plant nutritional content, which can alter insect community composition (likely in favour of generalist over specialist species)[95], [110], [111]. For example, long-term exposure to episodic ozone in a soil seed bank resulted in altered patterns of dominance in arthropod communities, ultimately altering food web dynamics [112]. Herbivorous insects fed on ozone treated plants generally exhibit performance responses that vary within and between species of insects and species of plants [113], [114], making it difficult to generalise effects across groups. For example, some species have been shown to experience negative effects from feeding on ozone exposed plants (possibly due to reductions in foliar quality or BVOC interactions) [111], [115], [116], while other species appear to experience no effects [117]. Conversely, some species experience positive effects, possibly due to reductions in host plant defences and BVOCs that attract their natural enemies (e.g. predators and parasitoids) [114], [118], with the result being greater rates of herbivory that causes increased damage to vegetation [119].

Responses to ozone also likely vary within species. For example, in the aspen leaf beetle (*Chrysomela crotchi*), that generally experiences a decrease in performance when reared on plants under elevated ozone, responses were also found to vary based on host plant genotype [113]. Similar results were found in cabbage butterflies (*Pieris brassicae)* where ozone differentially affected larval performance based on plant genotype [120]; and in Spider mites (*Tetranychus urticae*) where observed decreases in developmental time under elevated ozone varied by plant resistance lines [121]. The matter is further

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[viii] O_3 = 35.2± 0.6 ppb; NOx = 59.6± 1 ppb (≈116 µg/m^3) relative to control plots

complicated given that responses to ozone exposure also vary depending on the life stage of insects (larvae appearing more sensitive), and the life stage of the host plant (later ages appearing more sensitive) [94], [114], [115]. The effects of ozone may also depend on other atmospheric factors, such as CO_2 concentration. For example, the forest tent caterpillar (*Malacosoma disstria*) experienced benefits from feeding on host plants under increased ozone, but this effect was reversed when CO_2 was also elevated [122]. Conversely, the opposite effect was found in gypsy moths (*Lymantria dispar*), that experienced performance reductions after feeding on ozone exposed host-plants, but these reductions were mostly ameliorated under elevated CO_2 [116]. In order to gain a complete understanding of the impacts of ozone exposure for invertebrate communities, clearly future work should attempt to incorporate as many species and population specific interacting factors as possible.

Particulate Matter

Particulate matter (PM), often referred to as dust, consists of all non-gaseous organic and inorganic particles suspended in the air [123]. The compounds and materials that make up PM vary considerably in size, composition and origin [123]. Exposure to particulate matter has been linked to increased morbidity and mortality in humans and is associated with a significant global disease burden [124]. Particles measuring less than 2.5 micrometres in diameter ($PM_{2.5}$) are of particular concern to human health [124], [125]. PM affects human health more so than any other pollutant, and the WHO estimate that 4.2 million premature deaths can be attributed to ambient (outdoor) $PM_{2.5}$ exposure [125].

Ambient PM primarily originates from the incomplete combustion of solid fuels, such as coal and wood. Major primary anthropogenic sources of ambient PM include: industrial activity, energy generation, residential solid fuel use, agricultural activity, land transport, and biomass burning [123], [124], [126]. Natural sources of primary ambient PM include windblown dust, soil erosion, volcanic eruptions, forest fires and sea spray [123], [126]. Additionally, PM can be formed as secondary compounds from the reactions of precursor pollutants such as nitrogen and sulphur oxides (NOx and SOx), volatile organic compounds (VOCs), and ammonia (NH_3) [123], [126].

Impacts to invertebrates

The majority of research into the impacts of PM exposure on invertebrate health comes from studies of the free-living nematode *Caenrhabditis elegans* (*C. elegans*). *C. elegans* has long been used as a model organism for the study of ecotoxicity, partly because they are inexpensive, bioethical and easy to maintain [127]. Additionally, on the genetic level, they have remarkable similarity to humans across several important regions [127], [128]. Across these studies, $PM_{2.5}$, even at low levels, has been found to impact multiple essential biological functions including development, lifespan, locomotion, reproduction, neurobehaviour, and intestinal function [127], [129]–[131]. Consistently, prolonged exposure has been found to cause more severe impacts than acute exposure [127]. Genetic studies have also revealed altered expression of genes required for controlling oxidative stress responses following chronic exposure $PM_{2.5}$ [128]. Transgenerational effects have also been observed, whereby impacts on reproduction, lifespan, locomotion and intestinal development have been transferred across multiple generations [132]. In this study, the progeny of exposed individuals never fully recovered from $PM_{2.5}$ toxicity [132]. Transgenerational effects have also been recently observed in the red flour beetle (*Tribolium castaneum*), where chronic exposure to coal dust resulted in concentration-dependent severe and life-limiting physiological abnormalities that spanned multiple generations [133]. The effects of oxidative stress and impaired intestinal development and defecation behaviour have been identified as the major factors driving toxicity from prolonged $PM_{2.5}$ exposure in *C. elegans* [127], [129], [131], [132], [134], [135]. Sun et al., (2016) identified that the contribution of heavy metals from coal combustion was particularly harmful (especially lead, chromium and copper), with greater toxicity being caused by a combination of these metals than exposure to any metal alone (see section 9)[136].

Beyond the lab-studies of *C.* elegans, we know virtually nothing about the effects of PM for the vast majority of species [137]. We can predict, however, that airborne PM may be particularly harmful for winged and foraging invertebrate species, especially pollinators, that regularly come into prolonged contact with airborne dusts. It has long been known that the application of smoke to honeybees reduces antennal alarm pheromones [138]. More recently, it has also been shown that the fine hairs of bees (pubescence) promote the accumulation of electrical charges at the body surface. This charging attracts pollen but also other airborne particles including pollutants, and especially PM [139]. The attractant properties of bee pubescence to airborne pollutants are so effective that bees and bee products are commonly used as bioindicators of environmental pollution [140]. Bees have been found contaminated with a mixture of ultra-fine (<0.1 micrometres), fine and coarse PM, comprising heavy metals, quartz, calcite, baryte and clay minerals [139]–[141].

While bees are increasingly being used as bioindicators of environmental pollution, the direct effects of such exposure for the bees themselves have rarely been explored [141]–[144]. In those studies that have explored the impacts of direct exposure to PM, effects include both lethal and sublethal impacts (e.g., behavioural, genetic and physiological/cellular level alterations)[142], [145], [146]. Honey produced by contaminated bees living close to heavily trafficked areas displays fine and ultra-fine metal-based PM contamination [140]. Bees will therefore be directly exposed to PM not just via cuticular contact (and also presumably inhalation), but oral ingestion as well, from consuming contaminated pollen and honey (which represent a substantial portion of the bee diet) [140], [144]. When ingested, PM comes into direct contact with the gut. The bee gut microbiota consists of a simple but distinctive community of bacterial species that provide essential functions for bee health [147]. Acute and chronic ingestion of metal-based components of PM has been shown to alter the gut microbiota in the honeybee [148], and cause histological and cellular damage to midgut epithelial cells [145]. Honeybee gut dysbiosis[ix] has also been previously associated with an increase in disease susceptibility and greater mortality [137], [147], suggesting important impacts of PM ingestion (and particularly heavy metals (see section 9)) on honeybee health and survival. Pollutants incorporated into colony food stores or nesting material also accumulate over time, such that even subtle effects on individuals can translate into severe colony-wide effects over generations [137]. Effects are likely to vary among taxa, for example depending on foraging range, foraging mode and resource type [137]. Solitary species are also predicted to be more at risk of pollution, because foraging distances are shorter, food sources are generally less varied, and contaminated food is less avoidable (than for social species) though this remains to be tested [137].

Thimmegowda et al.,(2020) recently performed a field-based quantitative analysis of impacts of PM on the giant Asian honeybee (*Apis dorsata*). They found that exposure to a mixture of fine and coarse PM across field sites in Bangalore[x], India, was strongly associated with reductions in bee flower visitation, but also a number of important physiological attributes including survival, heart rate and haemocyte levels. They also found alterations to the expression of genes related to lipid metabolism, stress and immunity [146]. This study has received criticism for heavily weighting correlative evidence where confounding factors were not controlled for (which should include, at the very least, exposure to other pollutants)(see [143], and the authors reply [149]). However, Thimmegowda et al., (2020) were able to partially address this in their initial study by exposing fruit flies (*Drosophila sp.*) to the same pollutants at similar concentrations in a controlled lab environment. While different species may differ in their responses to air pollution, in this case the flies displayed very similar results across all aspects of physiology, behaviour and genetics examined. These results are also in agreement with Wang et al., (2017), who found that experimental exposure to concentrated PM increased rates of premature mortality, inflammation and oxidative stress in *Drosophila* [xi] [150]. Other studies have also found that exposure of fruit flies to food contaminated with ash in concentrations of 1% and 2%, resulted in genetic loads of 37.1% and 68.7% respectively [151]. This indicates that exposure to ash from industrial activity can also induce the accumulation of recessive mutations that affects individuals fitness [151]. Overall, given the severe implications associated with the loss of key pollinator species, there is a clear need for further research in this area. Ideally this would include causal work where confounding factors can be controlled for (e.g., floral abundance, bee age and condition, diet, source colony, and exposure to other pollutants) to confirm and further explore these results in giant Asian honeybees, and other species.

PM may also impact pollinator performance indirectly by obstructing the polarisation pattern of skylight – an important navigational cue utilised by several pollinating species to

[ix] An imbalance between the types of microorganisms present in the gut
[x] Concentrations of PM ranged from 28.32 – 98.59 $\mu g/m^3$. >80% reduction in pollinator survival was seen over concentrations of 50 $\mu g/m^3$
[xi] PM concentrations 52 – 91 $\mu g/m^3$

orient themselves in space [152]. Atmospheric PM can scatter skylight, lowering the degree of light polarisation, in some cases down to zero (e.g., in heavy dust storms) [108]. Recently, Cho et al., (2021) investigated the effect of a very heavy air pollution event[xii] on honeybee (*Apis mellifera*) foraging trip duration. They found that foraging trip duration increased by 71%, and this was associated with high concentrations of fine PM and a significantly reduced light depolarisation ratio [108]. It is worth noting that other factors such as quality and quantity of floral resources, and the direct effects of air quality on flight performance, were not accounted for in this study. In the painted lady butterfly (*Vanessa cardui*), flight duration and speed was significantly reduced in smoke polluted air (under all $PM_{2.5}$ concentrations tested[xiii]), relative to clean air [16]. While the mechanisms were not directly investigated, light polarisation was unlikely to play a factor in this case given the short distance between the butterflies and their light source. Instead, they suggest that reduced flight speed could be the result of a mechanical disturbance due to PM adhering to the wing surface – similar to the cause of reduced flight ability in mosquitos flying in foggy conditions [153]. They also suggest that spiracle closure under high pollution stress would have resulted in a lowered metabolism that may have limited flight duration [16]. These hypotheses remain to be tested.

Herbivorous invertebrates living close to sources of PM are likely to be impacted by dust deposited on foliage. Dust covering leaf surfaces may: 1) act as a structural barrier to edible leaf material, 2) reduce palatability and digestibility of leaf material, 3) inhibit photosynthetic activity that reduces foliar nutrient quality, 4) act as an abrasive layer causing mechanical damage to herbivores, and 5) act as direct toxicants when ingested [154]. Heavy-metal based PM from a petroleum production site was found to contaminate the host plant of Muga silk worms (*Antheraea assama*), which was thought to contribute to the decline of silk production from worms at this site [155]. The mechanisms by which PM exerts toxic effects on silk worms are unclear, but in the small brown butterfly (*Bicyclus anynana)*, prolonged exposure to PM pollution has been shown to increase mortality, restrict larval development and lower pupal mass [11]. In this case, these impacts were found to be a direct effect of PM [xiv], as opposed to being the consequence of exposure to polluted food sources [11]. Upon post-mortem examination, they did not find PM in the tracheal system of caterpillars, suggesting that the observed responses to PM were the consequences of either direct toxicity or increased spiracle closure, as opposed to blocked airways [11]. In other species of Lepidoptera (moths and butterflies), larvae have also been shown to experience progressive impacts on growth, digestion efficiency, development and survival when consuming abrasive minerals - possibly the result of mechanical damage [154]. Consumption of abrasive silica particles has previously been shown to result in permanent mandibular damage that reduces feeding efficiency and overall lifetime fitness in the African armyworm (*Spodoptera exempta*) [156]. Exposure of

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[xii] Heavy dust storm in May 2017. Average concentrations of $PM_{2.5}$ = 250 μg/m^3 and PM_{10} = 1000 μg/m^3
[xiii] 150, 180 and 750 μg/m^3
[xiv] Concentrations of PM between 50 (control) and 117 (treatment) μg/m^3

fruit flies to food contaminated with ash in concentrations of 1% and 2%, resulted in genetic loads of 37.1% and 68.7% respectively [151]. This indicates that oral exposure to ash from industrial activity can also induce the accumulation of recessive mutations that affects individuals fitness [151].

Some species may be able to exhibit behavioural plasticity to avoid the effects of contamination. In the leafmining moth *Stigmella lapponica*, females are able to alleviate the impacts of pollution for their offspring, by avoiding laying their eggs on highly polluted leaf areas [157]. In some species, behavioural plasticity may not be possible, or may only be possible for certain life-stages. For example, *Helicoverpa armigera*, a herbivorous moth, experienced reduced survival when late-instar[xv] larvae were fed on tomato leaves contaminated with coal dust [154]. Larvae were unable to adjust their behaviour to avoid consuming contaminated leaf material. Contrastingly, neonate (just hatched) larvae, when given a choice, showed a preference for uncontaminated leaves which allowed them to avoid the impacts of coal dust on their survival [154]. In some cases, individuals may alter feeding behaviour to increase overall consumption of a contaminated food source, in an attempt to counteract reduced nutritional content [154], [158]. Such behavioural adaptations could inadvertently increase exposure to contaminants. While evidence of this is lacking for PM, Slansky & Wheeler, (1992) found that the velvet bean caterpillar (*Anticarsia gemmatalis*) increased food consumption after caffeine contamination reduced the nutritional content of their host plant. This resulted in greater overall toxicity and decreased fitness in this species [158]. Future work would benefit from exploring the impacts of such compensatory feeding behaviour for invertebrates feeding on PM contaminated food sources.

Some species may be able to exert more long-term adaptive responses. A well-known example of selective adaptation to pollution is the industrial-melanism of the peppered moth (*Biston betularia*). In this case, following the industrial revolution, melanic forms of the peppered moth increased in frequency in some heavily industrialised locations in England, eventually becoming the dominant form over the wildtype (peppered white) in these areas. This rapid evolutionary change is generally believed to be the result of increased selection pressure to remain camouflaged against smoke-blackened trees [159]. The frequency of melanistic forms have since declined in parallel with a reduction in atmospheric pollution [159]. In other species where their ability to adapt is restricted, for example because of genetic limitations, or an inability to shift their range to less polluted environments, the impacts of pollution are likely to be much more severe.

[xv] A late phase of moulting during arthropod larval development.

Heavy Metals

Heavy metals and metalloids occur naturally in the Earth's crust and atmosphere, but anthropogenic activity can promote widespread heavy metal contamination above baseline levels, generating significant public health concerns for humans, animals and plants [9], [160][161]. Combustion constitutes the most important source of heavy metal emissions into the atmosphere. Primary sources include power generation, smelting, incineration and the burning of fossil fuels [161]. Heavy metal emissions generally arise from raw materials or trace metals in fuels, and - when combusted, are either emitted as vapours, particulate or both. Some metals are initially emitted as a vapour that then condense in the air to form ash [162]. Atmospheric sources of heavy metals result in metal pollutants spreading over large areas, where they interact directly with organisms in the air, but also following aerial deposition into topsoil and water [163], [164]. Heavy metals are unable to degrade, and so persist in the environment well after the source has been removed [160], [164].

While many heavy metals provide essential micronutrients for organisms (e.g. copper, manganese, selenium, zinc, cobalt and iron), they can quickly become toxic above trace levels. Other heavy metals have no beneficial biological function and are highly toxic even at low concentrations (e.g. cadmium, chromium, mercury, lead, nickel and arsenic) [9], [165], [166]. Both essential and non-essential metals accumulate in organismal tissue and are readily transferred through trophic levels [160], [165], [167].

Impacts to invertebrates

The toxic effects of heavy metals have been well documented in vertebrates, where impacts can include organ, skeletal and nervous system damage, carcinogenesis, and neurotoxicity [9], [168]. Even acute exposure to very low concentrations can be damaging. For example, the World Health Organisation (WHO) has stated that there are no safe levels of lead exposure for vertebrates [169]. The effects of metal pollution are more poorly understood in invertebrates, however there is an increasing body of evidence to suggest that many invertebrates accumulate high levels of trace metals, and are highly sensitive to metal pollution [9], [170]. For example, Monchanin et al., (2021) found evidence that non-essential metals tend to accumulate at higher levels in invertebrates than vertebrates, and that invertebrates may be more sensitive to their damaging effects [9]. This is particularly concerning because current safe environmental levels of metal pollutants are typically only determined by their effects in vertebrates (namely humans) [9], [161], [171]. Indeed, Monchanin et al., found evidence that levels of metal pollution currently considered permissible for humans are harmful for terrestrial invertebrates [9].

Invertebrates may absorb atmospheric heavy metals directly through contact with their exoskeletons, through inhalation, or indirectly through ingestion of contaminated soil or food [146], [160], [172]. Exposure to heavy metals in some invertebrate species has been shown to result in increased mortality [166], [173], [174], and specific lethal effects include cytotoxicity, carcinogenic and mutagenic effects [9]. Sublethal effects are also common and include impaired fertility and fecundity [166], [173], developmental delays and malformations [166], [173], [175], impaired cognition [176], impaired resistance to pathogens and disease [177], and altered behaviour (e.g. foraging/feeding, oviposition behaviour, and taxis[xvi] [9], [178], [179]. Negative effects on population parameters have also been observed [166], [180], and in studies where the impacts of multiple metals have been explored simultaneously, the combined toxic effects can be far greater than the effects of individual metals alone [136], [178], [181], [182].

Some species are known to accumulate heavy metals to a greater degree than others [160], [180]. However, impacts of heavy metals appear to vary considerably between invertebrate groups, with sensitivity varying by morphology, physiology, behaviour, habitat, and food preference, as well as concentration and type of heavy metal [183]. Despite this, multiple studies have attempted to generate patterns linking certain groups with heavy metal sensitivity [183], [184]. In a meta-analysis by Kozlov & Zvereva, (2011), they show that pollution-induced differences may vary across trophic levels, with secondary producers (e.g., predatory and parasitic invertebrates) generally appearing more sensitive and being more likely to decrease in abundance [185], [186], whereas primary consumers (e.g. herbivorous invertebrates) generally increase [185], [186]. Changes in trophic level composition can have drastic impacts on the environment, although it may be possible to recover if pollution levels are reduced. For example, Zvereva et al., (2016) found that declining pollution from a local nickel-copper smelter was associated with a decrease in abundance of herbivorous invertebrates, likely due to the return in abundance of their natural enemies [186].

Land snails are considered useful bioindicators of metallic pollution in terrestrial ecosystems [170], [187]. So-called “macro-concentrators”, snails are known to accumulate substantial amounts of heavy metals, with a limited ability to excrete them, and with the strongest levels of contamination occurring closer to sources (e.g., motorways and industrial sites) [188], [189]. Snails become exposed to heavy metals via respiration, oral ingestion, and dermal contact [170], [188]. Experimental and field studies across various terrestrial gastropods has shown that heavy metal accumulation impacts survival, growth, reproduction and feeding behaviour [170], [188]. The toxic effects of metals generally appear to occur as a result of oxidative stress in these species [170]. Owojori et al., (2022) explored the toxicity of lead and cadmium in the tropical snail *Archachatina papuracea*, finding that cadmium and lead accumulated in snail tissue progressively with increasing concentrations. They also found that cadmium was 10 to 30 times more toxic than lead[xvii] – consistent with the relative toxicity of cadmium for other soil organisms [190]. Other impacts from this study included decreased egg production.

[xvi] Movement of an organism in response to a stimulus
[xvii] Median lethal concentration (LC50) was 93±4.4 mg/kg and 1121±457 mg/kg for Cd and Pb respectively.

Ants and their nest material can also be used as indicators of heavy metal pollution in terrestrial ecosystems [180], [191]. While generally tolerating heavy metals better than many other species, ants can experience significant impacts from contamination on several population level parameters including: biodiversity, abundance, community structure and colony size [180], [191], and they may also experience behavioural impacts [192].

Honeybees (*Apis mellifera*) are also commonly used as bioindicators of heavy metal pollution, given the substantial evidence that they can bioaccumulate metals even at very low levels of pollution [171], [193]–[195]. The fine hairs coating their bodies are known to attract and accumulate particulate matter (including metal-based particles) (see section 8), which is then deposited into nesting material and food stores – spreading throughout the colony. Honeybees are also widespread, and forage over large areas [193], [196]. Contamination of honey and wax produced by Australian native bees (*Tetragonula carbonaria*) with lead and zinc, strongly correlated with both dust and soil concentrations across multiple sites (see table 1 in Zhou et al., 2018 [144]) indicating that this species makes a reliable bioindicator of environmental heavy metal contamination [144]. This study also found that contamination in honeybees and their wax corresponded well with concentrations of historic lead aerosols (1978 – 2004), indicating that these pollutants are persistent contaminants of biological samples [144].

In the honeybee, heavy metals have been shown to induce both acute and chronic effects. For example, cadmium and copper exposure increased developmental time, decreased feeding efficiency, and resulted in greater mortality for both larvae and adults alike [181]. These effects were dose-dependent, and the effects of both metals combined were greater than the effects of each metal alone[xviii] [181]. Similarly, honeybees (and their honey) sampled closer to urban and industrial areas were significantly more contaminated with lead and mercury[xix] compared to bees sampled from agricultural areas, and especially mountainous areas where no contamination was found [197]. In a lab-based study, where honeybee colonies were exposed to field-realistic concentrations of lead, bees raised under lead exposure [xx] experienced significantly reduced head size and impaired cognition (in the form of reduced olfactory learning) [176].

A number of correlational studies have found negative parameters of bee and colony health associated with gradients of heavy metal pollution. For example, Urbanisation was positively correlated with lead contamination in colonies of the common Eastern bumblebee (*Bombus impatiens)*, where elevated lead also correlated with a decrease in colony size (in terms of worker numbers and number of larvae present) [198]. Similarly, Moron et al., (2012) found a significant reduction in the abundance and diversity of

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[xviii] Individual concentrations of Cd and Cu ranged from 0 – 400 mg/L, and joint concentrations ranged from 0 – 800 mg/L

[xix] Highest concentrations of Hg and Pb in honey: 3.249 mg/kg and 0.238 mg/kg respectively. Highest concentrations of Hg and Pb on bees: 0.051 mg/kg and 0.489 mg/kg respectively.

[xx] 0.75 mg L^{-1} of Pb

multiple species of solitary wild bees along a gradient of heavy metal pollution (cadmium, lead and zinc) in two geographically distinct areas (one in the vicinity of an active smelter, and one in the vicinity of an inactive smelter) [199]. In a later study, increasing environmental concentrations of cadmium, lead and zinc was found strongly negatively associated with brood size and the proportion of dead offspring in red mason bees (*Osmia rufia)*, with heavily polluted sites experiencing a 30-40% increase in offspring mortality [200]. Heavy metals have also been shown to have a negative effect on the survival and reproduction of other pollinators, especially butterflies [201]–[203]. There do appear to be cases, however, where exposure to certain heavy metals does not appear to negatively impact pollinators. For example, in bumblebees, no correlation was observed between heavy metal contamination and species diversity or dominance, despite finding that bees were contaminated with moderate levels of lead and cadmium [204]. This could be due to species specific tolerance to the specific metals investigated, or a failure to capture other sublethal impacts.

Many invertebrates have evolved mechanisms to rid themselves of excess heavy metals. These adaptations can be behavioural such as avoiding contaminated food/sites [160]; physiological such as excreting metals in their faeces, and storing metals in the hepatopancreas; or genetic such as upregulating genes responsible for the production of detoxification enzymes [9], [160], [167], [190]. For example, honeybees contaminated with lead and mercury from industrial and urban pollution were found to have upregulated the expression of antioxidant enzyme genes, suggesting adaptation of these bees to oxidative stress [197]. Similarly, in the nematode *Caenorhabditis elegans* – a commonly used model lab organism for the study of ecotoxicity, exposure to cadmium, lead, chromium and arsenite resulted in the upregulation of several stress-response genes [205]. This response varied significantly by metal, with higher levels of stress responses observed for cadmium than the other metals. In this case, cadmium exposure also coincided with a deterioration of physiological parameters such as growth and reproduction, but whether this was a direct result of cadmium toxicity, or a side effect from the upregulation of stress responses, was unclear.

While these detoxification mechanisms may protect certain species from low concentrations of metals, many species have little to no tolerance of heavy metals. A number of species also appear unable to detect the presence of metal and metalloid contamination at all [178]. Some avoidance behaviours – such as increased motility, may also put individuals at greater risk of predation [178]. Resisting the toxic effects of heavy metals is also energetically demanding and will come at the cost of reduced energy availability for other metabolically demanding functions including reproduction, and defence against pathogens and disease [165], [166]. For example, in ground beetles (*Pterostichus oblongopunctatus*), a species of carabid beetle known for their tolerance to heavy metals (due to efficient mechanisms of detoxification), chronic exposure still comes at the cost of reduced egg quality and hatchability [167]. These impacts also appear in lab-reared offspring of field-collected beetles, suggesting intergenerational effects also occur [167]. Additionally, utilising metal detoxification mechanisms is also unlikely to protect individuals from sub-lethal effects [9]. In some cases, mechanisms of detoxification may simply not be effective under very high concentrations of heavy metals and be more effective for some metals than others. For example, lab-reared larvae of the Apollo butterfly *(Parnassius apollo)* exposed to leaf samples collected from several contaminated sites in Finland, were able to excrete considerable amounts of cadmium, iron, manganese and zinc in their faeces, but detoxification appeared ineffective for copper [201]. Furthermore, detoxification for all metals was completely ineffective when fed on leaves from the most polluted site, resulting in 100% mortality of larvae [201]. Apollo butterflies experienced significant declines and local population extinctions in Finland in the 1930's. It was suggested that aerial metal pollution was a significant contributing factor, and in support of this, recovery of these species has only occurred in areas where concentrations of airborne heavy metals have decreased [201].

Heavy metals can move through trophic groups, either becoming bio-magnified (more concentrated as they move from one trophic level to another) or bio-minimised (less concentrated as they move from one trophic level to another)[165]. Whether trophic-transfer of heavy metals occurs via bio-magnification or bio-minimisation will depend on each individual species involved, their tolerance and ability to detoxify and recover from heavy metal exposure, and the properties of the specific metals involved [160], [165]. If bio-magnification occurs, the impacts for whole ecosystems can be severe. Heavy metals in the air can be deposited onto plants, or accumulated heavy metals in soils can be transported to plant roots and eventually above-ground vegetation, where herbivorous invertebrates can be indirectly exposed [165]. This can result in significant loss of diversity and alterations to community composition. For example, Nesterkov & Vorobeichik, (2009) showed that, in close proximity to a copper smelter (of which copper, zinc, cadmium, lead and sulphur dioxide are among the primary aerial emissions), total above ground plant biomass decreased by 50%, with tolerant grasses gaining dominance. This was associated with a drastic alteration in invertebrate community composition: sucking herbivores (primarily *Cicadinea* and *Miridae*) dominated, with a reduction or complete disappearance of gnawing herbivores (e.g., molluscs and harvestmen).

Conclusions and Recommendations

Terrestrial invertebrates perform vital functions for numerous ecosystem services, but they are currently experiencing global declines. Pollution is now considered a global threat to invertebrates, and air pollution has received increasing attention as a significant risk factor, especially for pollinators.

It has been repeatedly acknowledged across studies, that the impacts of air pollution on invertebrates are understudied. In particular, research has focussed primarily on only a narrow set of indirect impacts (e.g., on habitat or resource loss), or on impacts from a limited number/type of pollutants (e.g., heavy focus on agrochemicals such as pesticides). Comparatively little attention has been paid to more direct effects, with a particular lack of knowledge on the impacts of air quality on invertebrate physiology and behaviour.

Recommendation 1: There is a need for future work to focus more on direct effects, particularly focussing on neglected areas, such as the impacts of air quality on invertebrate physiology and behaviour.

There have been several attempts to summarise trends across invertebrate groups. These seem to generally support that the impacts of air pollution to invertebrates disproportionately affect specialist and winged species over generalists [42]. In particular, a 2010 meta-analysis on the responses of terrestrial arthropods to air pollution, revealed that widespread adverse impacts were most clearly observed for decomposer and predatory arthropods [207]. This is likely due to the dependence of specialists on a narrower range of ecological conditions. Winged species are also often in prolonged contact with polluted air with a limited ability to avoid exposure. Generalist herbivores may also be able to take advantage of enemy-free spaces and altered plant defences potentially leading to shifts in species composition. General trends should be interpreted with caution, however, as research is still lacking. Furthermore, much research to-date is correlational with fewer studies able to provide causal evidence. There is also significant variation in effects both within and between species and ecological conditions. In general, pollution effects also depend on both temperature and precipitation in such a way that ecosystem-wide adverse effects are likely to increase under predicted climate changes [207].

The effects of airborne pollutants have also only been explored for a limited number of pollutants (often not at environmentally relevant concentrations), and in a very limited number of species [2], [11]. There is a paucity of research on the impacts of air quality to non-arthropod species in particular.

Recommendation 2: Future work would benefit from studying a more diverse range of invertebrate species. This should include different groups and populations that are likely to differ in their physiological and behavioural responses to air pollution, as well as their specific ecological vulnerability.

There has been a recent surge in the number of studies exploring the impacts of air pollutants on pollinators. Particular attention has been paid to the effects of NOx, VOCs and ozone. Some concerning impacts include the interference of pollutants with insect – plant communication. The combined influence of VOCs, NOx and ozone can diminish the ability of insect pollinators to locate and memorise floral resources, with potentially significant impacts to pollination services. Other direct and indirect impacts to pollinators can occur from exposure to particulate matter and heavy metals. Given that pollutants are never found in isolation in the atmosphere, but rather occur simultaneously and interact with one another constantly, our knowledge is severely limited by the lack of research exploring the impacts of pollutants in combination.

Recommendation 3: Future work would benefit from an increase in the number of studies exploring the combined impacts of exposure to multiple field realistic concentrations of pollutants on invertebrates. This would be especially beneficial for understanding the full impacts to pollinators that seem to be significantly

impacted by exposure to multiple pollutants. This may also reflect a wider need for the consideration of a more holistic approach to air quality risk assessment and future policy and targets.

Focus has largely been directed towards the study of the European honeybee (*Apis mellifera*). Whilst the honeybee is certainly a vital generalist pollinator that performs multiple ecosystem services, we know very little about the direct and indirect impacts of air pollution for other pollinating species.

Recommendation 4: To improve our understanding of the impacts of air pollution to pollination services, it is vital that we expand our knowledge across a wider range of pollinating species, including social and solitary bees, butterflies, flies, and moths. This could be particularly valuable when developing the air quality narrative in relation to ecosystem services and public engagement.

Overall, whilst this evidence review provides an important first step in addressing the major gaps and areas for future work, there is a great deal of complexity that cannot be captured in a review format.

Recommendation 5: It would be useful to generate a series of systematic reviews targeting specific pollutants, or groups of pollutants with interacting effects. Given the apparent diversity of invertebrate responses to air pollution, species specific reviews would also be beneficial. This would aid in the generation of more specific and actionable recommendations.

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Appendices

1. Search Strings

Each search consisted of an initial basic string to capture common search terms:

- **TOPIC**: Invertebrate OR insect OR arthropod OR pollinat* OR terrestrial OR hexapod OR beetle OR parasitoid OR wasp OR bee OR honeybee OR butterf* OR moth OR fly OR flies OR hymenoptera OR homoptera OR arachnid OR spider OR millipede OR centipede OR chilopod OR myriapod OR worm OR annelid OR nematode OR slug OR snail OR mollusc OR gastropod
- **AND TOPIC:** (air SAME pollut*) OR atmospher* OR (airborne SAME pollut*) OR (aerial SAME pollut*) OR (gaseous SAME pollut*) OR “air quality” OR aerosol OR emission OR smoke OR dust OR fumes OR diesel OR petrol OR smog OR (vehicle SAME emission) OR (vehicle SAME pollut*)
- **AND TOPIC:** expos* OR concentrat* OR dose OR toxic* OR “mode of action” OR lethal OR sub-lethal OR impact OR effect OR affect OR uptake
- **AND TOPIC:** physiolog* OR life-history OR reproduction OR fertility OR fecundity OR behaviour OR forag* OR development* OR respiration OR mortality OR survival OR stress OR lifespan OR learning OR memory OR olfactory
- **NOT TOPIC:** marine OR freshwater OR seawater OR sea OR ocean OR benthic OR aquatic OR swim OR mussel OR fish
- **NOT TOPIC:** pesticide OR fungicide OR insecticide
- **NOT TOPIC:** noise OR light

Each of the 6 separate searches consisted of specific additional search terms to capture the papers relevant to the associated pollutant type:

1. **TOPIC:** ammonia OR NH3
2. **TOPIC:** “nitrogen oxide*” OR NOx OR NO OR “nitrogen dioxide*” OR NO2
3. **TOPIC:** VOCs OR “volatile organic compound*” OR NMVOC OR “Non-Methane Volatile Organic Compound*” OR benzene OR 1,3-butadiene
4. **TOPIC:** ozone OR O3
5. **TOPIC:** particulate OR PM2.5 OR pm2.5 OR PM10 OR pm10
6. **TOPIC:** “heavy metal” OR “trace metal” OR metal OR (metal SAME pollut*) OR trace

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