REVIEW PAPER



Metals could challenge pollinator conservation in legacy cities

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Abstract

Metal contamination is a worldwide issue that is particularly present and ubiquitous in urban environments. Many pollinators, including species of bees, butterflies, and moths are found in heavily modified landscapes where they may be negatively affected by exposure to metal contamination. Increased efforts to convert vacant urban lands to habitat that benefits such communities necessitates a thorough understanding of the hazard and risks pollinators face in metal contaminated landscapes. This investigation revealed that bees and butterflies have complex species and population specific responses to metals. Exposure to these pollutants can have reproductive, immunological, behavioral, and developmental impacts. These include challenged reproductive efforts, longer developmental times, and elevated brood mortality for pollinators.

Implications for insect conservation This review shows that pollinator conservation efforts are threatened if we fail to recognize the importance of metal exposure within contaminated landscapes. Bees and butterflies are exposed to metal concentrations in legacy cities that can cause reproductive, development, or behavioral impacts.

Keywords Bee · Butterfly moth · Vacant land · Contamination · Post-industrial · Novel habitat · Ecosystem services · Urban · Ecological restoration

Introduction

Over 350 cities worldwide have experienced substantial population loss over the last half century (Luescher & Shetty 2013) largely due to deindustrialization and suburbanization (Lever 1991). A hallmark of these post-industrial 'legacy cities' is their large holdings of vacant land resulting from the demolition of abandoned infrastructure (Fig. 1A–D) (Seymour 2020). Legacy cities are characterized by long-term economic disinvestment, shrinking populations, suburbanization, and social and political conflicts (Martinez-Fernandez et al. 2012; Haase et al. 2014). Vacancy shapes the landscape pattern of legacy city by creating dynamic mosaics of occupied and abandoned structures, and patches of formerly occupied vacant land (Gardiner et al. 2013; Sampson et al. 2017). Diverse and abundant bee and butterfly communities

Anthropogenic activities such as transportation, manufacturing, construction, improper disposal of wastes, and demolition have contributed to metal pollution in cities worldwide (Sharma et al. 2015a; Nakajima & Aryal 2018) (Fig. 2). Even following the regulation of some major sources of metal pollution, a legacy of soil metal contamination remains as metals are generally stable and remain in place until remediated. For example, beginning in the 1970s and 1980s lead (Pb) was no longer used in the production of paint and gasoline in the United States (Kerr & Newell 2003). Nonetheless, Pb particles released from car exhaust and paint chips remain in urban soils (Schwarz 2016) and pose a risk to the local biodiversity (Gardiner & Harwood 2017). Likewise, metals such as chromium (Cr), copper



have been documented within urban vacant lots within legacy cities (Sivakoff et al. 2018; Dylewski et al. 2019; Turo et al. 2021), promoting conservation focused investments to manage these reclaimed greenspaces as pollinator habitat (Fig. 1E–F) (Burr et al. 2016; Dylewski et al. 2019). However, vacant lot soils can contain elevated concentrations of metals (Fig. 2) (Sharma et al. 2015a; Perry et al. 2021), and the potential of metal pollution to challenge urban pollinator health cannot be ignored (Harrison & Winfree 2015; Sánchez-Bayo & Wyckhuys 2019; Parreño et al. 2022).

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Fig. 1 The legacy city of Cleveland, Ohio (USA) has lost over 50% of its peak population, which has resulted in an overabundance of housing infrastructure (A), which is demolished (B) seeded with fescue grasses (C) and mown approximately once per month during the growing season. Monthly mowing supports bloom of urban spontaneous vegetation such as red clover (*Trifolium pratense*), white clover (*Trifolium repens*) and chicory (*Cichorium intybus*) (Perry et al. 2021), which is visited by a high species richness of wild bees (Sivakoff et al. 2018; Turo et al. 2021) (D). The City of Cleveland Land Bank manages over 27,000 vacant lots and has sought out ways

to reimagine these greenspaces to support biodiversity and provide ecosystem services to the community. The addition of pocket prairies containing native Ohio wildflowers (E) and adding ornamental flowering plants to urban farms (F) are management strategies currently employed to provide forage for urban pollinators. Over 100 bee species have been found foraging within Cleveland's vacant lots, thus there is an urgent need to identify the metal exposure risks associated with vacant land as bee habitat and provide recommendations on how to safely implement pollinator focused conservation within legacy cities



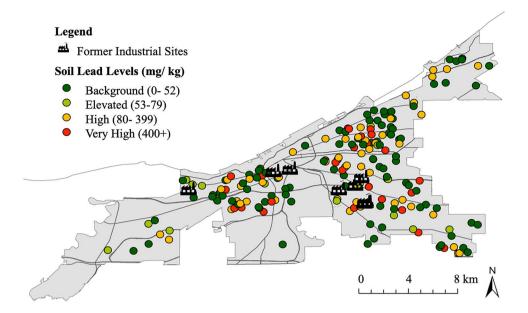


Fig. 2 Soil lead contamination is widespread throughout the city of Cleveland, OH, resulting in large part from historic manufacturing and industrial complexes (Jennings et al. 2002). The map shows locations of historic manufacturing and other industrial sites located in the city of Cleveland, OH, USA, and measured soil lead levels compared to background soil concentrations (51.7 mg/kg) (US EPA 2016). The soil metal data were collected from participants in the Ohio State University Extension's Summer Sprout Program. Vacant

lots under consideration as future garden sites within this programreceived complementary soil testing, which was completed by the Soil and Plant Tissue Testing Laboratory at the University of Massachusetts Amherst. Soil led levels from 190 vacant lots are shown, collected from 1997 to 2016. Historic industrial sites were identified using a USA Today investigation from 2012 ("USA TODAY Investigation Reveals Hazardous Levels of Lead in Neighborhoods Across the Country" 2012)

(Cu), and zinc (Zn) are commonly found in urban soils at elevated concentrations (Karim et al. 2014). Due to atmospheric deposition and surface runoff of metals, trace metals are not exclusive to heavily modified urban soils near former industrial, waste disposal, or construction locations and can redistribute across a landscape via erosion, air currents, and water runoff (Li 2018), sometimes several kilometers from a point source (Suvarapu & Baek 2017). Additionally, continuous modern inputs of metals, such as from the demolition of structures, traffic emissions, and improper waste disposal, contribute to elevated soil lead, as well as arsenic, cadmium, zinc, aluminum, and chromium in urban soils (Sharma et al. 2015b). It is difficult to predict where metal contamination is concentrated due to the ability of metal pollution to travel away from point sources, and from continuous modern input of metals from residential sources. Thus, high levels of metal contamination may not be isolated to one area of a legacy city (Fig. 3).

The success of conservation initiatives utilizing vacant land are threatened if we fail to recognize the consequences of metal pollution for pollinator community health (Harrison & Winfree 2015). The goal of our review is to examine potential metal exposure routes for urban bees and butterflies, (hereafter pollinators), summarize known

chronic and acute impacts of metal exposure on pollinator species, including lethal and sublethal effects, and identify hurdles to pollinator conservation using vacant land within cities. We performed literature searches using Google Scholar and Web of Science for articles published between the years of 1980 and 2021 using the keywords 'pollinator, bee, butterfly, moth, caterpillar, Lepidoptera, Apidae AND metals, heavy metals, metalloids, metal pollution, metal contamination'. The resulting articles were screened, and we omitted duplicates, articles for which we were unable to obtain the full text, or articles that did not measure physiological responses, such as immune function, growth and development, and reproduction. Due to the small number of studies assessing metal impacts on pollinators of conservation concern, we also included studies of honey bees, Apis mellifera, (Hymenoptera: Apidae) as they are documented bioindicators of metal pollution worldwide (Celli & Maccagnani 2003), and common pestiferous Lepidoptera. We recognize that these species not ideal proxies for all pollinators of conservation concern. Nonetheless, by examining how metals influenced these common flower feeding insects we have formulated a research agenda to advance our understanding of how these pollutants shape conservation investment within legacy cities.



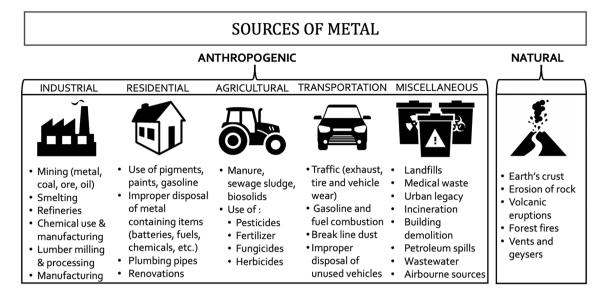


Fig. 3 Metals are byproducts of both natural and anthropogenic activities. Certain metals, such as iron, aluminum, and calcium make up large portions of the earth's crust and are released during erosion or volcanic eruption events. Anthropogenic sources of metals include pollution, traffic emission (tire and automobile wear particles, vehicle exhaust fumes, break line dust), the weathering of buildings and

machinery, industrial runoff, smelting, mining, fertilizers, domestic emission from the use of metal containing products, such as lead-based paint and leaded gasoline, and byproducts of urban legacy-materials that result from activities related to urban development and growth (Jennings et al. 2002; Wuana and Okieimen 2011a, b)

Possible metal exposure pathways

Within a contaminated habitat, pollinators could be exposed to metals through direct dermal contact with polluted water, air, or soil, and/or indirectly from ingesting contaminated resources or during grooming behaviors (Fig. 4). While the relative importance of these possible metal exposure pathways has not been identified, below we highlight possible metal exposure routes for urban pollinators.

Direct metal exposure pathways

Metal-contaminated dust, resulting from traffic emissions, fuel combustion, and construction and demolition processes is common within city landscapes (Aguilera et al. 2021). Metal-contaminated dust has been detected on tree leaves and other surfaces near roadways and industrial areas (Norouzi et al. 2015). Metal deposition on foliage surfaces represents a hazard to foliar feeding caterpillars that travel across and consume plant materials. Further, butterflies, moths, and bees could consume metal dust that settles on floral heads and within floral nectar and pollen provisions (Courtney et al. 1982; Clarke et al. 2017). Scanning electron microscope coupled with X-ray spectroscopy images revealed that metal particles concentrate on the head, wing margins, and corbiculae regions of honey bees (Negri et al. 2015). Thus, self-grooming and social bee allogrooming behaviors increase the possibility of ingesting metals (dust particles with metals sorbed to the surface and/or metal dust) affixed to hairs and body surfaces and incorporating metals into collected resources. Further, particles that gather on the corbiculae, structures involved in pollen collection, are likely to be incorporated into pollen loads that will be fed to developing bees, as it has been demonstrated that anthropogenic dust can adhere to pollen grain surfaces (Okuyama et al. 2007; Negri et al. 2015).

Urban stormwater runoff often contains both dissolved and particulate-bound fractions of metals (Sansalone & Buchberger 1997; Turer et al. 2001), in addition to other pollutants (Song et al. 2019). Bees drink and collect water for nest construction from contaminated puddles (Antoine & Forrest 2021), and puddling behavior may expose butterflies to nonessential metals (Inoue et al. 2015). Surface soils (approximately 15 cm depth from surface) store the bulk of metals from stormwater runoff (Turer et al. 2001; Suvarapu & Baek 2017) and settled airborne particulates (Yang et al. 2016). Ground nesting and mason bees are commonly found in cities (Camilo et al. 2017; Sivakoff et al. 2018) and regularly contact and ingest soil during nest construction. For example, metal concentrations in pollen (Cd: 0.89-9.31 mg/kg), lead (Pb: 42.05-356.16 mg/kg), and zinc (Zn: 55.90–592.42 mg/kg) collected by Osmia bicornis (Hymenoptera: Megachilidae, previously Osmia rufa) near smelting sites in Poland were positively correlated with metal concentrations measured in surface soils at foraging sites, even though specific exposure routes were



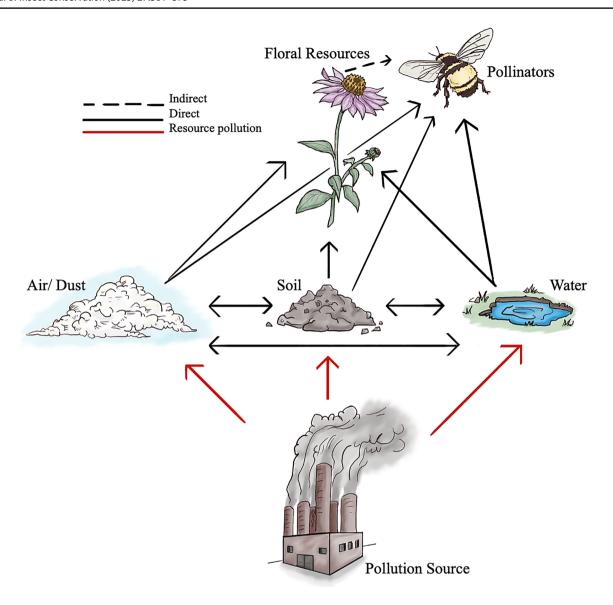


Fig. 4 Heavy metal exposure routes. Resources are directly contaminated from pollution sources, such as smelting operations, industrial manufacturing, and domestic use of metal containing items. Once resources are contaminated (air, soil, water), contamination can be transferred between resources; air and soil (dust erosion and deposition), air and water (evaporation and precipitation), soil and water (runoff). Additionally, plants can become contaminated from dust particulate landing on foliar surfaces as well as metal uptake from soil and water. Pollinators may be exposed to metals in the environ-

ment either directly or indirectly. Direct exposure routes may include consuming contaminated water, directly contacting contaminated soil during nest construction or travel, or contacting dust particulate while foraging on floral resources. Indirect exposure routes include consuming contaminated food resources, such as nectar or plant materials, taken up by the plant from the soil. Many unknowns remain surrounding pollinator metal exposure routes and impacts of metals on pollinator species

not confirmed (Moroń et al. 2012). Metal contamination of surface soils also presents a hazard to foliar feeding caterpillars, which travel across and consume soils to enhance their intestinal microbiota (Hannula et al. 2019).

Local soil conditions such as pH, soil type and texture, and organic matter content influence metal toxicity through changing metal bioavailability and movement through the environment (Rieuwerts et al. 1998; Turner & Mawji 2004). The reactive fraction of metals in the soils,

not the total concentration, dictates overall risk to flora and fauna (Liu et al. 2018). For example, pH influences metal solubility with generally high solubility under low pH conditions, while high organic carbon content in soil can adsorb certain metals and reduce bioavailability (Hou et al. 2020). Generally, water soluble and exchangeable forms of metals are more bioavailable to organisms than precipitated or particle bound species (Kim et al. 2015). Therefore, it is difficult to predict metal toxicity and risk

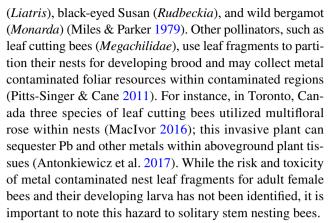


to pollinators by quantifying soil total metal concentrations alone.

Plant uptake and translocation of heavy metals

Certain plants are capable of translocating metals from contaminated soil or water to aboveground structures, including leaves and shoots, and pollen and nectar provisions (Meindl & Ashman 2015; Xun et al. 2017, 2018). Plants have evolved complex and efficient mechanisms for obtaining essential nutrients from the environment, even if present in extremely low concentrations. These mechanisms are also involved with the uptake, translocation, and sequestration of toxic elements (Tangahu et al. 2011; Singh et al. 2016). Plants can be classified into three major groups: metal excluder, indicators, and metallophytes/ hyper-accumulators (Bhalerao et al. 2013). Metal excluder species limit the translocation of metals from substrate and can maintain a low level of contaminant in their tissue over a wide range of metal concentrations. Indicator plant species accumulate metals in their biomass to levels that are usually reflective of soil metal concentrations (Cole & Smith 1984). Metallophytes, or hyper-accumulator plants, can take up metals from the roots and accumulate them in above ground tissues at concentrations 100-1000 fold higher than observed in non-hyperaccumulating species, all without experiencing any negative toxic effects (Singh et al. 2016). To date, over 450 metal hyper-accumulator species have been identified across 45 angiosperm families (Suman et al. 2018), with a majority of species in the *Brassicaceae* family, followed by Asteraceae, Rubiaceae, and Fabaceae (Morel et al. 2006), many of which contain important pollinator forage species.

Unfortunately, there is some evidence that urban plants commonly utilized by pollinators for foraging and nesting can accumulate metals (Simon et al. 1996; Zhu et al. 2001; Eskov et al. 2015; Pietrelli et al. 2022). Most plant metal uptake studies focus on metal concentrations in vegetative plant parts such as roots, shoots, and leaves (Shahid et al. 2017). Many crops commonly produced in urban agroecosystems (Mirecki et al. 2015), as well as urban spontaneous vegetation found within vacant lots, can accumulate metals in these plant parts, such as chicory (Cichorium intybus), dandelion (Taraxacum officinale), common milkweed (Asclepias syriaca), and clovers (Trifolium) (Simon et al. 1996; Zhu et al. 2001). Foliar metals represent a risk to developing caterpillars (Li et al. 2010; Pietrelli et al. 2022), as caterpillars have similar body metal profiles and metal concentrations as found in plant foliage after feeding on metal contaminated host plants (Wong & Cheung 1986; Ooik & Rantala 2010; Mitchell et al. 2020). Some genera of native plants recommended for pollinators in the Midwestern US (Xerxes Society 2017) can also accumulate metals in their above ground vegetative tissues including blazing star



Fewer studies have examined the ability of plants to accumulate metals in flowers (Simon et al. 1996; Zhu et al. 2001; Xun et al. 2017; Pietrelli et al. 2022), nonetheless there is evidence that contaminated nectar and pollen could represent an exposure route for foraging pollinators, as demonstrated by metal content in honey bee honey (Conti & Botrè 2001). For instance, several bee visited plants within urban lots can accumulate metals within their flowers, including red clover (*Trifolium pratense*), chicory (*Cichorium intybus*), Queen Anne's lace (Daucus carota), and narrowleaf plantain (Plantago lanceolata) (Simon et al. 1996; Zhu et al. 2001; Eskov et al. 2015; Pietrelli et al. 2022). The nectar of common crops from urban agroecosystems such sunflowers (Helianthus) (McCutcheon & Schnoor 2003), mustards (Brassica) (Bennet et al. 2003), radish (Raphanus sativus) and summer squash (Cucurbita pepo) (Hladun et al. 2015; Xun et al. 2017) have also been shown to contain metals. However, even closely related plants can vary in their translocation abilities of different metal species, which complicates identifying bioavailability and exposure. For example, the goldenrod species Solidago canadensis bioaccumulates Pb and Zn in its leaves, inflorescences, and roots (Bielecka & Królak 2019), while Solidago gigantea has high bioaccumulation but low translocation ability to move cadmium (Cd), Cu, Cr, iron (Fe), and nickel (Ni) from below ground to foliar tissues (Dambiec et al. 2022). Therefore, limiting pollinator exposure to metals when creating habitat will require testing of specific plants and metals as information from related species may not be representative.

Secondary effects of metals on resource availability and quality

Metal contamination in soils can influence plant physiology, community composition, and cause shifts in host plant range, which in turn alters available pollinator forage resources (Pandey et al. 2014; Chowdhury & Maiti 2016). Soil metal contamination can cause reduced seed production and germination, decreased seedling height, stunted growth, reduced fruit production, decreased root and shoot growth,



and morphological deformities (Kabata-Pendias 2011; Ahmad et al. 2012). These effects vary depending on the metal properties, concentration, and plant species (Cheng 2003). Metal pollution can significantly impact pollen germination and tube length, decrease pollen vitality and negatively impact plant reproductive biology (Mulder et al. 2005; Muradoğlu et al. 2017). Deformed flowers and plants receive fewer pollinator visits than normal flowers (Ohashi & Yahara 1998), resulting in lower pollination, genetic diversity, and reduced seed set.

Within contaminated sites, metal-tolerant genotypes dominate plant communities within a short timespan (Ryser & Sauder 2006). Physiological stress from metal exposure slows down succession in grasslands, which benefits early successional plants such as the fritillary butterflies host plant, Viola calaminaria (Salz & Fartmann 2017). Some critical nectar plants of butterflies are sensitive to metals and have reduced vigor in response to metal pollution. For instance, certain early spring host plants, annuals, and highly producing nectar plants are highly sensitive to metal pollution (Mulder et al. 2005). Butterfly population shifts in metal contaminated habitats may be a secondary effect of metal stress on host plant vigor, reduced nectar or pollen availability, and changes in species presence (Mulder et al. 2005). Interestingly, certain plants preferred by moths are almost twice as tolerant of metals compared to plants visited mainly by butterfly species (Mulder et al. 2005) which may lead to shifts in plant community structure and subsequent changes in lepidopteran population dynamics from shifting host plant ranges.

Metals and pollinator health

Metal pollution has direct negative impacts on pollinator survivorship (Di et al. 2016; Ali et al. 2019), reproduction and fitness (Moroń et al. 2014; Scott et al. 2022), morphology (Szentgyörgyi et al. 2017), and behavior (Burden et al. 2016, 2019) (Fig. 5). Clearly, mortality from metal exposure negatively impacts pollinator populations (Sgolastra et al. 2018a, b), however, the sublethal effects of metal exposure are more nuanced.

Reproductive success

Pollinators exposed to metals can experience reduced reproductive success (Moroń et al. 2014; Sivakoff et al. 2020; Scott et al. 2022)For instance, the fecundity of the solitary, stem nesting red mason bee, *Osmia bicornis* (Hymenoptera: Megachilidae), declined with proximity to two smelters in Poland and the UK that contaminated the soil with Cd, Pb, and Zn (Moroń et al. 2014). Females foraging near the smelters collected provisions with elevated Zn concentrations and

constructed fewer brood cells; their offspring sustained twice the larval mortality as individuals in uncontaminated sites with 50-60% overall brood mortality (Moroń et al. 2014). Within the legacy city of Cleveland, Ohio (USA), colonies of the common eastern bumble bee, Bombus impatiens (Hymenoptera: Apidae) were more likely to contain measurable concentrations of Cr (0.39 mg/kg), Cu (23.9 mg/kg), Fe (119.5 mg/kg), Ni (0.63 mg/kg) and Zn (93.2 mg/kg) within forager bodies and collected provisions compared to colonies located outside the city (Sivakoff et al. 2020). Chronic consumption of provisions contaminated with As, Cd, Cr, or Pb caused 40 to 90% bumble bee brood mortality, three times that of unexposed colonies (Scott et al. 2022). Additionally, honey bee fitness is negatively affected when jointly exposed to Cd and Cu in the laboratory, causing an increase in larval development duration and mortality (Di et al. 2020). A larger impact of metals on immature insects compared to adults could be because developing brood express fewer detoxification genes than adult females (Xu et al. 2013; Di et al. 2016). For instance, Hunt's bumble bee, Bombus huntii (Hymenoptera: Apidae) express varying levels of genes associated with immune response and detoxification across life stages, and to a greater extent than other genes (Xu et al. 2013).

Fitness consequences likely result from physiological trade-offs between metal detoxification and reproduction in insects (Bashir-Tanoli & Tinsley 2014; Schwenke et al. 2016). This has been demonstrated in honey bees whereby queens stressed by pesticide exposure produce fewer eggs than unstressed queens in similarly sized colonies (Wu-Smart & Spivak 2016). Similarly, exposure to a mix of pesticides and fungicides reduced ovarian maturation and shortened the lifespan of Osmia bicornis (Sgolastra et al. 2018a). It is highly likely that detoxifying metals would activate similar physiological pathways in solitary bees and therefore may result in decreased reproduction, but this requires further investigation. Yet, species vary in their tolerance of metals, for instance, metal exposure has different impacts on pestiferous lepidopteran species. The tobacco cutworm, Spodoptera litura (Lepidoptera: Noctuidae), fed artificial diet with 300-750 mg/kg of Zn have a shortened egg laying period and reduced oviposition rate compared to individuals not fed metals (Shu et al. 2009). Similarly, the beet armyworm, Spodoptera exigua (Lepidoptera: Noctuidae) copulate less and produce fewer eggs when fed artificial diet containing 51.2 mg/kg of Cd-spiked food (Su et al. 2021). Conversely, Zn tolerant female cabbage white butterflies, Pieris rapae (Lepidoptera: Pieridae), produce more eggs and have higher reproductive efforts under nonpolluted conditions (Shephard et al. 2021). Physiological responses to metal exposure are complex, and species and population specific, thus potential risks should be assessed at the species level.



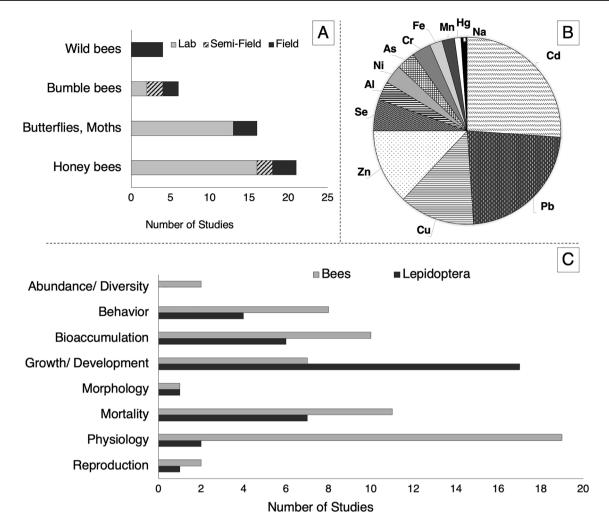


Fig. 5 Summary of studies measuring the impact of metals on pollinators. Summary graphs of literature search using Web of Science and Google Scholar from years 1980–2021, using search terms: pollinator; bee; solitary bee; butterfly; bumble bee; honey bee; Lepidoptera; AND heavy metal; metal; metal pollution; metal contamination resulted in 48 articles that fit our search criteria. A Research articles were classified as field based, semi-field (outdoors with manipulation), or lab based per group. B Pie chart sections represent the most common metals tested in bee and butterfly literature combined C Major effects of metal exposure on pollinators that were identified

within each study. Some articles addressed multiple topics within the study. All bee groups (honey bees, bumble bees, solitary bees) were combined into 'bees' (n=32), and 'butterflies and moths' include some common pestiferous lepidopteran species (n=16). 'Physiology' category contains the following topics combined: cellular physiology (Bees: 1; Leps: 0), gene expression (Bees: 6; Leps: 0), immune function (Bees: 1; Leps: 0), metabolomics (Bees: 2; Leps: 0), microbiomics (Bees: 2; Leps: 0), physiology (Bees: 7; Leps: 1) and tolerance (Bees: 0; Leps: 1)

Growth and development

Metal exposure at toxic levels can result in pollinator morphological abnormalities, such as reduced eye (Philips et al. 2017), head (Monchanin et al. 2021) and wing size (Szentgyörgyi et al. 2017; Shephard et al. 2020), which have clear implications for dispersal and foraging success. Increased incidence of morphological deformities such as deformities of pupal body and improper molting in Cd-exposed northern armyworm, *Mythimna separate*, moths have also been noted (Wei et al. 2020).

Butterflies reared on food containing field realistic concentrations of Cd, Cu, Fe, Pb and Zn can exhibit reduced consumption and growth rates, lower pupation weight and a smaller adult body size (Nieminen et al. 2001; Fred & Brommer 2005; Ali et al. 2019; Shephard et al. 2020). For instance, autumnal moth, *Epirrita autumnata* (Lepidoptera: Geometridae) caterpillars reared on metal polluted bilberry leaves (As: 1.02 mg/kg; Ni: 12.9 mg/kg; Pb: 0.85 mg/kg) grown near smelting locations in Finland exhibited reduced body mass and growth rates compared to caterpillars fed uncontaminated bilberry leaves and had significantly higher levels of metals in their bodies compared to caterpillars



reared on uncontaminated leaves (Eeva et al. 2018). Importantly, these developmental effects vary among pollinator species. Non-native pest species often exhibit a greater tolerance to metal exposure and may have enhanced detoxification ability due to recent selection from targeted insecticide management (Shephard et al. 2020), compared with species of conservation concern which are usually protected from such management techniques. For example, monarch caterpillars, Danaus plexippus (Lepidoptera: Nymphallidae) have reduced survivorship to pupation when reared on diets containing 344 mg/kgZn in the laboratory, whereas cabbage white butterfly caterpillars fed the same diet exhibited increased survival (Shephard et al. 2020). The cabbage white butterflies that consumed Zn did, however, experience a tradeoff through prolonged developmental time and a smaller adult body size (Shephard et al. 2020).

Response to stressors

Metal exposure impacts insect immune function (van Ooik et al. 2008), gene expression (Johnson et al. 2012), stress response (Martinek & Hedb 2020), and survival when exposed to multiple environmental stressors (Rothman et al. 2020; Jiang et al. 2021). Investing in immune responses to parasites, diseases, or pathogens may reduce a pollinator's ability to detoxify other contaminants (Goulson et al. 2015; Gong & Diao 2017). For example, honey bees exposed to 1.0 mg/kgCd demonstrate severe cellular damage of fat bodies and reduced immunocompetence, resulting in decreased ability to combat bacterial infection (Polykretis et al. 2016). Conversely, sometimes a mild stressor can upregulate a conserved metabolic pathway and thereby synergistically enhance an organism's ability to combat another environmental threat. Honey bees that are orally exposed to sublethal doses of pesticide and fed ad libitum have increased survivorship when challenged with an additional stressor, possibly through hormesis (Dickel et al. 2018). Similarly, pollution exposure enhances immune function of female autumnal moths, but not in males (Ooik & Rantala 2010).

Metal exposure alters honey bee microbiome composition, metabolite profile, detoxification compounds (Rothman et al. 2019b), and alters gut microbial community composition and relative abundance of specific core biota in bumble bees (Rothman et al. 2019a). Insect detoxification and microbiota symbiosis influence the severity of metal exposure and cause multigenerational impacts of these contaminants for pollinator health. Gut microbiota contribute to digestion, development, pathogen resistance, and other physiological processes including detoxification (Jing et al. 2020), as well as influence the survival, size, and egg production in some insects (Coon et al. 2016), so a disruption to the microbiome can negatively impact metabolism, immune function, and health (Raymann & Moran 2018; Rothman et al. 2019b).

Bumble bee queens' gut microbiome changes across key life stages from eclosion to egg laying, and likely play important roles in egg development and fecundity (Wang et al. 2019). Furthermore, microbiota inoculation increases survival for bumble bees exposed to field realistic doses of selenate (0.75 mg/L) compared to uninoculated bees (Rothman et al. 2019a). The microbiome increases survival for bees exposed to metalloids (Rothman et al. 2019b), therefore, may play a significant role in bee fecundity and success or failure in contaminated landscapes.

Foraging behavior

Some bee species do not avoid foraging on metal contaminated flowers, as they are unable to detect nectar qualities until inspection (Hladun et al. 2015; Sivakoff & Gardiner 2017; Xun et al. 2017). For example, honey bees do not avoid Ni-contaminated resources when presented with a choice (Meindl & Ashman 2014, 2015), and bumblebees are not able to detect naturally occurring concentrations of nectar toxicants within choice feeding assays (Tiedeken et al. 2014). However, pollinators have been found to alter their foraging activity at contaminated resources with certain compounds after resource inspection. For instance, honey bees and wasps take fewer and shorter visits to nectar feeders containing concentrations of metals commonly found in roadside soils (Cd: 0-0.8 mg/kg; Cu: 0-50 mg/kg; Pb: 0-3 mg/kg; Sb: 0-0.8 mg/kg; Zn: 0-100 mg/kg) (Phillips et al. 2021). Bumble bees and honey bees forage for shorter durations at sunflowers (Helianthus) grown in Pb contaminated soil (Sivakoff & Gardiner 2017), Impatiens capensis (Balsaminaceae) flowers contaminated with aluminum (Al) (Meindl & Ashman 2013) and at *Hosta* flowers where metal contaminated nectar was added (Zn: 80 mg/L; Cu: 55 mg/L; Ni: 50 mg/L; Pb: 55 mg/L) (Xun et al. 2018). The inability of pollinators to detect and avoid metal contaminated food until consumption suggests contaminated nectar can be a direct exposure route (Meindl & Ashman 2015; Burden et al. 2019).

Oral metal exposure can impair pollinator memory, cognition, long-term recall, and learning (Burden et al. 2016; Monchanin et al. 2021), which can also influence their foraging behavior. For example, manganese (Mn) exposure alters honey bee brain biogenic amine levels that causes premature transition from in-hive functions to foraging behaviors and results in poor foraging by these precocious and inexperienced workers (Søvik et al. 2015). Chronic oral exposure to trace amounts of Pb results in impaired cognition and reduced olfactory learning performance (Monchanin et al. 2021), critical for successful foraging bouts. Any reduction in foraging efficiency can reduce food resources that are available for developing brood, and poor pollination services



for the plant, ultimately leading to a decline in seed set (Steffan-Dewenter & Tscharntke 1999; Webber et al. 2020).

Hurdles to urban pollinator conservation

Metal contamination remains a ubiquitous, yet largely under investigated challenge to urban pollinator conservation (Fig. 5A–C). To date, the majority of studies that have assessed the lethal or sub-lethal impacts of metal exposure on wild pollinators have been conducted in the laboratory, with metal concentrations that may or may not be field relevant (Fig. 5A). Further, most studies have targeted honey bees and pestiferous Lepidoptera-few have focused on species of conservation concern (Fig. 5A). Likewise, not all common metal contaminants have received equal focus, with most studies examining how exposure to Cd, Pb, Cu and Zn influence pollinator health (Fig. 5B). Although these are common soil contaminants within many legacy cities (Sharma et al. 2015a) other metals, such as As, Cr, Ni, and Fe, are also frequently found at elevated concentrations (Sharma et al. 2015a, b; Pietrelli et al. 2022) and could represent a significant risk to pollinators. There is a major need to invest in assessing the physiological effects of metal exposure on pollinators of conservation concern. Fewer than 20 studies have examined physiological effects of metals on pollinator heath, with growth and development, survivorship, and bioaccumulation being the most studied to date (Fig. 5C).

Field-relevant metal toxicity and multiple stressors

Focusing on field-relevant doses of metals is fundamental for determining realistic risks in contaminated environments. Specifically, soils contaminated with the metal byproducts of industrial activity, both biologically available and unavailable, often contain elevated concentrations of several pollutants and the additive or synergistic effects of exposure to these toxins warrants further study. Further, presence of a metal in the environment does not necessarily mean toxicity, so understanding the risk posed by environmentally relevant metal concentrations is paramount. Likewise, the frequent use of indicator species such as honey bees is unlikely to accurately illustrate mortality risks of acute metal exposure for all pollinators (Arena & Sgolastra 2014; Franklin 2019). For example, a meta-analysis comparing sensitivities of honey bees versus non-honey bee Apiformes to pesticides found high variability of sensitivities between species, with certain species having ten-fold higher sensitivity than honey bees to chemicals (Arena & Sgolastra 2014). Metal toxicity can also vary by life stage, sex, feeding behaviors, and genetic background (Tchounwou et al. 2012) as well as functional traits such as nesting substrate, floral specialization,

and capacity for dispersal, necessitating studies accounting for these differences. In fact, the importance of soil metal contamination as a driver of pollinator distributions is virtually unknown with just two studies measuring bee species diversity and abundance across a contamination gradient (Moroń et al. 2012, 2014). To our knowledge no studies have examined butterfly diversity across a contamination gradient, or the influence of environmental metal contamination on the distribution of pollinator functional diversity in legacy cities.

Sublethal effects and tolerance

To date, just 17 studies have measured the effects of chronic exposure to sublethal metal concentrations on wild pollinator behavior, physiology, and morphology (Fig. 5C, see Appendix S1). Metal exposure is known to alter gut microbiota which in turn can impact nutrient availability, immune function and detoxification across an insect's lifecycle (Jing et al. 2020). Understanding how metals, in combination with other urban stressors such as elevated temperatures, reduced habitat quality, and the presence of additional pollutants influence pollinator health is challenging but necessary to advance conservation planning. A pollinator's physiological condition, such as their nutritional status, is likely to vary across urban landscape contexts and this could influence the severity of health impacts resulting from metal exposure (Tchounwou et al. 2012). For example, bumble bee queen development in reproductive colonies is impacted by available nutrition (dos Santos et al. 2016), and exposure to metals may differentially influence queen production in colonies with suboptimal versus optimal nutrition.

Animals found in stressed environments can develop a tolerance to metals (Singh 2005; Merritt & Bewick 2017), but to our knowledge the capacity of pollinators to do so is not known. Certainly, a high species richness of bees and butterflies are found in contaminated sites (Sivakoff et al. 2018; Turo et al. 2021), but as highly mobile insects, differentiating between populations that have experienced chronic metal exposure versus individuals that have recently emigrated from outside of the contaminated region is difficult. Life history traits may influence a pollinators' likelihood to adapt, specifically if the nesting habits of certain species are more likely to expose them to stressors and/or if their host plants hyperaccumulate metals.

Identifying exposure routes

Understanding metal exposure routes and bioavailability for pollinators is critical to advancing urban conservation planning and implementation. Assessments of metals' risks to pollinators by airborne particulates, soil, and water are needed to develop best management practices to minimize



harmful exposure. Pollinators may also be exposed to metals via plant uptake from contaminated soil. The accumulator status of urban spontaneous vegetation growing in ruderal locations, which represents a major source of urban pollinator forage, is largely unknown. This information could guide best practices for urban pollinator habitat establishment and management. For instance, if plant uptake is a major exposure route, frequent mowing of urban vegetation to prevent bloom could be practiced within contaminated vacant land to limit pollinators' dietary exposure (Rascio & Navari-Izzo 2011). Additionally, plant exposure to metals may negatively influence the quality of the nectar and pollen and further harm bees by providing poor quality food (Muradoğlu et al. 2017).

Low-cost remediation strategies

Metals represent a hazard to humans and wildlife living in human dominated areas, as metal contamination is present where large proportions of human populations live. The objective of any soil remediation effort is to be protective of and reduce overall risk to human, plant, and animal health (Wuana and Okieimen 2011a, b). Several options for in situ and ex situ remediation techniques that use chemical, physical, or biological methods are available, including phytoremediation, soil amendments, immobilization and soil washing (Wuana and Okieimen 2011a, b; Li et al. 2019). Additional cost-efficient methods to reduce the chances of metal exposure include frequent mowing of blooming species in contaminated areas, and sowing plant species that do not uptake metals into the biomass. However, we need to understand exposure routes, metal speciation, and bioavailability to appropriately design a successful remediation strategy. Soil contamination needs to be characterized to establish type, distribution, and amount of metal in the soil and the desired end concentration must be established (Wuana and Okieimen 2011a, b). Therefore, to identify a metal remediation goal, we first need to determine environmental quality guidelines for pollinator metal exposure levels that can be used to inform remediation efforts.

Conclusions

This review was motivated by the enthusiasm that community leaders within legacy cities demonstrate for urban pollinators and their willingness to establish bee habitat utilizing reclaimed vacant land. These individuals recognize the risk metals may pose to their conservation plans and seek low-cost tactics to reduce or eliminate pollinator exposure within urban habitats. For example, Bee City USA is a national program that encourages local communities to implement pollinator focused plantings and make commitments to conserve

native pollinators through conscious action. Cities, towns, and counties are encouraged to "...create and enhance pollinator habitat on public and private land by increasing the abundance of native plants and providing nesting sites" ("Bee Campus USA Commitments" 2020). These plantings could include vacant lots or border highways, where metal exposure could be a concern. For instance, the Bee City USA volunteers in the city of Lynchburg, Virginia, USA collaborated with the city Buildings and Grounds department to reduce mowing and herbicide use in vacant lots and on local roadways in an effort to provide food and habitat for pollinators ("Affiliate Spotlight" 2021). Such dedication to aiding urban pollinator communities deserves research-based guidelines for the selection of sites, plant communities and management practices to diminish the risks posed by metals.

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Declarations

Competing interest The authors declare no conflict of interest.

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