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REVIEW

Effects of heavy metals and metalloids on plant-animal interaction and biodiversity of terrestrial ecosystems—an overview

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Abstract Heavy metals and metalloids are ubiquitous and persistent in the environment. Anthropogenic activities, including land use change, industrial emissions, mining, chrome plating, and smelting, escalate their distribution and accumulation in terrestrial ecosystems. Priority metals, including lead, chromium, arsenic, nickel, copper, cadmium, and mercury, pose enormous risks to public health, ecological safety, and biodiversity. The adverse effects of heavy metals on plant-animal interactions, pollen viability, species fitness, richness, and abundance are poorly understood. Hence, this review summarises the critical insights from primary investigations on the key sources of heavy metal pollution, distribution pathways, and their adverse effects on plants and pollinators. This study provides insights into how heavy metals compromise nectar quality, pollen viability, plant-pollinator growth, and reproduction. Biotic pollinators are responsible for approximately 90% of the reproduction of flowering plants. Heavy metals adversely affect pollinators that rely on angiosperms for nectar and pollen. Heavy metals interrupt pollinators' and plants' growth, reproduction, and survival. Evidence showed that bees near gold mines had their olfactory learning performances and head sizes reduced by 36% and 4% due to heavy metals exposure. Cadmium (Cd) interrupts the redox balance, causes oxidative stress, alters gut microbiota, and reduces the survival rate of *Apis cerana cerana*. Excess Cd exposure reduced the flight capacity, loss of mitochondria, and damaged muscle fibre of *Bombus terrestris,* while Zn stress reduced egg production and hatchability of *Harmonia axyridis.* Furthermore, heavy metals alter flower visitation, foraging behaviour, and pollination efficiency.

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Introduction

Plant-animal interactions represent a significant channel of energy transfers via ecosystems, thus contributing significantly to the functioning of terrestrial ecosystems (Banerjee et al., 2022). Heavy metal pollution is a rising problem that negatively affects terrestrial ecosystems, human health, and the global environment in recent decades. Heavy metals are harmful environmental constraints that threaten many life forms, including pollinators (Kumari et al., 2024). Plant-animal interactions embody significant energy transfer channels via ecosystems where antagonistic and positive interactions contribute to ecosystem functioning (Banerjee et al., 2022). These interactions usually form complex networks involving diverse species of antagonists and mutualists vital for ecosystem functioning (Rodríguez-Rodríguez et al., 2017). Plants-animals interactions are diverse and serve as ecological and evolutionary forces for angiosperms, insects, and many assemblies of vertebrates (Leal et al., 2017). Global concerns about the decline in biotic pollinators have gained considerable momentum. The decline is mainly due to certain anthropogenic activities with their associated consequences, including the global climate nexus (Janousek et al., 2023). Biotic pollinators are responsible for approximately 90% of the reproduction of flowering plants (Newton et al., 2023). Based on prime data from 200 countries, vegetables, fruits, or seed production from 87 global leading food crops rely on biotic pollination (animal pollination). Although beetles (Coleoptera) are excellent pollinators of both early and modern plants, including the rare orchid *Disa forficaria* (Cohen et al., 2021), the exposure of female *Harmonia axyridis* (ladybug) to Zn stress reduced egg production and its hatchability, indicating the negative effect of Zn exposure on fertility (Shi et al., 2020). The exposure of *Serangium japonicum (*Coleoptera*; Coccinellidae)* affected its development, reproduction, alteration in gene expression, and physiological trade-offs due to alteration in enzymatic activities (Khan et al., 2024a, 2024b), confirming the toxicity of Cd to insect pollinators.

In contrast, 28 crops do not require biotic pollination (Klein et al., 2007). Studies suggest that biotic pollinators (insects and other animals) pollinate most angiosperms, while a minority utilise abiotic pollen vectors, essentially wind (Ollerton et al., 2011). In addition, persistent organic pollutants such as agrochemicals have been linked to the global decline in the population of bees in the past few decades (Botina et al., 2023). The exposure of bees to agrochemicals during feeding and foraging activities has been linked to a decline in bee (*Partamona helleri*) population as the pollutants affect the gut microbiota associated with insect nutritional health and immunocompetence (Botina et al., 2019). Biotic pollinators, such as insects and other animals, play critical roles in reproducing many vast global crops, particularly angiosperms, and the health of natural ecosystems (Stanley & Raine, 2016). Biotic pollinators, including diverse species of insects and vertebrates, provide critical ecological services through pollination, sustaining plant diversity (Potts et al., 2010). Pollination improves the fertilisation rates of angiosperm species, thus enhancing both the quantity and quality of seeds and fruits (Toledo-Hernández et al., 2022). Yet many of these biotic pollinator species have recently witnessed global declines. The global decline in insect pollinators such as honeybees, bumblebees, flies, and pollinators, in general, has far-reaching catastrophic implications for biodiversity, plant reproduction, and agricultural production, thus, global food security (Nicolson, 2011). Many studies have highlighted the decline of animal pollinators (Biesmeijer et al., 2006; Ollerton et al., 2011). Similar findings have been made about insect pollinators such as bumblebees (Bommarco et al., 2012; Cameron et al., 2011) from a global perspective due to anthropogenic activities resulting in habitat changes and climate.

Different factors are responsible for the pollinator population's declining menace, including habitat changes, landscape composition, and environmental contamination (LeBuhn & Vargas Luna, 2021). However, environmental pollution by potentially toxic elements (TEs) is of great concern given their non-gradable, persistent, and bioavailable nature. Ecological pollution, particularly by potentially toxic elements due to anthropogenic activities, causes drastic changes in global habitats, resulting in a decline in species composition, population, and abundance (LeBuhn & Vargas Luna, 2021). Evidence showed that environmental contaminants such as heavy metals reduce the species diversity of wild bees (Shi et al., 2023). Bees are critical insect pollinators that encounter environmental contaminants while foraging on contaminated plants (Rothman et al., 2019). *Apis mellifera* (honeybees) forage widely and collect food from divergent sources exposing them to environmental contaminants (Waiker et al., 2022). Recent studies indicated that the population of the native Asian honeybee *Apis cerana* is declining. Surveys with 116 local beekeepers in the Jumla District of Western Nepal revealed a 44% decline in occupied beehives and a 50% decline in honey production per hive from 2012 to 2022 (Kortsch et al., 2024). For instance, LeBuhn and Vargas-Luna attributed the decline in the pollinator population to the loss of habitat and the deposition of potentially toxic elements, including pesticides and nitrogen, in terrestrial ecosystems (LeBuhn & Vargas Luna, 2021). The accumulation of heavy metals in the terrestrial environment poses a global challenge to human health and ecological safety (Yang et al., 2022). The exposure of honeybees to Cd subtly altered their general microbiome and metabolome composition (Rothman et al., 2019). Chronic exposure of bumblebees to Cd at field-realistic concentrations significantly reduced their flight duration, average velocity, and distance. Transcriptome evaluation further showed impairment of carbon metabolism and mitochondrial dysfunction in the bees' flight muscles. Cadmium (Cd) contamination adversely affects ecosystems due to its potential transfer up the food chain (Gao et al., 2024). The exposure of *Bombus morio* and *Bombus atratus* (neotropical bumblebee species) to 0.2 ppb mercury for 48 h by ingestion adversely severely impacted the fat body cells (oenocytes and trophocytes) and pericardial cells, thus morphology and HSP70 expression (de Andrade Nogueira et al., 2019). The exposure of *Apis mellifera* to a sublethal dose of Pb altered their body proteins and reduced the catalase activity regardless of the diet's nutritional quality (Schmarsow et al., 2023). The exposure of *Apis mellifera* adults to The LD_{50} and the lowest benchmark dose of Cr as $Cr(NO_3)_3$ showed low acute oral toxicity bee foragers (Sgolastra et al., 2018).

Plants can accumulate heavy metals from the soil and translocate them into different parts of the plant, including its floral organs, thus hampering its productivity (Xun et al., 2017). Metals persistently existing in the soil may be accumulated by plants and translocated to different parts of the plant, including leaves, flowers, and tissues. These metals can ultimately enter the biosphere and accumulate in trophic levels of the food chain (Priya et al., 2023). Due to this phenomenon, some studies have suggested that *Apis mellifera* and its products, such as propolis, beeswax, and pollen, are suitable bioindicators for assessing environmental pollutant contamination (Farias et al., 2023). The morphological features of *Apis mellifera* make them potential carriers of atmospherically deposited toxic substances such as heavy metals, radioactive elements, or persistent organic pollutants (e.g., pesticides) on plant surfaces (Bargańska et al., 2016). Conti et al. recently confirmed that bees, propolis, wax, and pollen accumulate high amounts of potentially toxic elements from the surrounding environment. The study revealed that bees and pollen accumulated the highest Cd surplus.

In contrast, toxic metal concentration in honey was several times lower compared to the lower concentration threshold (Conti et al., 2022). Seasonal dust, particularly during the summer (June–August) dust containing heavy metals, settles on surfaces of different plant parts such as leaves and flowers, leading to exogenous pollution of pollen and nectar (Dang et al., 2022). Foliar dust concentration of potentially toxic elements in urban areas was higher compared to suburban and rural areas, highlighting the role of dust in heavy metal accumulation in different plant parts (Subpiramaniyam et al., 2021). Floral organs of plants may accumulate heavy metals by translocation mechanism via the roots in polluted soils or atmospheric deposition (Moroń et al., 2012). For instance, *Rosmarinus officinalis labaiatae* (Rosemary: *Lamiaceae*) exhibited a higher concentration of heavy metals such as Pb, Ni, Zn, and Cu in its floral organs due to soil pollution in Jordan (El-Rjoob et al., 2008).

Bees are considered herbivorous insects due to their consumption patterns of nectar and pollen via their life cycle; simultaneously, they are one of the most dominant flower pollinators (Nicolson, 2011). The range, richness, and abundance of different wild pollinators have declined, while the global area of pollinator-dependent crops has increased over the past decades, raising concerns about biodiversity (Senapathi et al., 2021). Globally, increasing evidence suggests a decline in pollinators, hindering agricultural production and crop pollination. However, there is also an increase in pollinator-dependent crops, which means more biotic pollinators, indicating the critical need to protect biotic pollinators to ensure sustainable agriculture production globally (Mashilingi et al., 2021). Besides the effects of heavy metals and persistent organic pollutants on animal-plant interactions, these pollutants also adversely affect human health. For instance, heavy metals, including mercury (Hg), chromium (Cr), arsenic (As), cadmium (Cd), and lead (Pb), pose severe risks to human health from direct or indirect exposures via air, water, and food (Balali-Mood et al., 2021). The toxicity of these heavy metals can lead to several health complications, including brain damage and the dysfunctioning lungs, kidneys, liver, and other vital organs in humans. Other health consequences include muscular, physical, and neural deteriorating processes, which mimic ailments such as Parkinson's disease, muscular dystrophy, multiple sclerosis, Alzheimer's disease, and cancer (Jaishankar et al., 2014). Although scientists are generally interested in how interactions among species of organisms (plant-animal) alter their abundance, distribution, diversity, and composition, the effects of heavy metals on these traits require further investigations (Velma et al., 2009). Hence, this study seeks to (i) evaluate the sources and distribution pathways of heavy metals in the terrestrial ecosystem, (ii) elucidate the effects of heavy metals on pollination, nectar quality, and pollinator fitness, (iii) assess the effect of heavy metals on plant growth and reproduction, and (iv) examine the drivers of pollinator decline. Scattered studies have highlighted heavy metal effects on pollination, plants, and pollinators. However, given the scattered nature of some of these findings, it is difficult to understand the issues regarding global pollinator decline and strategies to mitigate the menace. This review, therefore, comes in handy to harmonise isolated findings into a formidable piece to guide policy reforms towards biodiversity conservation strategies and provide better insights concerning pollinator-plant relationships.

Methodology

The relevant papers for this study were retrieved from many scientific and academic databases, notably Web of Science (WoS), Springer Nature, Scopus, Science Direct, Google Scholar, Semantic Scholar, and PubMed Central. Literature and information search shortcomings were overcome by using additional search tools such as Scite, R Discovery, SCISPACE, Publish, or Perish 8.0 during the search process. The keywords used in the search were heavy metals, plant-pollinator interaction, biotic pollinators, the interaction between plants or animals and heavy metals, pollination, nectar, pollen, and plant secondary metabolites. Search retrieval of articles was restricted to English-published articles. As part of the screening, the titles and abstracts of popped-up articles during the search were evaluated thoroughly to determine their suitability for inclusion in the relevant paper pool. The titles and abstracts of the screened papers were further scrutinised to ensure they were relevant to the study goal. At the same time, the entire contents of the articles were additionally appraised in cases of any ambiguity to ensure the sampling strategies, methodology, and data analytical procedures were correct and appropriate. All relevant materials and information concerning the topic from the above scientific and academic databases, as much as practicable, were assessed and considered, particularly peer-reviewed articles. Contents from 'doubtful and predatory' sources were excluded as practicably as probable. Most of the empirical data analysed in this study were primary studies conducted on the related keywords. As a third screening layer for the retrieved literature, three experts in plant-animal interaction and heavy metals were consulted for their suggestions and critiques, aiming to achieve a robust screening process. Overall, 390 heavy metals, metalloids, and plant-animal interaction-related materials were retrieved using various search tools available. After a rigorous screening, 200 articles passed the screening processes and were ultimately retained for this study, as shown in Fig. 1.

Sources of heavy metals in terrestrial ecosystem

Heavy metals are naturally occurring elements in the earth's crust (Tchounwou et al., 2012). However, their environmental distribution and concentrations vary based on their point sources. Heavy metals are released into terrestrial ecosystems via natural or anthropogenic sources (Mohammad Saghir Khan et al., 2011). Most often, anthropogenic activities are responsible for the widespread emission of potentially toxic elements into the terrestrial environment via industrial productions, mineral extractions, agricultural activities, smelting, and application of fossil fuels. The continuous, accelerated disturbance and exploitation of these elements by humans, thus the geochemical cycle of metals, lead to the terrestrial environment accumulating potentially toxic elements above the permissible thresholds (Bradl, 2005). When the concentration of the potentially toxic elements exceeds the established background values, they tend to pose severe risks to not only humans but also plants, animals, microorganisms, and ecosystem services and functions. The distribution and circulation pathways of potentially toxic elements in the terrestrial environment may be natural, such as volcanic blasts, soil erosion, soil formation, or geogenic and lithogenic activities (Bradl, 2005). Anthropogenic-wise, heavy metals may be distributed via industrial effluents, sewage disposal, landfills, mining, agricultural activities, and industrial emissions (Tchounwou et al., 2012). Evidence suggests that the bulk of heavy metal accumulation in the terrestrial environment is via anthropogenic activities such as rapid

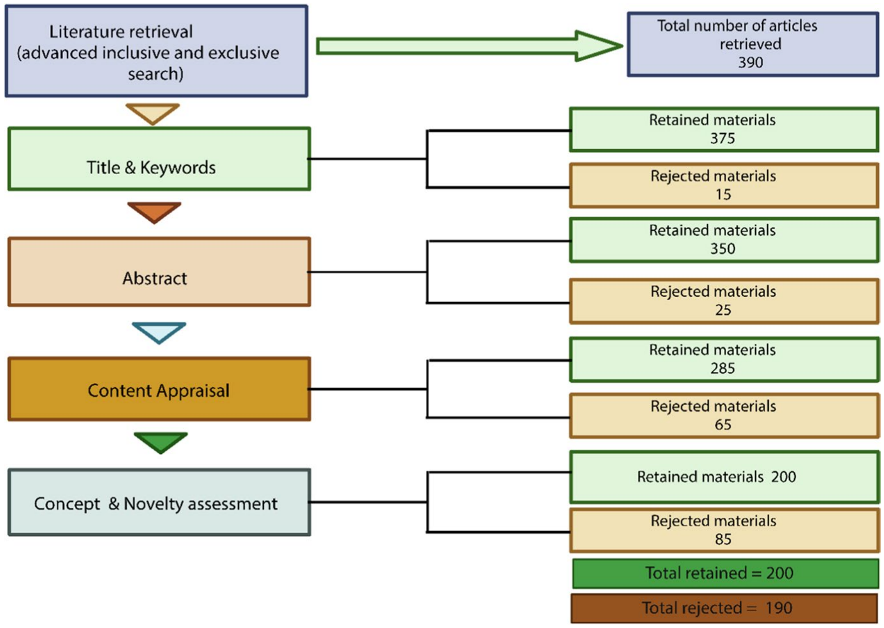

Fig. 1 Schematic illustration of advanced literature search and screening

urbanisation, commercialisation of agriculture, population growth, and robust industrialisation (Pujari & Kapoor, 2021). The terrestrial environment embodies soil and soil or air interface and the biological species and communities therein. Large species, including organisms, are linked to the interface between the belowground (ground) and aboveground partition, concurrently or otherwise interacting with both divisions (Tarazona & Ramos-Peralonso, 2014). As illustrated in Fig. 2, anthropogenic activities are the dominant and reoccurring sources of potentially toxic elements in terrestrial ecosystems.

Natural sources of heavy metals

Rocks such as sedimentary, magmatic igneous, and metamorphic are vital sources of heavy metals in terrestrial environments. The igneous rock is formed due to the solidification of the molten magma, which originates from the earth's mantle and may be transported to the topmost part of the soil via many geological processes, including volcanic eruption, plate tectonics, or seismic activities (Bradl, 2005). The magma comprises diverse constituent chemical elements, including potentially toxic elements, released during natural phenomena such as volcanic eruptions, rock weathering, and plate tectonic activities (Bradl, 2005). Many rocks, especially sedimentary rocks, possess properties such as porosity and permeability, allowing them to hold and transport fluids. The rocks also contain deposits of heavy metals. During soil formation, rock weathering, and plate tectonic activities, these potentially toxic elements are released into the environment, thus causing environmental pollution (Bradl, 2005). High concentrations of cadmium (Cd) and mercury (Hg) in Austria were traceable to rock weathering activities involving eluvial bedrock (Reisinger et al., 2009). The surface and deep-depth soil profiles were heavily enriched with heavy metals such as Cd, Zn, and Pd. The phenomenon was partly due to relatively high concentrations of base materials such as limestone and sandstone bedrock, thus suggesting the natural origin of the heavy metals (Fuge et al., 1991). Soils developed from serpentine rocks are strongly enhanced in potentially toxic elements such as chromium (Cr) and nickel (Ni) due to the elevated levels of these elements in the bedrock and the availability of other minerals (Proctor & Baker, 1994).

Anthropogenic sources of heavy metals

Anthropogenic activities threaten environmental quality more than natural phenomena (Li et al., 2023). Anthropogenic-induced sources of heavy metals are numerous, ranging from mining tailings, smelting,

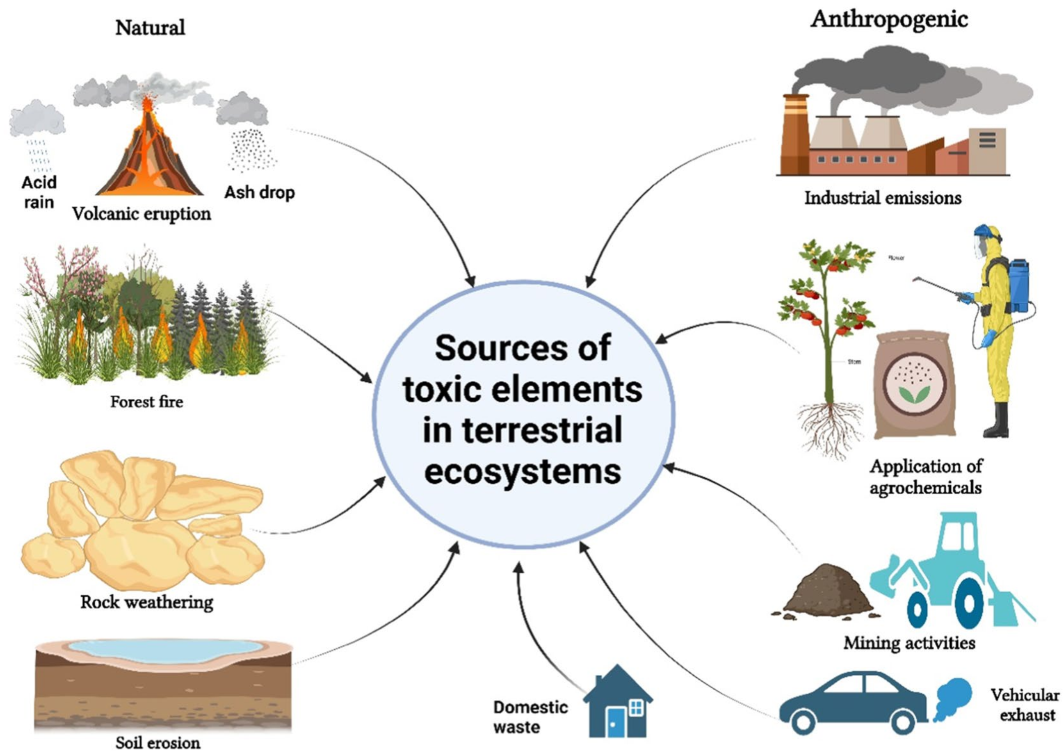

Fig. 2 Sources of toxic elements in terrestrial ecosystems

effluents, solid waste and landfills, deforestation, forest fires, fossil fuel combustion, coal combustion, industrial emission, and agrochemicals such as fertilisers, pesticides, and weedicides (Briffa et al., 2020; Wuana & Okieimen, 2011). Industrialisation is a critical human-induced activity that results in the accumulation of heavy metals in terrestrial ecosystems. Emissions from chimneys are a vital input source of heavy metals in the atmosphere. Hg release into the atmosphere is prevalent in South Africa, attributed to coal combustion activities and mining (Fayiga et al., 2017). The released heavy metals can travel short or longer distances depending on the prevailing weather conditions and elevation of the chimney vents. Higher chimneys contribute significantly to long-range transboundary heavy metals in terrestrial environments (Ji & Ma, 2022). Warmer temperatures and windy atmosphere enhance the travelling length of gaseous aerosols and particulate toxicants by convection and side currents and vice versa. Transport exhaust fumes such as vehicles, ships, and jet engines emit heavy metals into the atmosphere, often transported by moving clouds and prevailing winds to farther distances, thus contaminating the terrestrial environment (Briffa et al., 2020). For instance, road traffic emission is a crucial source of antimony (Sb) in the atmosphere or surface environment (Philippe et al., 2023). De Silva et al. found that the concentrations of heavy metals such as cadmium (Cd), zinc (Zn), lead (Pb), platinum (Pt), rhodium (Rh), and palladium (Pd) in roadside soil samples were higher compared to the global mean crustal values raising severe concerns about vehicular emission of heavy metals into the terrestrial environment (De Silva et al., 2021). The extraction of mineral resources via mining activities releases heavy metals into the terrestrial atmosphere, particularly the improper disposal of mining tailings and acid mine drainage. A recent study reported that the global demand for six metal elements such as copper (Cu), lead (Pb), nickel (Ni), zinc (Zn), aluminium (Al), and iron (Fe), will probably continue to rise till 2100 with two- to sixfold depending on the element (Watari et al., 2021). Wastewater discharge from industrial and domestic sources is a vital cause of the accumulation of potentially toxic elements in the terrestrial environment. Similarly, agricultural activities, including applying chemical or inorganic fertilisers, insecticides, and weedicides and using adequately treated wastewater for irrigational purposes, contribute significantly to the accumulation of heavy metals in terrestrial environments (Ali et al., 2019; Rimawi et al., 2009).

Burning fossil fuels such as coal and crude oil by manufacturing companies, industries, thermal power plants, and the transportation industry releases heavy metals in the terrestrial environment. Industrial activities and operations emit the heaviest metals in the terrestrial environment (Mitra et al., 2022). Potentially toxic elements such as lead (Pb), cadmium (Cd), chromium (Cr), zinc (Zn), mercury (Hg), tin (Sn), antimony (Sb), arsenic (As), nickel (Ni), thallium (TI), copper (Cu), and cobalt (Co) are released into the atmosphere. The rampant industrial and booming transportation activities result in these heavy metals in the atmosphere accumulating on the vegetation cover and soils (Vouk & Piver, 1983). Napier et al. found that, in the UK, automobiles were the critical sources of Cu, Zn, and polycyclic aromatic hydrocarbons (PAHS) emissions in the environment (Napier et al., 2008). In recent years, there has been a global shift from internal combustion engines to electric vehicles (EVs) in response to urgent calls to mitigate the growing concerns about climate change and its devastating consequences on humanity and ecosystems. Hence, there is increasing demand for lithium-ion battery-powered automobiles. This major shift is driving the need for battery minerals, and it has been projected that essential raw materials (metals) for the manufacture of batteries will rise by 20-fold or more in the next three decades (Nkrumah et al., 2022). It means the increasing exploitation of potentially toxic elements such as Ni, Co, and Li via conventional methods will likely increase their potential release into the terrestrial environment, thus increasing the risks of exposure to humans, animals, microorganisms, and ecosystems. In cement industries, every production stage produces dust containing potentially toxic elements such as Hg, As, Cd, and Pb, which are released into the atmosphere as particulate matter (Das et al., 2023). Recent evidence suggests that roadside habitats, ubiquitous parts of terrestrial ecosystems, are significant sources of heavy metal pollution to pollinators (Meinzen et al., 2024).

Distribution pathways of heavy metals in terrestrial ecosystems

Heavy metals spread in the terrestrial ecosystem via atmospheric deposition, soil erosion, leaching, volcanic eruptions, chimney emissions, vehicular exhaust, agricultural activities, and mining and smelting operations (Madhav et al., 2023). The forms and nature of potentially toxic elements deposited in the terrestrial environment vary depending on the pathway. For instance, heavy metals can accumulate in the terrestrial environment via dry atmospheric deposition in dry particulate matter, dust, gases, aerosols, and fossil fuel combustion (Bradl, 2005; Pujari & Kapoor, 2021). Heavy metals in the form of aerosols are categorised into two main types: primary and secondary aerosols. The primary aerosols are released into the atmosphere directly from the earth's surface.

In contrast, secondary aerosols occur due to chemical interactions in the atmosphere, where gaseous particles and water vapour react with existing contaminants to form new species of toxins (Sievering, 1999). It may also occur through wet deposition in precipitation, fog, acid rain, and permafrost. Heavy metals can accumulate naturally in the terrestrial environment via pedogenic activities, including weathering of serpentine rocks and the parent material (Jayakumar et al., 2021). The movement of soil and sediment due to soil erosion and atmospheric deposition contributes to the distribution of heavy metals in the terrestrial environment (Singh & Kumar, 2017).

Although the atmosphere may be categorised into five key strata, the stratosphere and troposphere are the primary transportation channels of heavy metals. The troposphere is the nearest stratum to the earth, while the stratosphere lies above the troposphere, within which the ozone is located. Due to the vigorous vertical mixing effect in the troposphere with consistent air circulation and pattern, heavy metals are transported quickly. However, heavy metals emitted close to the earth's surface may not move far from the emission source due to confined airflow and turbulence effect and thus may accumulate in nearby ecosystems (Briffa et al., 2020). Heavy metals may accumulate in terrestrial environment runoffs, application of inorganic fertilisers, pesticides, weedicides, and improperly treated effluent and sewage sludge for irrigational activities (Gall et al., 2015). Vehicular emission is a crucial route via which heavy metals are released into terrestrial ecosystems in the form of exhaust fumes from the combustion of fossil fuels (Zwolak et al., 2019). Zhou et al. found that sewage irrigation, fertiliser application, and atmospheric deposition were significant sources of anthropogenic input of potentially toxic elements such as Zn, Pb, Ni, Hg, Cd, As, and Cr in Huanghuai Plai (Zhou et al., 2014). As depicted in Fig. 3, the below and above-ground routes via which plants accumulate heavy metals in terrestrial ecosystems have been illustrated.

Effects of heavy metals on nectar quality and pollination

According to the Food and Agriculture Organization of the United Nations (FAO), approximately 90% of all wild angiosperm species rely on biotic pollination to some extent, highlighting the significant role of insects and other animal pollinators (Food & Agriculture Organization, 2016). Animal-plant interaction is the most critical ecological symbiotic relationship between plants and pollinators, without which many plants, particularly angiosperms, may not produce seeds and reproduce (Ollerton et al., 2011). Plant-pollinator interactions play a vital role in the dynamics of plant communities. For instance, the *Dionaea muscipula* (Venus flytrap) plant requires biotic pollinators to move pollen within and across other plants for successful reproduction (Hamon et al., 2024). However, pollination services depend on the abundance and the foraging behaviour of pollinators and the availability and distribution of floral resources (Nottebrock et al., 2017). Heavy metals are a global concern in pollination due to the global decline in pollinators and heavy metals' persistent, harmful, and bioavailability properties in terrestrial environments (Jing et al., 2018). The accumulation of heavy metals by plants, either from the soil or from atmospheric deposition, influences the chemical properties of nectar, thus affecting the reproductive fitness of

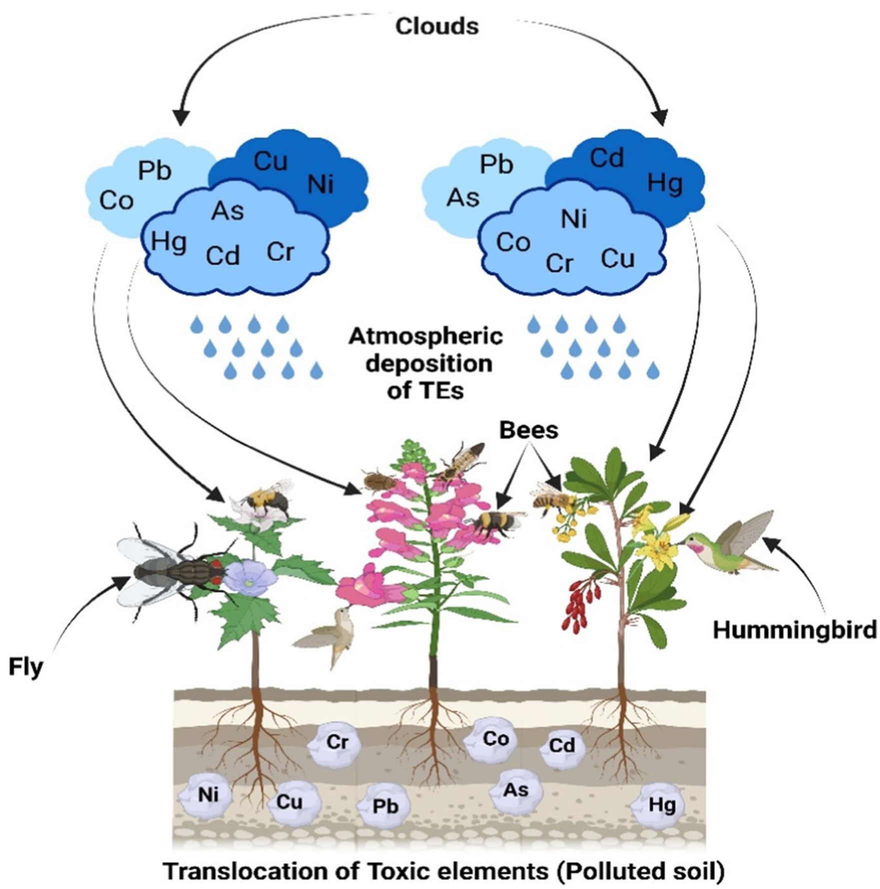

Fig. 3 Above and below-ground accumulation pathways of toxic elements by plants in terrestrial ecosystems

the plant and the behaviour of pollinators and floral antagonists (Xun et al., 2018). Due to their persistent properties, heavy metals can accumulate in different tissues of plants and living organisms via bioconcentration and biomagnification mechanisms (Mahdavian and Somashekar, 2009). For instance, Cd has high accumulation and mobility potential, thus making its transfer within trophic levels less complicated in terrestrial ecosystems (Xia et al., 2024). Meindl and Ashman found that the growth of *Strptanthus polygaloides*, a hyperaccumulator of Ni on Ni-enriched soil, did not affect the flower's morphology, anther size, or nectar quantity.

Nevertheless, the accumulation of heavy metals by plants in their leaves and floral parts indicates that pollinators visiting and foraging on the tissues of such plants expose them to potential harm. In a greenhouse study, Hladun et al. exposed *Raphanus sativus* to Cu, Cd, or Pb, finding that Cu accumulation was the highest in the flowers among the metals (Hladun et al., 2015). Cadmium (Cd) and Cu exhibited the highest translocation indices and bioconcentration factors compared to Pb, which showed less mobility. Thus, Cu exhibited the highest risk because of its high translocation capacity within the plant tissues (Hladun et al., 2015). *Apis mellifera* colonies treated with Cu or Cd had more dead pupae within the capped cells than untreated colonies. Colonies treated with selenium (Se) exhibited lower total worker bees' weights than untreated colonies. In contrast, Pb showed a minimal effect on the colony's performance despite the many bees from the significantly accumulated quantities of the metal (Hladun et al., 2015).

However, Ni was accumulated in the nectar and pollen-filled anthers. Due to the floral accumulation of Ni, fewer visitations occurred by bees and flies compared to plants grown in a controlled environment (Meindl & Ashman, 2014). Thus, heavy metals alter the chemical composition of nectar (Xun et al., 2018). For instance, the alkaloid gelsemine in the nectar of *Gelsemium sempervirens* (yellow jasmine or Carolina jasmine) decreased the visitation of pollinators. However, it showed no significant effect on nectar robbers, thus reducing the reproduction of female plants' natural ecosystems (Adler & Irwin, 2012). *Helianthus annuus L.* (sunflowers) grown in high Cd-contaminated soil reduced the frequency and time of visits by bumblebees, while increasing Cd concentration reduced sunflower height (Sivakoff et al., 2024). Sucrose solution (artificial nectar) spiked with As, Cd, Cr, or Pb, and another nectar spiked with all four heavy metals were exposed to *Bombus impatiens* (bumblebees) for 15 or 30 days in flight tents. Colonies fed with all the heavy metals recorded a significantly higher proportion of dead brood than those fed with single metals (Scott et al., 2022). When fed by pollinators, heavy metals in nectar reduce their fitness and increase their susceptibility to diseases and pathogens, thus jeopardising their survival rate (Feldhaar & Otti, 2020). *Apis mellifera* exposed to particulate matter ($PM_{2.5}$ and PM_{10}) in bowl traps mounted near incense-controlled colonies resulted in a depressed bee population, deterioration in olfaction, and flight performance (Khan et al., 2024a, 2024b). The mechanisms of heavy metal toxicity in insect pollinators relate to the interaction with the thiol group or a sulfhydryl group (–SH molecules). Exposure to heavy metals such as Hg, Pb, Cd, and Cu can disrupt the locomotor performance and mating behaviour of insect pollinators (Oliveira et al., 2022). Evidence showed that both bumble bee larvae and adults can accumulate higher amounts of heavy metals in their bodies when exposed to these toxicants via nectar foraging (Scott et al., 2024).

Quinn et al. observed that plants' selenium (Se) accumulation affects plant-arthropod interactions. Due to its hyperaccumulation capability, *Stanleya pinnata* (*S. pinnata*) can accumulate potentially toxic elements such as Se from the soil and translocate them to the floral parts. *Brassica juncea* (brown mustard) accumulated a higher content of Se in its leaves compared to the flowers cultivated on Se-enriched soil. They further observed that a higher concentration of Se in *B. juncea* flowers inhibited pollen germination while showing no effect on pollen germination in *S. pinnata* (Quinn et al., 2011). Sikakoff and Gardiner found that cultivating sunflower plants on Pb-enriched soil reduced the visitation time of bees but did not affect the frequency of visitations (Sivakoff & Gardiner, 2017). Lead (Pb) altered the sensitivity of honeybees towards the evaluation of sucrose after ingesting the metal or after antennal stimulation (Burden et al., 2019).

Cucurbita pepo L. cv. (Golden Apple) grown on potentially toxic elements contaminated soils such as Ni, Pb, Zn, and Cu showed the accumulation of these metals on the floral organs with varied concentrations depending on the potentially toxic element. The proliferation of the heavy metals by the squash plant reduced the foraging time of honeybees compared to those grown on controlled soils. Increased concentrations of the heavy metals led to a reduction in seed weight, pollen transfer, and pollen viability, as well as the visitation behaviour of pollinators (Xun et al., 2017). Soil chemical properties, such as the amount of potentially toxic elements in a particular soil, can alter floral traits such as morphology and floral properties (Meindl & Ashman, 2013; Sivakoff & Gardiner, 2017). This phenomenon could affect the plant and pollinators' interaction positively or negatively (Meindl & Ashman, 2015). Meindl and Ashman observed that the foraging time of bumblebees reduced due to the accumulation of Ni in the nectar of flowers in Ni-polluted soil. It also hampered the visitation by bees to neighbouring flowers in the contaminated area (Meindl & Ashman, 2013).

In contrast, the accumulation of heavy metals in nectar also serves as a check mechanism against nectar' thieves', thus serving a beneficial purpose to plants (Xun et al., 2018). It means that the contamination of nectar by heavy metals could play antagonistic and mutualistic roles in flowers. For effective foraging by bees, they must first learn flower location, nectar profitability, and flower manipulation skills to extract the nectar. Floral traits include colour, scent, size, and morphology; therefore, pollinators must first locate the flower and learn how to manoeuvre their ways (Laverty, 1994). Biotic pollination is an essential ecosystem service provided by pollinators. Studies showed that about 75% of the major global food crops demonstrate improved fruit or seed set due to animal pollination (Klein et al., 2007). One way to enhance pollinator-plant interaction in terrestrial ecosystems is to reduce land-use intensity on agricultural grasslands, which benefits pollinator diversity, such as bees and enhances pollination service delivery (Scheper et al., 2023). It is important to note that, besides potentially toxic elements that hinder pollination services by biotic pollinators, the complexity of floral organs also affects the foraging efficiency of biotic pollinators, exceedingly naïve pollinators (Laverty, 1994). For instance, naïve bees can locate nectar from shallow cup-shaped flowers with exposed nectar and many long-tubed flowers with an open entry on their first attempts. However, bees may spend up to 30 min on flowers with concealed nectar to achieve learning adeptness and about an hour to attain flower-handling competence (Laverty, 1994).

Nectar chemistry significantly influences biotic pollinators' visitation frequencies, behaviour, and dynamics (Barberis et al., 2023). Heavy metals in nectar, such as bumblebees, deter flower robbery and could affect mutualistic biotic pollinators (Barlow et al., 2017). Nectar is generally an energy source due to the presence of sugars, but it may provide pollinators such as bees more than sugar. Studies have shown that pollen provides various nutritional benefits (constituents) to bees, such as lipids, minerals, vitamins, and protein, which are vital for their larvae (Nicolson, 2011). Nectar exposed to heavy metals leads to the alteration of its quality, thus affecting the foraging behaviour of pollinators and reducing the foraging time (Xun et al., 2018). Besides the decline in pollinators, the accumulation of heavy metals in nectar reduces pollination services and inbreeding by plants, reducing nectar quality (LeBuhn & Vargas Luna, 2021). Nectar is the main benefit directly gained by biotic pollinators. Hence, the chemical properties and constituents influence the behaviour and fidelity of pollinators (Bogo et al., 2021). Nectar sugar and amino acid contents in old flowers are significantly higher compared to flower buds. Nectar contamination by floral visitors enhanced nectar amino acid quantity and diversity. Nectar exposed to biotic pollinators exhibited more yeast cells than flowers not visited by biotic pollinators, though low to cause variation in glucose/fructose ratio (Bogo et al., 2021). It suggests that many exogenous and endogenous parameters influence nectar chemical composition during ecological interactions in complex processes, thus altering plant–insect interactions. Nectar secondary metabolites (alkaloids) are typical floral nectar, like in leaves and flowers, although in a lower concentration. However, their presence in nectar significantly affects biotic pollinator visits and the duration per flower by free-range bumblebee pollinators.

Thus, the effect of nectar alkaloids on biotic pollinators' behaviour and activity depends on the concentration or dose (Manson et al., 2013). These secondary metabolites, such as nicotine, caffeine, grayanotoxins, aconitine, thymol, linalool, and lupanine, serve as defence mechanisms against nectar robbers but can also affect mutualists (Stevenson, 2020). The toxic effects of these alkaloids may be similar to synthesised heavy metals. For instance, caffeine is considered a potential natural biopesticide (Hollingsworth et al., 2002). Its toxic effects in insects include paralysing and intoxication via the inhibition of phosphodiesterase activity, thus increasing intracellular levels of cyclic adenosine monophosphate (AMP) (Nathanson, 1984) and inhibiting feeding in *Spodoptera litura* (tobacco armyworms) (Uefuji et al., 2005). The effect of nectar secondary metabolites on pollinator interactions varies depending on the mix or combination. For instance, Muth et al. demonstrated that combining tyramine and octopamine in a concentration range similar to natural nectar did not affect insect behaviour. However, when mixed with caffeine, they altered critical traits of bumblebees' behaviour, such as floral preferences, long-term memory, and sucrose responsiveness (Muth et al., 2022). Marchi et al. found that arginine and caffeine increased honeybee learning performance. However, insect memory retention increased significantly only when fed with treatment with the combination of the two compounds (Marchi et al., 2021).

Effect of heavy metals on biotic pollinators

The increase in global emissions from anthropogenic activities such as industrial production, manufacturing, mining, transportation, and application of agrochemicals increases the pollution burden of ecosystems. Most of this anthropogenic-induced environmental pollution endangers well-being and alters the interaction between animals and plants (Margaoan et al., 2024). The chronic exposure of pollinators to heavy metals negatively affects individual pollinator health. Thus, it ultimately affects pollinators' population and community levels, thus jeopardising the integrity of terrestrial ecosystems (Tovar-Sánchez et al., 2018) by As adversely affecting wild bee diversity (Shi et al., 2024). Monchanin et al. found that bees sampled from a nearby gold mine site reduced their olfactory learning performance by 36% and head sizes by 4%. Additionally, the three-dimensional scans of the bees' brains revealed that the olfactory centres were 4% smaller, suggesting neurodevelopmental challenges due to exposure to heavy metals (Monchanin et al., 2024). Pesticides pose sublethal effects on the pollinator community, particularly bees, ranging from reproduction to learning difficulties. Pollinators provide critical services to wild ecosystems and crops. However, their diversity and abundance are threatened due to habitat loss (Meinzen et al., 2024). The effects of neonicotinoids on pollinators, especially bees, are worsened when bees are starved, highlighting the importance of nectar resources for the survival of bees exposed to heavy metals (Fischer et al., 2024). The treatment of strawberry plants with active ingredients from commercial formulations of pesticides such as Cuprozin® Progress and SWITCH® affected the plants. For instance, the exposure of the plants to Cuprozin® Progress resulted in reduced emission of floral volatiles and reduced pollen protein concentration. In contrast, the treatment with SWITCH® led to higher emission of floral volatiles. Still, it delayed the first visitation and the visitation frequency by bumblebees compared to the control plants (Voß et al., 2023), highlighting the adverse effects of agrochemicals on plant-animal interaction. Stanley et al. found that more bees became foragers when colonies of bumblebees were sequentially exposed to 10 parts per billion (ppb) of thiamethoxam, a neonicotinoid pesticide, and were later released. The bees also visited *Lotus corniculatus* flowers more than the control species. Bumblebees were exposed to thiamethoxam-collected pollen quite frequently compared to the controls; however, controlled bumblebees efficiently handled flowers following a couple of visits compared to the bees exposed to the pesticide. This suggests that the sublethal effect of agricultural pesticides such as thiamethoxam can potentially influence the foraging behaviour of bumblebees during pollination (Stanley & Raine, 2016). Neonicotinoid agrochemicals reduce effective foraging, cognitive functions, and colony fitness in pollinators, particularly bumblebees (Gill & Raine, 2014; Moffat et al., 2015; Stanley & Raine, 2016). When honeybees were exposed to 80 parts per billion (ppb) of ozone (O_3), it decreased olfactory recall (Démares et al., 2024). Cd disrupts the redox balance of bees, causes oxidative stress, alters the gut microbiota, and reduces the survival rate of *Apis cerana cerana* (Li et al., 2024a, 2024b). Extreme Cd exposure at field-realistic concentrations reduced the flight capacity of *Bombus terrestris* (bumblebees) and caused mitochondrial loss and muscle fibre damage (Gao et al., 2024). Honeybees respond actively to environmental stressors such as Pb and Hg derived from cities. The concentration of Hg and Pb were highest in urban areas' bees and honey compared to montane and agricultural areas, highlighting the emissions risks in cities to pollinators (Gizaw et al., 2020). The exposure of *Apis mellifera* to Cd and Cu altered the expression of genes for catalase and superoxide dismutase, while Pb exposure only affected superoxide dismutase gene expression. The results further showed that even the lowest concentration of Cd reduced catalase activity (Nikolić et al., 2016). Honeybees exposed to a low concentration of Pb (0.1 mg/L) caused a biphasic effect on acetylcholinesterase activity, while a higher dose of 10 mg/L induced acetylcholinesterase activity in the honeybees. Exposure of the honeybees to 0.001 and 0.01 mg/L of cadmium chloride ($CdCl_2$) led to a significant reduction in acetylcholinesterase activity (Nikolić et al., 2019). Agrochemicals such as pesticides, insecticides, and weedicides, particularly neonicotinoids, have been identified as critical abiotic drivers altering the bee community in the terrestrial environment (Wood & Goulson, 2017). Czerwinski and Sadd found that applying pesticides alters immune function and thus influences bumblebees' fitness and survival rate (Andrew et al., 2017). The overreliance on synthetic pesticides for agricultural purposes globally depletes beneficial insects, including insect pollinators (Bakker et al., 2020). The exposure of the bumblebee colony to imidacloprid (neonicotinoids) resulted in reduced nest condition and growth compared to unexposed colonies. Thus, extreme exposure of bumblebees to neonicotinoids affects development and nest conditions and increases neuronal vulnerability to mitochondrial dysfunction (Moffat et al., 2015). The exposure of *Partamona helleri* (stingless bee) to copper sulphate ($CuSO_4$) and spinosad altered its survival rate, while $CuSO_4$ exposure altered its respiration. This highlights the adverse effects of agrochemical exposure on bees' survival and foraging behaviour (Botina et al., 2019). The application of field-recommended rates of 200 and 8.16 μg of active ingredients of copper sulphate ($CuSO_4$) and spinosad, respectively, per *Partamona helleri* (bee), caused a reduction in bee survival. In addition, 0.03 or 0.08 μg of active ingredients of spinosad reduced the body weight and increased the number of deformed bees (Botina et al., 2023).

Ollerton et al. found that the proportion of biotic-pollinated species increases from an average of 78% in temperate communities to 94% in tropical communities. Based on latitudinal richness trends in angiosperms, the global proportion and amount of biotic pollinated flowering plants are estimated to be 87.5% and 303,006 at species level richness (Ollerton et al., 2011). Apart from the acute and chronic consequences of neonicotinoids on biotic pollinators' foraging history, it also alters the preferences of pollinators towards flowers from which they collect pollens, indicating the harmful effects of pesticides (Gill & Raine, 2014). This highlights the significant role of biotic pollinators (insects and other animals) in sustaining most terrestrial ecosystems' functionality. Hence, the accumulation of potentially toxic elements in the terrestrial environment severely threatens and undermines the ecological relationship between plants, insects, and other animal pollinators. Evidence suggests that most tropical angiosperm species rely heavily on biotic pollinations (insects and other animals) for fertilisation, meaning that tropical plants (angiosperms) could suffer most from the global decline of pollinators heavily impacted by anthropogenic activities (Vizentin-Bugoni et al., 2018). Heavy metals and pesticides are at the top of the list of environmental pollutants that directly endanger the survival and reproduction of *Apis cerana cerana* (Asian honeybee) due to their toxicities (Li et al., 2024a, 2024b).

Effects of heavy metals on symbiotic relationships

Excess concentrations of heavy metals impede normal cell division, increase membrane lipid peroxidation, and prevent antioxidant enzyme activities (Rizwan et al., 2018). For instance, Cd inhibits physiological processes, including photosynthesis, transpiration rates, cell growth and elongation, respiration, nitrogen metabolism and mineral nutrition, biomass reduction, and subsequent plant death (Morkunas et al., 2018). Excess concentration of heavy metals poses a significant threat to symbiotic relationships between plants and microorganisms such as legumes and rhizobia (El-Tahlawy & Ali, 2021). The exposure of *Symphytum officinale* to heavy metals reduced the network species' material and signal exchanges, leading to a worse community composition stability. It further drastically reduced the symbiotic relationship between microorganisms. Cadmium (Cd) and Pb exposure led to *Pseudomonas* stress (Ma et al., 2024). Lead (Pb), Cd, and Ni accumulation by *Phaseolus vulgaris* caused photosynthetic pigment reduction and nodule characteristics. Cadmium (Cd) exhibited the most substantial toxicity effect on symbiosis compared to Ni and Pb (Hammami et al., 2022).

Additionally, there were significant reductions in shoot and root dry weights, root and shoot nitrogen content, number of nodules, and number of pods due to the presence of heavy metals in the soil, confirming the adverse effects of heavy metals on symbiotic activities of *Phaseolus vulgaris* (Hammami et al., 2022). Xiao et al. observed that pectin methyl esterase enhanced Cd accumulation in the leaf cell walls of *Arabidopsis thaliana* and inhibited its redistribution to silique (Xiao et al., 2022). The accumulation of Mn by *Sargassum cymosum* resulted in cellular destruction with organelle disruption and disorganisation of cell wall fibrils. Both medium and higher Mn concentrations caused metabolic stress in *Sargassum cymosum* (Costa et al., 2017).

Other factors

Besides the above-highlighted effects of heavy metals, some other essential factors negatively affect the adequate performance of pollinators. These include floral traits, plant, pollinator fitness, and survival. Ultimately, pollinators and plant species richness, diversity, and abundance are negatively influenced by these factors, posing threats to their survival in terrestrial ecosystems. Assessing environmental drivers that regulate the functional composition of different organisms, including pollinator species, is essential to establishing a more direct linkage between community structure and terrestrial ecosystem functions (Coutinho et al., 2018).

Effects of heavy metals on pollen viability, reproduction, and plant growth

Heavy metal pollution is one of the fundamental abiotic factors that negatively affect the productivity of plants (Asgher et al., 2023). Globally, there are contrasting estimations about angiosperm species. At the same time, Ollerton et al. estimated the number to be 308,006 (Ollerton et al., 2011), Jiang et al. put the total number of angiosperms at 288,735 species globally (Jiang et al., 2023). Whatever the number of angiosperms, empirical evidence suggests that floral phenological shifts due to natural or anthropogenic activities alter the plant-pollinator interactions, affecting adequate pollination and seed fruit development (Rafferty & Ives, 2011). Evidence showed that plants could accumulate heavy metals such as Cu, Zn, Pb, and Cd in different parts of plants, such as roots, stems, xylem, flowers, leaves, and pollens (Sumalan et al., 2023). For instance, the accumulation of heavy metals by pollens affects their viability and development. The accumulation of heavy metals such as Hg, Cu, Cd, and Pb significantly reduced pollen germination and tube growth in apricots and cherries. Copper (Cu) exhibited the most significant toxicity effect on the pollen of apricot, while Pb showed the slightest effect. The pollen germination and tube elongation in cherries were significantly inhibited by Cd and compared to Pb (Nazmi & Aykut, 2008). The accumulation of heavy metals by plants in excess concentrations results in deleterious consequences regarding plants' physiological and biochemical processes due to the alteration in the morphology of the vegetative and reproductive parts (Li et al., 2023).

As already discussed earlier, sources of heavy metals in terrestrial ecosystems vary. Notwithstanding their origins, their effects on plants are devastating, ranging from oxidative stress to cell membrane destruction. Arduini et al. found that the exposure of *Pinus pinea L.* and *Pinus pinaster Ait* plants (seedlings) to 5 μM of Cu inhibited root growth of both species within 3 h. They also noted that cell elongation in the plants was very sensitive to Cu compared to cell division. Exposure of the two species to 1 μM of Cu resulted in cell membrane destruction after 10 days, confirming the negative consequences of potentially toxic elements on plant development (Arduini et al., 1995). Due to the ability of many plants to accumulate potentially toxic elements from the atmosphere, mainly from human activities, including Zn, Cd, Pb, Cr, and Cu, in higher concentrations, these elements tend to induce adverse effects (Turkyilmaz et al., 2020). Many plants readily accumulate heavy metals such as Cr in the atmosphere, ultimately hindering their growth due to their high concentrations (Sulhan et al., 2023). When *Aulosira fertilissima* was exposed to Pb treatment, it resulted in the retardation of chlorophyll-a, -b, total, phycobilin, and carotenoids. In addition, metabolites such as carbohydrates, phenols, and proteins also reduced in content after Pb exposure (Nirmal Kumar et al., 2009). Exposure of Ni to *Arabis alpina* (Brassicaceae) impeded pollen germination and pollen tube elongation. The pollen tubes exhibited abnormalities, including swelling of the tip, coiling, or burst, and variation among the specimens with a reduction in pollen fertility (Pavlova, 2016).

The *Nicotiana tabacum* (tobacco) exposure to Hg, Al, Zn, Cu, Ni, Pb, Co, and Cd reduced the pollen germination rate and pollen tube elongation. Ni, Hg, and Cu exhibited the most toxic effects on the elongation of pollen tubes (Tuna et al., 2002). In cherry plants, fruit set is significantly influenced by pollen germination and tube growth. When ten sweet cherry cultivars in vitro were exposed to increasing concentrations of heavy metals such as Cu, Pb, Hg, and Cd, it reduced pollen germination and tube growth in all cultivars (Sharafi et al., 2017). When the concentrations were increased to 250 ppm for each metal, tube growth and pollen germination were almost reduced to zero in most cultivars, highlighting the toxicity of these metals on cherry pollen germination and tube elongation. Cadmium (Cd) exhibited the highest toxic effect on pollen germination rate and tube elongation among the cultivars (Sharafi et al., 2017). Cadmium (Cd) toxicity inhibited the pollen germination and tube growth of *Nicotiana tabacum* and *Lilium longiflorum*. When the concentration was increased to 10(−2) M, the pollen germination rate was completely stopped, and pollen exhibited the propensity to burst within an hour (Sawidis, 2008). Similarly, when *Picea wilsonii* pollens in vitro were treated with Hg, Cd, and As led to an irregular increment in the diameters of the pollen tubes and swelled tips with distinct cytoplasmic vacuolation (Wang et al., 2015). Arsenic (As) exhibited the highest toxicity effect on pollen germination, followed by Hg and Cd, while Cu and Cr showed a minimal effect, suggesting that different heavy metals have a varied effect on *Picea wilsonii* pollen germination and tube growth (Wang et al., 2015). The exposure of *Cydonia oblonga* and *Prunus domestica* to Cd, Pb, Hg, and Cu in a culture medium resulted in a drastic reduction in pollen germination and tube growth. Cadmium (Cd) showed the highest inhibitory effect on pollen germination and tube elongation in *Prunus domestica,* while Cu exhibited the least inhibition. For *Cydonia oblonga,* Cu had less effect on pollen germination and tube growth, with Hg exhibiting the highest toxicity (Gür & Topdemir, 2005). Muradoglu et al. found that when three apple cultivars, namely Fuji, Gala, and Braeburn, were treated with Pb, Hg, Cd, Co, and Zn, the pollen germination and tube elongation significantly reduced (Muradoglu et al., 2017). In contrast, Braeburn showed the highest pollen viability, 81.85%, indicating that different apple cultivars have variable sensitivity to heavy metal exposure. Increasing concentration of the metals inhibited pollen germination and tube growth, with Hg exhibiting the highest effect on all the cultivars (Muradoglu et al., 2017). Heavy metals accumulated in plants produced free radicals and reactive oxygen species (ROS) in plant cells, followed by unrestrained oxidation and chain reaction with nuclei acids, lipids, and proteins, leading to oxidative stress and cell destruction. The consequences of heavy metals in plants include redundant growth, biomass reduction, and alteration in metabolism, resulting in decreased yield output (Goyal et al., 2020). Heavy metals deform plants' growth and development and cause ionic imbalance. They also degrade chlorophyll and chloroplast, thus reducing the rate of photosynthesis and altering the elemental composition and water balance in plants (Kumar & Aery, 2016). Cadmium (Cd) inhibits oxygen evolution in plants, thus affecting photosynthesis at the photosystem II level. The inhibition is enhanced by Ca concentration since Cd competitively binds to Ca in the photosystem II site in photoactivation (Faller et al., 2005). According to (Baszyński, 2014), Cd-induced the inhibition activity of Photosystem II due to thylakoid membrane destruction. The effects of heavy metals on plants vary depending on the species. Nevertheless, the result could be direct or indirect on the growth and development of the plants. Direct effects of heavy metals on plants include reducing biological and physiological activities, destroying plants' cellular structure and functions due to oxidative stress, and inhibiting cytoplasmic enzymes. The indirect consequences may include replacing essential plant nutrients due to cationic exchange activities in plant cells (Kumar & Aery, 2016). Heavy metals' generation of ROS in plants leads to peroxidation, damaging the cell membrane and the related organelles of plants. Heavy metals in plants also substitute Mg ions from chlorophyll, thus affecting chlorophyll biosynthesis. Other heavy metals disrupt electron transport during light reactions and alter different enzymes during dark period reactions, thus affecting plants' growth and reproductive function (Rai et al., 2016). Although Zn is a vital micronutrient, it alters many of the metabolic activities of plants. A reduction expresses the phytotoxicity of Cd and Zn in plants' growth and development, metabolism, and induced oxidative destruction of different plant species, including *Phaseolus vulgaris*. Zinc (Zn) toxicity due to extreme concentrations results in stunted growth of roots and shoots, simultaneously causing chlorosis in new leaves (Nagajyoti et al., 2010). Heavy metal accumulation in cereals resulted in visible physiological changes such as stunted growth and chlorosis (Vasilachi et al., 2023). Heavy metals such as Cd cause stunt shoot and root growth, impede photosynthetic activities, stomatal conductance, and plant biomass reduction (Li et al., 2023). Plants' exposure to high Cd concentrations results in brown colouration of root tips, growth inhibition, and eventual mortality in plants. The Cd also alters Fe (III) reductase activity by roots, thus leading to Fe (II) deficiency in plants, affecting photosynthetic activities in plants. Similarly, Cd interrupts the effective uptake of essential nutrients such as K, P, Mg, and Ca and water balance in plants. Cd inhibits nitrate reductase due to a reduction in the absorption of nitrate and its translocation from roots to shoots (Nagajyoti et al., 2010). Plants' exposure to extreme concentrations of Ni leads to chlorosis and necrosis in various species of plants due to alterations in plants' physiological properties. The exposure of plants to higher concentrations of Ni causes nutrient balance impairment, leading to distortion of cell membrane functionalities. Hence, lipid composition and H-ATPase activities of the plasma membrane are altered, as notably reported in *Oryza sativa* shoots (Rahman et al., 2005; Ros et al., 1992). Higher absorption of Ni by plants reduces water content, particularly in monocot and dicot plant species. Excessive Ni uptake reduces water uptake by plants, which suggests that heavy metals, including Ni, are harmful to plants (Gajewska et al., 2006). Plants' exposure to high Co concentration resulted in limiting Fe, chlorophyll, catalase, and protein activities in cauliflower leaves. Cobalt (Co) also inhibits P, Mn, Zn, S, and Cu translocation from the roots to the branches of the cauliflower. However, in contrast to other heavy metals such as Cd, Cu, and Cr, Co drastically reduces the transpiration rate and water potential (Chatterjee & Chatterjee, 2000).

Although a reduction in photosynthetic activities in plants may be partly due to Mn deficiency, many studies showed that excess accumulation of Mn in plants disrupts Mn homeostasis, particularly in acidic and poor-drainage soils where Mn tends to be in extreme concentrations. Excess accumulation of Mn in plants' leaves leads to a decrease in the rate of photosynthetic activities (Alejandro et al., 2020). Abbas et al. found that extreme accumulation of As by plants leads to a disruption of the effect functioning of plant metabolites, thus bringing about retarded growth and poor yield (Abbas et al., 2018). The translocation of Arsenate (As^{+5}) to different cellular membranes by PO_4^{3-} transport proteins results in PO_4^{3-} supply imbalances in plants. In the process of phosphorylation interaction, it may compete with PO_4^{3-} bringing about arsenate adducts, which are usually unstable and short-lived. It reported that chronic As exposure brings about the generation of ROS, which can result in the production of antioxidant metabolites and many enzymes involved in the defence of antioxidants (Finnegan & Chen, 2012). Chronic exposure to As by plants is also associated with biomass and chlorophyll reduction in plants and low germination rate (Nath Barbhuiya et al., 2023). Zhang et al. observed that the uptake of As by plants in excess quantities induced the generation of ROS, hence lipid peroxidation and impairment of cellular membranes (Zhang et al., 2021).

Lead (Pb) adversely affects plants' growth, physiology/morphology, and photosynthetic processes. Lead (Pb) inhibits the germination of different plant seeds such as wheat (*Triticum aestivum* L.) (Yang et al., 2010), Sorghum (Osman & Fadhlallah, 2023), *Peganum harmala* L. (Nedjimi, 2020), and *Lolium perenne* L. (Gholinejad et al., 2020). Evidence showed that high accumulation of Hg by plants resulted in injuries and plants' physiological disorders due to severe phototoxicity in plant cells. Mercury (Hg) in the cellular cell can destroy and block essential molecules such as enzymes and polynucleotides, translocation of important ions, displacement of basic cations such as Mg from chlorophyll, inactivation of proteins, and cell membrane destruction (Gworek et al., 2020). High accumulation of Hg by plants inhibits mitochondrial functions, thus inducing oxidative stress due to the production of ROS. The consequent effect is the interruption of cellular metabolism and biomembrane lipids in plants (Dutta et al., 2018; Jia et al., 2015).

Chromium (Cr) has known toxic effects on plants due to its ability to produce ROS like many other harmful elements in the terrestrial environment. However, some plants have the potential to resist the adverse effects of Cr in low concentrations, such as 3.8×10^{-4} µM (Huffman & Allaway, 1973). The toxicity of Cr depends on its speciation, which influences absorption, transport, and accumulation. Chromium (Cr) adversely affects crops at 5–5.0 mg/mL concentrations in a nutrient solution, which varies from 5 to 100 mg/g in soil (Oliveira, 2012). According to Davies et al., Cr is toxic to higher plants at a concentration of 100 µ/kg (dwt) (Davies et al., 2002). The harmful effects of Cr on plants include ROS generation, which is an agent of oxidative stress in plants (Sharma et al., 2020). Cr inhibits the primary physiological process of plants; thus, seed germination and the extent of inhibition vary based on the type of seeds. Chromium (Cr) has reduced the germination rates of different plants, such as *Echinochloa colona* seeds, by 25% with a concentration of 200 µM (Rout et al., 2000). *Phaseolus vulgaris* seed germination was reduced by 48% with a concentration of 500 ppm (Dreyer Parr & Taylor, 1982). Lucerne (*Medicago sativa* cv. Malone) seeds germination declined by 23% with 40 ppm of Cr (Peralta et al., 2001). Sugarcane bud germination by 32–57% with a concentration of 20 and 80 ppm (Jain et al., 2000). These highlight overwhelming empirical evidence about the inhibitory effects of Cr on the germination of seeds of different plant species. Jun et al. found that a concentration of 0–3.2 mM of Cr strongly affected the germination rate, coleoptile, and root length of *Lablab purpureus* and *Glycine max* (Jun et al., 2009).

The exposure of 1.5 mM Cr to *Solanum lycopersicum* (forty-five tomato genotypes) reduced the percentage of germination in all genotypes by 90% compared to the control; shoot lengths of all genotypes were affected, and half of the genotypes exhibited an apparent reduction in terms of seedling survival rate (Hafiz & Ma, 2021). *Cicer arietinum* exposed to Cr with 20 to 100 ppm concentrations inhibited seed germination and coleoptile growth. The xylem and phloem of *Cicer arietinum* were severely destroyed with the lowest amount (Medda & Mondal, 2017). The exposure of *Vigna radiata* (L.), green gram, to Cu concentration between 100 and 250 mg/kg resulted in reduced biomass production, growth, and nutrient content, suggesting that higher Cu concentration adversely affects the physiological functions of green gram. In contrast, low Cu concentration (50 mg/kg) instead promoted the general growth, dry matter yield, and nutrient content significantly (Manivasagaperumal et al., 2011). This indicates that Cu plays a mutual and antagonistic role in some plants depending on the concentration. Extreme Cu concentration exposure to plants reduced Fe and Zn in leaves and Mg in the roots of plants. The consequent effects were the reduction in leaf area and root elongation due to the toxicity of Cu (Cruz et al., 2022). Besides the direct consequences of heavy metals on biotic pollinators, plant growth, and reproduction, the indirect effects of heavy metals in the terrestrial environment include the inhibitory effects of plant physiological processes. This directly affects the interaction between plants and biotic pollinators. Figure 4 illustrates how heavy metals affect different stages of plants' life. Plants' accumulation of heavy metals affects the concentrations of vital cations such as K, Mg, and Ca in plants, which are critical for plant growth, ultimately leading to their deficiencies (Tomczyk et al., 2023).

Drivers of pollinators decline

Globally, compelling evidence exists concerning the decline in biotic pollinators, including bee richness (Zattara & Aizen, 2021). Different factors, including habitat loss and land-use change, significantly contribute to global pollinator declines (Zattara & Aizen, 2021). This phenomenon implies that pollen limitation will be exacerbated, thus decreasing plants' reproductive success (Thomann et al., 2013). Insect pollinators play a role in the ecological process of plant-pollinator interactions. Nearly 75% of cultivated crop species (Klein et al., 2007) and over 80% of wild plants (angiosperms) (Potts et al., 2010) depend on insects for pollination, particularly wild bees for seed and fruit production. Graham et al. observed a 61% reduction in wild bee abundance and a 33% reduction in richness between 2004 and 2006 and between 2013 and 2014 sampling periods in blueberry fields. The potential cause of these reductions was the increased application of insecticides coupled with extreme spring weather that caused widespread destruction to flowering plants, thus limiting pollinator nectar resources (Graham et al., 2021). Other factors, including landscape composition, greatly influence bumblebees' diversity, abundance, and community structure globally (Bennett & Isaacs, 2014). Bumblebees are critical pollinator species that provide pollination services for crops and wild plants (Kleijn et al., 2015;

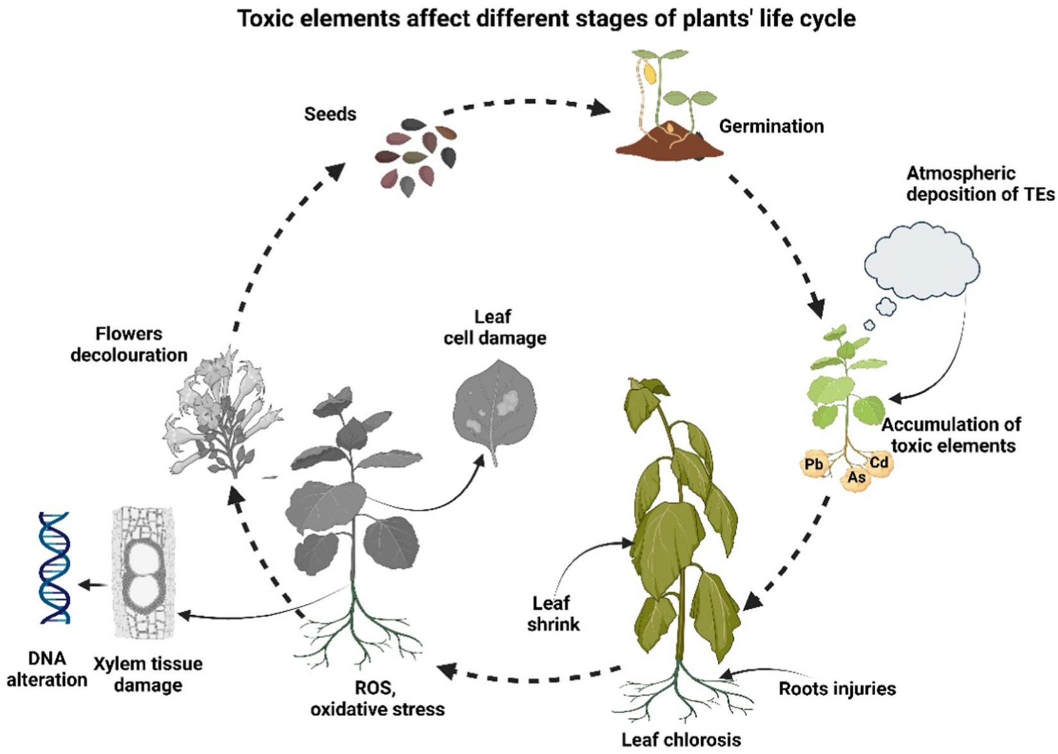

Fig. 4 Effects of toxic elements on plant's growth and reproduction

Stanley & Stout, 2014). Climate variation has diverse effects on wild bees, including their timing of life history or phenology, phenological shifts at individual species levels, and threatening critical pollination service provided by wild bees (Wyver et al., 2023). Mason bees (*Osmia* spp) are efficient fruit plant pollinators (Osterman et al., 2023).

Animal pollinators facilitate the reproduction of diverse plant species. Based on the foraging theory, biotic pollinators prefer similar plant species in natural communities and transitory single-species specialisation during foraging sessions (Schmid et al., 2016). The global reduction in the richness and diversity of biotic pollinators, such as insects, maybe attributed to disease occurrence, pesticide exposure, and loss of habitats (Moffat et al., 2015). Habitat conversions and landscape homogenisation due to intense anthropogenic activities such as agriculture with high synthetic chemical inputs disrupt plant-pollinator communities and pollination services in terrestrial ecosystems (Kovács-Hostyánszki et al., 2017). Tolede-Hernandez et al. found that habitat loss, climate, agrochemicals, limited resources, and exotic species invasion (including pathogens) drive the global stingless bee community decline (Toledo-Hernández et al., 2022).

Basnett et al. observed that abiotic factors such as elevational gradient were limitations for pollinator services. They found that auto-fertilisation and higher pollen limitation were among species at a higher elevational gradient. Increasing elevational gradient increased visitations by bumblebees and flies (Diptera) while decreasing birds' visitation to flowers (Basnett et al., 2019). At higher elevational gradients in alpine and arctic terrestrial environments, the richness of biotic pollinators is often low due to harsh and unfavourable climatic conditions, thus resulting in poor plant-pollinator interaction variability and success (Totland, 1994). Pollination services by biotic pollinators are affected by climate and weather. For instance, microclimate alters flower opening time, extrusion of anther and dehiscence, germination, and survival of pollen grains (Corbet, 1990). Temperature also plays a critical role in regulating the developmental processes of plants and insects. Hence, climate variation can lead to the phenological separation of pollinator-plant mutualistic interaction. Plant allogamy and reproduction stages are susceptible to stress caused by abiotic factors such as climate variation-induced drought because of the limited water availability to terrestrial ecosystems (Descamps et al., 2021). The ecological interaction between biotic pollinators and angiosperm species is altered by drought. Drought affects plant growth, flower production, floral display, shape, colour, size, and the composition and quantity of olfactory compounds, nectar volume, sugar concentration, and pollen (Descamps et al., 2021). Parasites and novel pests have also been identified as possible factors responsible for global declines in biotic pollinators (Graham et al., 2021).

Prospects

A detailed understanding is critical to ensure a deeper appreciation of the effects of potentially toxic elements on terrestrial ecosystems' health and sustainability under a global climate regime. This would provide a better prediction of the impact of potentially toxic elements on terrestrial ecosystems and enhance biodiversity conservation strategies in the future. The preliminary finding shows that potentially toxic elements negatively affect pollinator visitations to flowers, foraging behaviour, and nectar quality. More insights are required to elucidate how potentially toxic elements influence nectar chemistry and tastes, ultimately reducing biotic pollinators' foraging preferences. Investigating the effects of potentially toxic elements on pollen production and quality is essential since a potential deterioration in quality and quantity could negatively affect pollination processes and fruit production in the long term.

Further studies are needed to understand the contribution of different land use systems and practices, including how the application of agricultural chemicals such as pesticides, weedicides, and chemical fertilisers affect pollinator diversity and abundance. This has significant implications for reduced yields of healthy and quality fruits and vegetables, threatening global food safety and security. Additional investigations are necessary to ensure adequate available data to predict the level of biotic pollinator decline globally to boost our understanding and help scientists in modelling to predict its implications for biodiversity conservation better. It is critical to investigate the bioaccumulation mechanisms in biotic pollinator species (invertebrates and vertebrates) and the relationship with plants' morphological, physiological, and anatomic changes that may influence the population dynamics of pollinators. The response of pollinators to environmental changes, mainly in the tropics where insect diversity is the highest, is understudied and must be probed further. The nuanced insights from such further studies will provide empirical guidance and inform policy formulations and biodiversity conservation strategies, particularly the impact of global climate on terrestrial ecosystem functions. Although the evidence showed that bumble bees (adults and larvae) could bioaccumulate heavy metals in their bodies during nectar foraging activities, further investigation is required to ascertain how sublethal concentrations of heavy metals, including Pb and Cd, could alter their behaviour, including brood care, flight navigation, and foraging. Contrary to the long-standing established understanding that pollinators are attracted to flowers purposely for nectar and pollen rewards, new insights suggest that pollinators, particularly bees and wasps (Hymenoptera) and flies (Diptera), may be lured to flowers by plants via sexual mimicry (Cohen et al., 2021). Further studies will be necessary to understand the mechanism behind the attraction of male beetles to flowers by the novel macrolide isolates from the floral scent.

Conclusion

Chronic exposure to heavy metals by pollinators and plants negatively affects both pollinators and plants due to persistent and toxic properties. The accumulation of heavy metals in terrestrial ecosystems alters plant-pollinator interactions, species biodiversity, and abundance. Heavy metals occur in terrestrial ecosystems via two significant sources: natural and anthropogenic sources. However, the predominant source is human-induced emissions from industrial production, coal smelting, mining, and agrochemicals. Heavy metals in terrestrial ecosystems alter pollinators' foraging behaviour and preferences, affecting pollination efficiency. The effect of pesticides on pollinators, particularly bumblebees, is exacerbated when bees are starved, suggesting that limited nectar rewards could further jeopardise the survival of bees exposed to heavy metals. The accumulation of heavy metals by flowers reduces flower visitations by pollinators and hence may reduce yields of healthy and quality fruits and vegetables. In addition, heavy metals such as Hg, Pb, As, Cu, Co, Ni, Cd, and Cr act as xenobiotics to plants in higher concentrations. Heavy metals in excess concentrations directly affect plants' physiological processes, metabolism, and reproduction. The depletion of essential cations in plant leaves, such as Mg, due to extreme exposure and accumulation of heavy metals ultimately reduces the chlorophyll content, thus negatively affecting photosynthesis and plant metabolism.

Most heavy metals produce ROS, which induces oxidative stress, cellular destruction, and alteration of the enzymatic activities in plants. The accumulation of heavy metals in terrestrial ecosystems could further exacerbate the global decline in biotic pollinators, which raises serious concerns about the prospects of angiosperm biodiversity and healthy yields of fruits and vegetables in the future, given that an overwhelming percentage of angiosperms is pollinated biotic pollinators. Evidence suggests that the structural complexity of habitats at both local and landscape scales could significantly influence pollinator bees' abundance and richness patterns. High management intensity negatively affects the response traits of bees; thus, below-ground nesting bees and social bees demonstrated varied abundance patterns, indicating that utilising hybrid management practices at the local scale could enhance both species richness and abundance of different bees with particular response traits in agroecosystems. Nevertheless, further community-cluster response traits studies are critical, given the potential trade-offs.

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Author contribution Baba Imoro Musah conceived, designed, and executed this study. BIM conducted a literature search and retrieval, analysed and synthesised the data, and drafted, revised, and wrote the final manuscript. This paper is the author's work and does not have a gifted author.

Data availability The author declares that the data supporting the findings of this study are available within the paper.

Declarations

Ethics approval and consent to participate Ethical approval and consent to participate are not required for this study.

Competing interests The authors declare no competing interests.

Hazards and human or animal subjects Not applicable.

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