



Review

Drivers of toxic element accumulation in terrestrial ecosystems across elevational gradients

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ABSTRACT

Terrestrial ecosystems, account for approximately 31% of the global land area and play a significant role in the biogeochemical cycling of toxic elements. Previous studies have explored the spatial patterns, effects, and drivers of toxic elements along urban gradients, agricultural lands, grasslands, and mining sites. However, the elevational patterns of toxic elements in montane ecosystems and the underlying drivers remain largely unknown. Atmospheric deposition is a crucial pathway through which toxic elements accumulate along terrestrial elevational gradients. The accumulation of toxic elements exhibited seasonal variability along elevational gradients, with higher deposition occurring in summer and winter. Approximately 46.77% of toxic elements (e.g. Hg) exhibited increasing trends with elevation, while 22.58% demonstrated decreasing patterns (Ba, Co). Furthermore, 8.06% displayed hump-shaped distributions (Ag), and 22.58% showed no distinct patterns (As and Zn). The accumulation of these elements is influenced by several key factors, including atmospheric deposition (26.56%), anthropogenic activities (14.11%), and precipitation (10.37%) primarily via wet deposition of atmospheric pollutants. The accumulation of toxic elements threatens terrestrial biodiversity by disrupting food chains, altering community structures, and causing individual mortality. These disruptions also pose risks to human health through contaminated food sources and food webs, potentially leading to health issues like cancer, organ damage, and reproductive challenges. This review offers key insights into the factors affecting the accumulation and distribution of toxic elements along elevation gradients. It also lays the groundwork for further study on how toxic elements impact ecosystem functions, which is crucial for protecting biodiversity under climate change.

1. Introduction

Terrestrial ecosystem pollution by toxic elements poses a critical threat to biodiversity, ecosystem health, and sustainability (Liu et al., 2023). Toxic elements have naturally occurred in the Earth's crust since their creation. Anthropogenic activities (such as mining, agricultural activities, and oil combustion) and natural phenomena (such as rock weathering and formation, soil erosion, and volcanic eruptions) are critical sources of toxic elements in terrestrial ecosystems (Briffa et al., 2020). Many of these elements such as arsenic, cadmium, chromium, lead, nickel and mercury are highly toxic and rank among priority pollutants, even at low concentrations, posing significant health risks to both humans and wildlife. For example, mercury is known for its neurotoxic effects, while cadmium is a potent carcinogen even at lower

levels of exposure (Tchounwou et al., 2012). Certain metals, including mercury, cadmium, lead, chromium, and nickel, can easily migrate through air, water, and soil, posing risks to the environment. Their ability to accumulate in food chains and their harmful effects on biodiversity highlight the need for focused attention on these toxic elements (Briffa et al., 2020).

Nearly one-quarter of the Earth's land surface is occupied by montane ecosystems (Abbott and Brennan, 2014). Montane ecosystems are most likely to be affected by global climate warming, with a significant loss in biodiversity, as predicted by species distribution models (Weiskopf et al., 2020). Approximately 60 % of montane ecosystems are under extreme anthropogenic disturbances and pressure (Elsen et al., 2020). Elevational gradients are characterised by steep variations in physical environmental traits, including sunshine, temperature,

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ultraviolet radiation, geology, precipitation, and biotic environment (Boy et al., 2022). These gradients provide unique characteristics suitable for unravelling the underlying drivers of spatial variations in toxic element accumulation patterns in terrestrial ecosystems.

The rapid increase in global emissions has exacerbated the concentrations of toxic elements, particularly in terrestrial ecosystems, which serve as sequestration sinks. This could lead to drastic changes in regional and seasonal climatic patterns (Zitoun et al., 2024).

Most studies in recent decades have focused on the accumulation of toxic elements in urban settlements (El-Khatib et al., 2020), agriculture, and grasslands (Chai et al., 2015; Wen et al., 2022). Meanwhile, patchy areas have attempted to unravel the elevational patterns and drivers of toxic elements in terrestrial ecosystems. However, this knowledge gap hinders accurate predictions and assessments of montane ecosystems concerning future environmental contamination in the context of climate change. Furthermore, limited studies have examined the specific drivers of toxic elements and their accumulation patterns in different ecosystem compartments. The accumulation patterns of toxic elements and the drivers underpinning differences along elevational gradients in terrestrial ecosystems remain largely unclear. Quantifying the accumulation patterns of toxic elements and identifying their drivers along elevational gradients will enable to develop models for predicting the impacts of natural and anthropogenic emissions of toxic elements on biodiversity and ecosystem function (Sundqvist et al., 2013). This review clarifies the ambiguities concerning accumulation patterns and potential drivers of toxic elements along elevational gradients in terrestrial ecosystems. We explored the accumulation patterns in different ecosystem compartments and the effects of toxic elements on ecosystem functions. Specifically, this review aims to (i) provide a better understanding concerning the sources of toxic elements in terrestrial ecosystems, (ii) provide better insights about the inputs of toxic elements in terrestrial ecosystems via different environmental compartments (e.g., plant parts; soil; precipitation and snow), (iii) elucidate the drivers influencing the accumulation of toxic elements along elevational gradients, (iv) clarify the effects of toxic elements on biota and (v) examine the effects of toxic elements on ecosystem functions such as nutrient cycling and litter decomposition.

2. Methodology

2.1. Literature search and eligibility criteria

In determining the appropriate search databases to utilize, several crucial factors, including the databases' alignment with the research topic, their subject-specific depth, the caliber of the indexed journals, and the availability of advanced search capabilities were considered. The main literature search platforms or databases were the Web of Science Core Collection, MEDLINE, Elsevier Scopus, Elsevier ScienceDirect, GEOBASE, Semantic Scholar, Embase, SAGE, and Google Scholar. Additionally, data search software such as Scite, R Discovery, SCISPACE, Publish or Perish 8.0 were used to overcome search shortcomings. Multiple optimised keywords, such as "elevational distribution", "elevational patterns", "along elevation", "altitudinal gradient", "toxic elements", and "heavy metals", "drivers", "terrestrial ecosystems" were used during the literature search process. The process for determining eligibility consisted of two crucial stages essential for selecting studies for the review. The first step was to consolidate multiple reports of the same study, while the second involved using the available data to identify which studies met the inclusion criteria (Higgins and Green, 2008). The rationale behind this approach was to prevent duplicate publications, which could introduce significant bias into the research findings (Tramer et al., 1997). To effectively eliminate duplicates from the same study, we used reference management software (Mendeley, Elsevier Inc.) and a Spreadsheet Review Matrix. The underlying rationale was to prevent duplicate publications, which could introduce substantial bias into the research findings (Tramer et al., 1997). To

effectively eliminate duplicates from the same study, we used reference management software (Mendeley, Elsevier Inc) and a Spreadsheet Review Matrix. We excluded conference papers, magazine articles, and newspapers from this review. Only papers published in English were considered. The titles and abstracts were scrutinised to remove clearly irrelevant publications. The titles and abstracts of the papers were carefully reviewed to eliminate obviously irrelevant studies. Full texts of potentially relevant articles were then retrieved. Any duplicate reports of the same study were identified and linked, and the full texts were assessed against the eligibility criteria. The literature was then evaluated and synthesised using SCISPACE to ensure only the appropriate information was included in the analysis (Khan et al., 2019). Ultimately, 225 articles were selected and shared with several experts in the field, who assessed and provided recommendations on whether to exclude each study from the final analysis. The steps and results of our literature search are detailed in Fig. 1.

3. Sources of toxic elements in terrestrial ecosystems

Human activities and natural events are the primary sources of toxic elements in terrestrial ecosystems (Fig. 2). The concentration of toxic elements in terrestrial ecosystems is the sum of the inputs from anthropogenic and lithogenic sources minus the losses due to plant uptake, leaching, soil erosion, and gaseous volatilisation (Palansooriya et al., 2020). Natural processes such as volcanic eruptions, mineral weathering, and soil erosion mobilize toxic elements, establishing baseline concentrations amplified by human activities (Okerefor et al., 2020; Shen et al., 2019). Lithogenic sources, derived from geological formations, determine elemental baselines as weathering releases these elements into soils, sediments, and water (Tian et al., 2021). Volcanic activity can abruptly elevate local toxic element levels (Okerefor et al., 2020), while concentrations vary with rock type, geophysical conditions, and geography (Asaf et al., 2020). Though natural events like landslides and floods contribute to pollution, their impact is dwarfed by anthropogenic influences (Biswas, 2019). Soil erosion and parent material weathering drive element mobilization, enhancing bioavailability for plant uptake and ecological transfer (Bosiacki et al., 2014). These processes underscore the interplay between geogenic factors and ecosystem vulnerability, emphasizing the need to distinguish natural contributions from human-induced contamination in environmental risk assessments.

The major geographic regions for the deposition of typical elements (such as Pb, As, Hg, Cr, Cd) was summarized in Fig. A.1. Atmospheric deposition is a crucial pathway for the spread of toxic elements into terrestrial ecosystems. Aerosols, fine particulate matter, and tiny toxic substances are transported in the atmosphere from nearby or distant point sources, such as the chimneys of factories. They are transported by wind and eventually deposited on vegetation canopies by wet or dry atmospheric deposition (Allen et al., 2019; Wang et al., 2021). For instance, atmospheric deposition is the most critical source of Hg in the high-elevation Tibetan Plateau and the Himalayas. Long-range transboundary transported human-induced emissions from the Indo-Gangetic Plain to the Himalayas through convective storms and mid-tropospheric circulation. This phenomenon accounts for over 50 % of the total Hg⁰ at the Lhasa city site (Yu et al., 2022). The surface soil concentrations of Cd and Pb were remarkably higher in northwest, south, and southwest China. This phenomenon has been attributed to atmospheric deposition via long-range transboundary tropospheric transport, condensation from ore mining, fuel and coal combustion, and nonferrous smelting activities (Bing et al., 2021).

Tropospheric deposition is the primary pathway for transporting toxic elements in remote terrestrial ecosystems (He et al., 2023). Toxic elements, such as Hg, As, and Cd, are considered to be in the atmospheric vapour (gaseous) phase, making their transport over long-range distances very easy by wind (Liu et al., 2024). The main form of Hg in the precipitation was soluble, suggesting that gaseous Hg was present in

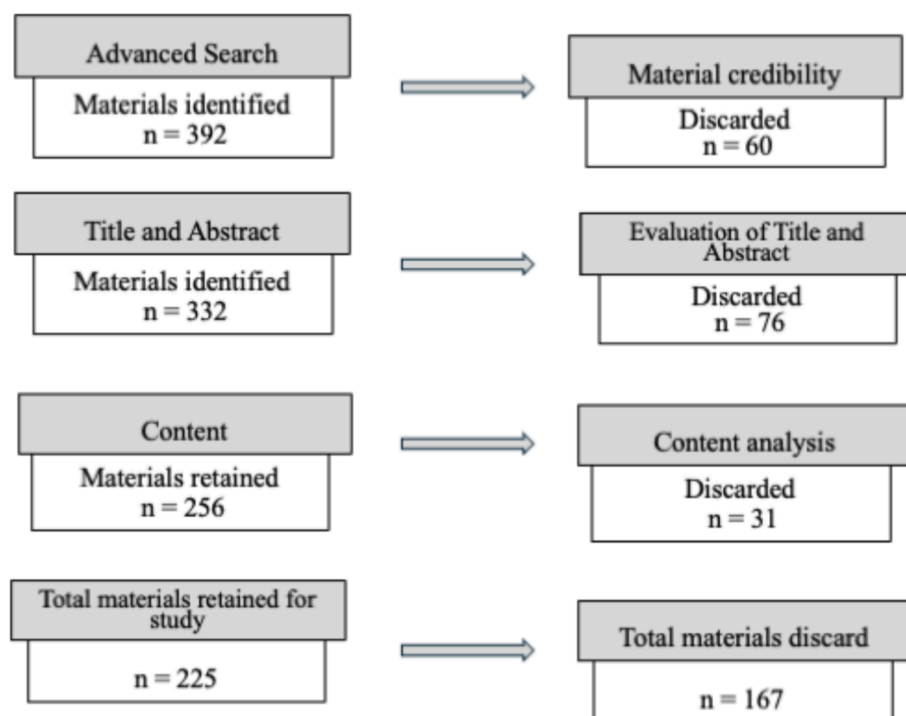


Fig. 1. A schematic description of the literature search.

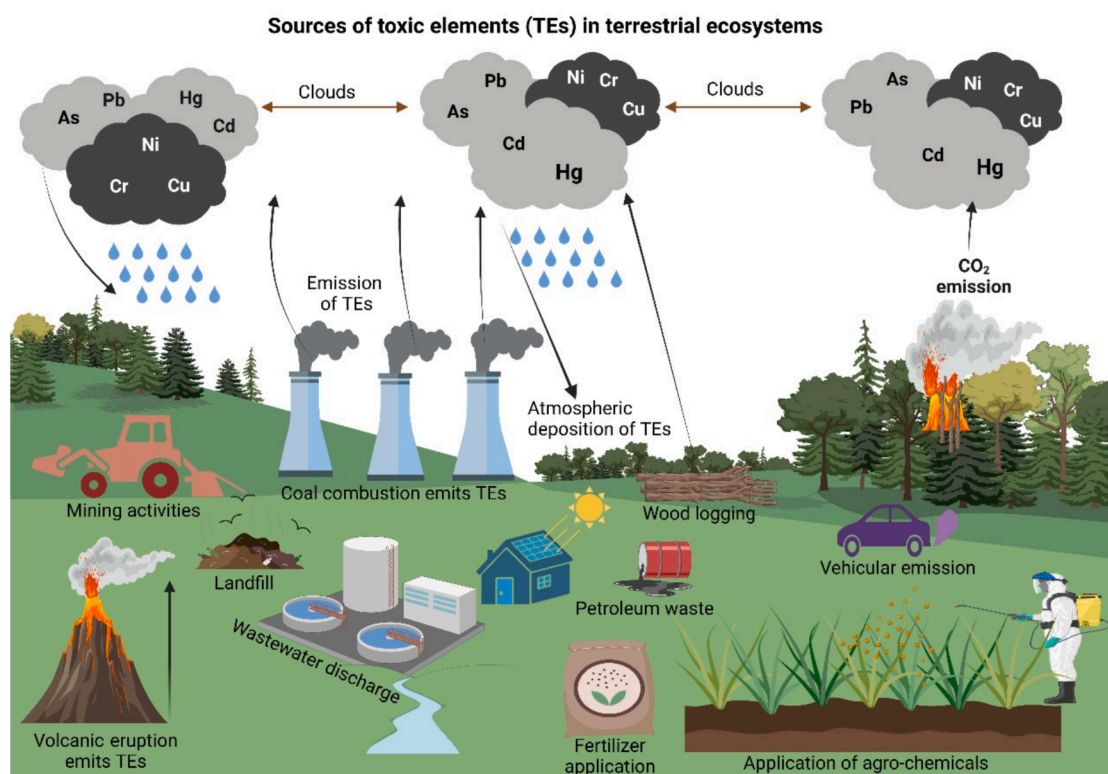


Fig. 2. Sources of toxic elements in terrestrial ecosystems.

the cloud-scavenged atmospheric wet Hg deposits (Huang et al., 2015). Unlike Cd inputs, there was a positive relationship between wet deposition and coal and oil consumption for soluble Cr and Pb. The atmospheric deposition of Cr, Pb, and Cd via precipitation is a vital source of toxic elements in natural terrestrial ecosystems in China (Zhu et al., 2016).

Anthropogenic activities explain the global terrestrial ecosystem pollution linked to socioeconomic factors (Newbold et al., 2015). In the coniferous forests at the tree line on the eastern edge of the Tibetan Plateau, China, anthropogenic emissions from India and China are proposed as the likely sources of Hg deposition in the forest ecosystem (Tang et al., 2015). The concentrations of Cu, Cd, Zn, Pb, and Hg in snow

samples from high-altitudinal glaciers in the Nyainqentanglha mountain region of the southern Tibetan Plateau indicated that anthropogenic activities significantly influenced its deposition in the high-elevational atmosphere of the southern plateau (Huang et al., 2013). Anthropogenic activities contribute to the release of toxic elements into terrestrial ecosystems from various sources. In Huai'an, China, terrestrial mosses exhibited significant accumulation of Zn, Cu, Cr, Pb, Co, and Cd, with concentrations considerably higher than those observed in Albania, a well-known hotspot for toxic element pollution in Europe. The primary sources of pollution included metal smelting (28.86 %), agricultural practices and textile dyeing (20.29 %), mining (19.83 %), traffic emissions and coal combustion (13.04 %), as well as natural pathways (17.98 %) (Zhou et al., 2022).

4. Elevational patterns of toxic elements in terrestrial ecosystems

Forest ecosystems are the largest sinks of atmospheric toxic elements among terrestrial ecosystems. For example, 500 to 1100 gigagrams of Hg is stockpiled in topsoil and vegetation (Wang et al., 2022b) in forest ecosystems. The higher the elevation, the higher the potential for toxic element accumulation in soils from atmospheric deposition (Ding et al., 2017). An increase in elevation creates a microclimate that enhances precipitation, thereby increasing the chances of wet atmospheric deposition of toxic elements. As illustrated in Fig. 3, atmospheric deposition is the primary pathway through which toxic elements are deposited in montane terrestrial ecosystems due to climatic variability, vegetation cover, and vegetation type. Wet and dry atmospheric deposition interact with the canopy over a long period, leading to significant variability in the water-soluble metal concentrations on foliage accumulated over a range of spatial scales from millimetres to kilometres (Lindberg et al., 1982). The relationship between elevation and the concentrations of toxic elements is complex and varies across different geographical regions.

Overall, the relationship between elevation and the concentrations of toxic elements is multifaceted, exhibiting increasing, decreasing, hump-shaped patterns and no patterns across different studies and geographical regions. Understanding these patterns is crucial for assessing environmental health and the impacts of atmospheric deposition on ecosystems at varying elevations. Based on the reviewed literature, the distribution patterns of toxic elements along elevational gradients revealed that 46.77 % exhibited an increasing trend (e.g. Hg), 22.58 % demonstrated a decreasing trend (e.g. Ba, Co), 8.06 % displayed a hump-shaped pattern (Ag), and 22.58 % showed no discernible pattern (As and Zn), as illustrated in Fig. 4 and Table A.1 in the Supplementary Materials. Terrestrial ecosystems are intricate environments where toxic

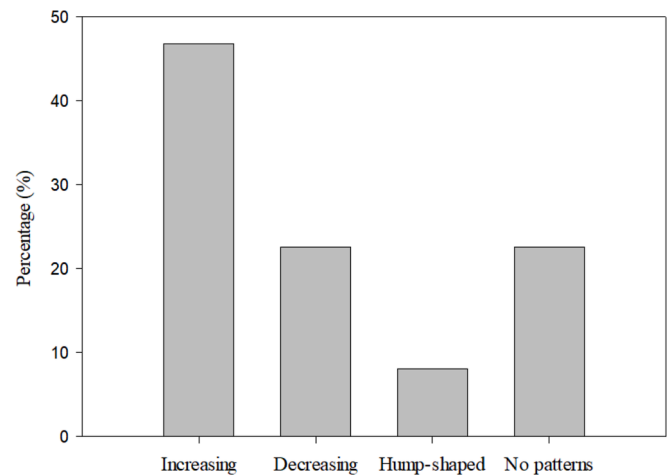


Fig. 4. Distribution patterns of toxic elements along terrestrial elevational gradients.

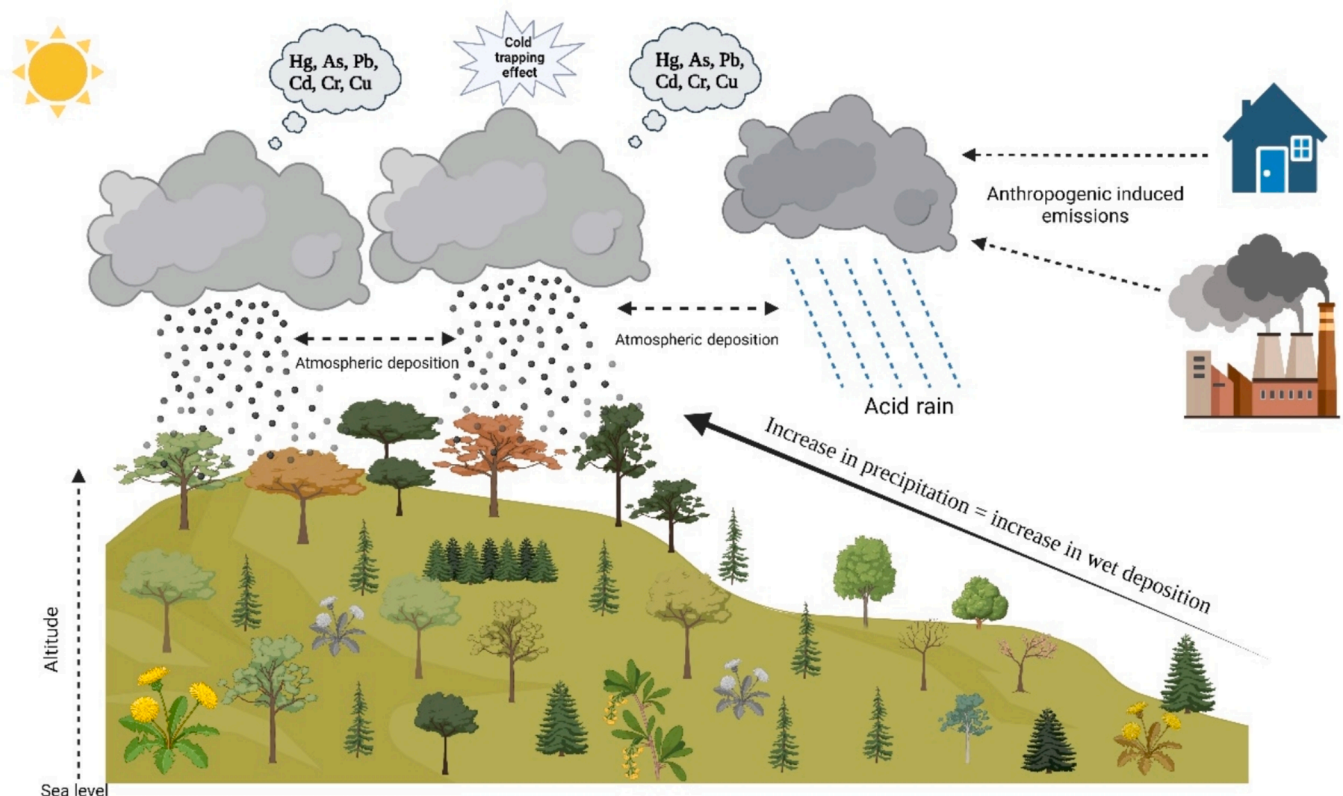


Fig. 3. Schematic illustration of anthropogenic-induced atmospheric deposition of toxic elements in terrestrial ecosystems along elevational gradients.

elements may accumulate and display distinct distribution patterns, frequently characterized by hump-shaped concentration trends along specific environmental gradients. These trends emerge from a combination of natural and anthropogenic sources, coupled with complex biogeochemical processes that regulate the mobility, transformation, and eventual fate of these elements (Yu et al., 2020).

Plant species, root exudates, and soil microbes jointly regulate toxic element accumulation across environmental gradients. Hyperaccumulators (e.g., *Sedum alfredii*) use specialized transporters to uptake metals, altering rhizosphere bioavailability (Wu et al., 2020). Root exudates like organic acids chelate elements (e.g., Pb, As), enhancing solubilization or immobilization depending on soil pH and redox conditions (Chen et al., 2017). For example, *Brassica juncea* mobilizes Cr (VI) via citrate exudation (Bortolotti and Baron, 2022). Soil microbes, including mycorrhizal fungi and metal-resistant bacteria, degrade organometallic complexes or immobilize metals via biosorption, reducing plant uptake (Barra Caracciolo and Terenzi, 2021). Microbial activity also influences nutrient cycling (e.g., N, P), indirectly affecting metal bioavailability (Tian et al., 2025). Along elevational or pollution gradients, interactions shift: cold-adapted microbes at higher elevations slow degradation, increasing metal retention, while lowland soils enhance detoxification via redox transformations. Multi-component analysis of soil–plant–medium systems is critical for understanding toxic element cycling.

4.1. Elevational patterns of toxic elements in plant foliage, shoots, and roots

Plants employ distinct strategies to respond to stress of toxic elements. Hyperaccumulators, such as *Thlaspi caerulescens*, sequester high concentrations of metals (e.g., Zn, Cd) in shoots via specialized transporters and vacuolar storage, enabling survival in contaminated soils (Rascio and Navari-Izzo, 2011; Pasricha et al., 2021). Excluders, like *Silene vulgaris*, restrict metal uptake through root exudates or cell wall binding, minimizing translocation to shoots (Van Hoof et al., 2001). Sensitive species, such as *Glycine max*, exhibit toxicity symptoms (e.g., root growth inhibition under metal stress) due to impaired nutrient uptake and oxidative damage (Kochian et al., 2004). These responses reflect evolutionary adaptations to environments with toxic elements, balancing tolerance and detoxification. The foliage is a suitable bioindicator for examining the accumulation of toxic elements in terrestrial ecosystems. Mosses are optimal bioindicators for atmospheric toxic element deposition due to their high surface-area ratio, cuticle-free surfaces, and ion-exchange capacity, enabling efficient pollutant absorption and retention (Lucaciu et al., 2004; Vergel et al., 2020). Species like *Pleurozium schreberi* and *Hypnum cupressiforme* track As, Cd, and Pb in European surveys. Lichens, though air-quality sensitive, are less reliable for quantitative monitoring due to slow growth and SO₂ susceptibility (Kolli et al., 2022). Ferns (e.g., *Pteris vittata*) hyperaccumulate specific elements but interact with soil, limiting atmospheric studies (Kolli et al., 2022). Supported by initiatives like UNECE ICP Vegetation, mosses remain the gold standard (Lucaciu et al., 2004; Vergel et al., 2020).

The effect of atmospheric deposition of toxic elements increases with elevation owing to orographic and cold trapping effects (Camarero, 2017). Specifically, atmospheric Hg, particularly Hg⁰, accumulates in foliage, accounts for a proportionate amount of atmospheric Hg deposition and alters the geochemical cycle of Hg. Foliage Hg accumulation arises from the net results of uptake, adsorption, fixation, and re-emission, among other processes (Liu et al., 2022b). In addition to atmospheric sources, lithogenic activities represent significant contributors to the release of toxic elements into terrestrial ecosystems. Roots, therefore, also serve as effective bioindicators for assessing the potential accumulation of toxic elements (Ali et al., 2019).

Plants accumulate toxic elements in various tissues (foliage, twigs, stems, shoots, and roots) at different concentrations depending on

exposure sources. For example, mean total arsenic (As) concentrations were 0.12, 0.35, and 0.48 mg/kg in foliage, twigs, and roots, respectively, while total mercury (Hg) concentrations were 0.0121, 0.0078, and 0.0171 mg/kg. Hg concentrations were highest in litter, followed by roots, leaves, and twigs, while As also peaked in litter. Significant positive correlations were observed between Hg concentrations in leaves and twigs ($R^2 = 0.2482$, $p < 0.05$) and in leaves and litterfall ($R^2 = 0.3453$, $p < 0.05$). Similarly, As in leaves correlated with twigs ($R^2 = 0.6113$, $p < 0.05$), indicating shared pollution sources and proximity (Tang et al., 2015). On the Eastern Tibetan Plateau, lead (Pb) and cadmium (Cd) concentrations were higher in twigs (2.551 mg/kg Pb and 0.101 mg/kg Cd) than in needles (1.291 mg/kg Pb and 0.034 mg/kg Cd). Pb concentrations increased with elevation, especially near anthropogenic sources, while Cd levels declined (Jia et al., 2021).

The distribution of toxic elements in plants varies significantly along elevational gradients, influenced by both local and long-range atmospheric transport. On the Tibetan Plateau, Hg concentrations in foliage increased at mid-elevational gradients (timberline), while As levels declined. In the Shergyla Mountains, total Hg in mosses and conifer needles showed a strong positive correlation with elevation on both western ($R^2 = 0.98$, mosses; $R^2 = 0.95$, conifer needles) and eastern slopes ($R^2 = 0.87$, conifer needles), whereas $\Delta^{199}\text{Hg}$ isotopic ratios exhibited an inverse relationship with elevation, reflecting reduced local emissions and increased long-range atmospheric contributions at higher altitudes (Jia et al., 2021).

In Appalachian Mountain red spruce (*Picea rubens*), toxic element concentrations increased with elevation, contributing to dieback disease (Gawel et al., 2022). Conversely, Cu and Zn in foliage reduced Hg accumulation at 800–1000 m a.s.l. (Gawel et al., 2022). In South Poland's Tatra National Park, ferns (*Athyrium distentifolium*) at low elevations (1000–1500 m) exhibited low toxic element concentrations. However, Pb increased significantly at mid-elevations (1501–1700 m), while Ni, Zn, Mn, Cr, and Cd were elevated at higher elevations (1701–2050 m) (Samecka-Cymerman et al., 2012). At Mt. Amiata, Pb concentrations in epiphytic lichens (*Hypnum cupressiforme*) increased along an elevational gradient (120–1730 m), with significant accumulation in mosses above 1300 m (Ancora et al., 2021). Similarly, in the Alps, Pb, Zn, Cd, and S concentrations in mosses rose with elevation, attributed to higher precipitation rates (Zechmeister, 1995).

Litterfall Hg deposition at Mt. Ailao, Southwest China, also increased with elevation, with rates of 12.0 $\mu\text{g}/\text{m}^2/\text{yr}$ (850–1000 m), 14.9 $\mu\text{g}/\text{m}^2/\text{yr}$ (1250–2400 m), and 23.1 $\mu\text{g}/\text{m}^2/\text{yr}$ (2500–2650 m) (Li et al., 2022). Toxic element concentrations in mosses on the Tibetan Plateau exhibited contrasting patterns. Sr, Cd, Ba, Zn, Pb, Cr, and Ni concentrations decreased with elevation, with higher levels observed at 1600–2200 m (e.g., 52.2 $\mu\text{g}/\text{g}$ for Sr) compared to 2800–3650 m (e.g., 37.8 $\mu\text{g}/\text{g}$ for Sr) (Xiao et al., 2021). By contrast, total Hg (13.1–273.0 ng/g) and methylmercury (MeHg) concentrations in mosses and lichens (20.2–345.9 ng/g) increased with elevation (1983–5147 m), showing strong positive correlations with altitude (THg: $R^2 = 0.362$; MeHg: $R^2 = 0.281$; $p < 0.01$) (Shao et al., 2017). These findings highlight complex spatial patterns of toxic element distributions, driven by elevation-specific interactions between atmospheric transport, local emissions, and vegetation uptake.

In the forest floor, Hg accumulation from litter inputs exceeded wet atmospheric deposition, as evidenced by a negative $\Delta^{199}\text{Hg}$ in topsoil analyses. In a dry-hot shrub valley, Hg deposition via litterfall increased along an elevational gradient, ranging from 12.0 $\mu\text{g}/\text{m}^2/\text{year}$ at 850 to 1000 m a.s.l. Similarly, concentrations of Ni, Cu, As, Pb, Co, and Mn in mosses increased along the elevational gradient on the Tibetan Plateau (Shao et al., 2017). Litter Hg concentrations ranged from 15 to 81 ng/g, with a mean of 35 ± 16 ng/g, while surface soil (0–8 cm) showed the highest Hg concentration, averaging 70 ± 37 ng/g. The Hg pool in the 0–60 cm soil horizon was 23 ± 9 mg/m², significantly lower than reported for other regions (Wang et al., 2017). A strong correlation between soil Hg concentration and litterfall Hg was observed ($R^2 = 0.69$, p

< 0.01) (Wang et al., 2019), emphasizing the linkage between soil and plant Hg distribution patterns along elevational gradients, although specific mechanisms may vary across regions and elements.

4.2. Elevational patterns of toxic elements in soil

Toxic element distribution in topsoil demonstrates clear elevation-dependent patterns, with enrichment factors for certain elements increasing significantly at higher altitudes. Mercury (Hg) and lead (Pb) in particular show pronounced accumulation trends in the topsoil with rising elevation. For instance, Hg and Pb concentrations in the topsoil increased fourfold at higher altitudes, driven by enhanced atmospheric deposition and long-range transboundary pollution (Stankwitz et al., 2012). Similarly, Hg concentrations in topsoil samples at approximately 1200 m above sea level (a.s.l.) were many times higher than those at 200 m a.s.l., with mean values of 503.5 ± 18 ng/g (Townsend et al., 2014). In contrast, while cadmium (Cd) also exhibited an increasing trend with elevation, zinc (Zn) did not display a similar pattern (Li et al., 2018).

Studies from various regions reinforce this elevation-dependent pattern of Hg accumulation. For example, in forest floor on Shergyla Mountain in the Tibetan Plateau, Hg concentrations increased consistently with altitude, showing significant positive correlations on both western ($R^2 = 0.56$, $p < 0.05$) and eastern slopes ($R^2 = 0.72$, $p < 0.05$) (Liu et al., 2019). Likewise, in the Catskill Mountains, USA, Hg concentrations in organic soil layers at approximately 1200 m a.s.l. were 4.4 times higher than those at lower elevations (200 m) (Townsend et al., 2014). Pb concentrations in topsoil also exhibited strong elevation correlations. For example, Pb levels in topsoil (0–5 cm) correlated significantly with elevation ($R^2 = 0.89$, $p < 0.001$) (Ancora et al., 2021). Similarly, Pb accumulation in organic soil horizons increased markedly with altitude, with Pb concentrations peaking at 2.12 g/m² in the coniferous zones (Stankwitz et al., 2012). This pattern underscores the role of altitude in influencing the deposition and retention of atmospheric Pb.

Regional studies also highlight spatial differences in toxic element accumulation patterns. For example, in the eastern Tibetan Plateau, arsenic (As) levels in A-layer soils were elevated in westward directions, whereas Hg concentrations were higher in southeast-facing slopes (Tang et al., 2015). Similarly, Cd and Pb concentrations in Mt. Luoji, southwest China, peaked at high altitudes, which was significantly influenced by anthropogenic inputs (Li et al., 2018). Conversely, Zn levels declined with increasing altitude, showing a contrasting accumulation pattern compared to Cd and Pb (Li et al., 2018). In the Serra dos Órgãos Mountain range, southeastern Brazil, Hg concentrations in rainforest soils increased significantly with elevation ($R^2 = 0.38$, $p < 0.001$), averaging 250.7 ± 79.4 µg/kg (Huang et al., 2015). However, Hg levels were lower in cloud forests and high-altitude grasslands, reflecting ecosystem-specific deposition and retention dynamics (Huang et al., 2015). These findings collectively emphasize the intricate interplay between elevation, ecosystem type, and the atmospheric deposition of toxic elements. The mobility and toxicity of toxic elements are governed by pH, organic matter, and redox conditions, which modulate their bioavailability and uptake by organisms (Kodirov et al., 2018). Chemical speciation, elemental interactions, and receptor-binding affinities further determine toxicity, reflecting the complexity of these dynamics (Peijnenburg et al., 2014). The addition of nano-montmorillonite reduced Cd bioavailability, leading to decreased Cd uptake by plants and alleviating Cd toxicity to soil microorganisms (Liu et al., 2022a). These interconnected physicochemical factors—pH, redox states, and organic matter—collectively influence metal bioavailability, complicating toxicity assessments. A holistic evaluation of these parameters is essential for accurate environmental risk analysis (Zhang et al., 2014).

While metals naturally occur in the environment, organisms have evolved adaptive mechanisms to regulate essential elements (e.g., Zn, Cu, Fe) for metabolic functions and mitigate excess exposure (Peijnenburg et al., 2014; Zhang et al., 2023). Microorganisms,

particularly bacteria and fungi, are pivotal in governing metal speciation, mobility, and bioavailability through redox reactions, complexation, and precipitation (Fomina et al., 2005). These microbes employ diverse strategies (such as biosorption, biotransformation, and efflux systems) to counteract metal toxicity, even under stress conditions that disrupt cellular membranes (Ayangbenro and Babalola, 2017). For instance, *Thiobacillus* and iron-oxidizing bacteria enhance metal bioavailability by dissolving minerals, while others immobilize contaminants, reducing ecological risks (Fomina et al., 2005). Similarly, fungi like ericoid and ectomycorrhizal species thrive in metal-rich environments via specialized detoxification mechanisms. Such microbial processes underpin biogeochemical cycles, influencing ecosystem health by balancing metal availability as both nutrients and toxins (Gerwien et al., 2018). Crucially, these interactions can be leveraged for bioremediation: microbial activities that solubilize or immobilize metals offer sustainable solutions for decontaminating polluted sites. By integrating microbial metabolic versatility with environmental management, bioremediation harnesses natural processes to mitigate heavy metal pollution, emphasizing the dual role of microbes as both mediators of metal dynamics and tools for ecological restoration.

4.3. Elevational patterns of toxic elements in cloud, rainfall and snow

At Stratton Mountain, Vermont (1,075–1,180 m), Hg deposition via aerosols, vapor, and liquid phases was 2–5 times greater than in surrounding low-elevation areas (Miller et al., 2005). In a high-elevation spruce-fir forest (1,204 m a.s.l.), Hg concentrations in cloud throughfall were 2.3 times higher than in cloud water. Additionally, other toxic elements (e.g., Ni, Cu, Sr, and Mn) were 2–34 times more concentrated, suggesting that cloud water interacts with tree canopies, leaching elements and transporting them into the soil (Lawson et al., 2003).

In the Qilian Mountains, toxic element concentrations (e.g., Cu, Pb, Ni, Cr, Cd, As, and Hg) in rainfall were higher at altitudes of 2,850–3,050 m in areas with dense vegetation compared to those with low or moderate coverage (Zang et al., 2021). Similarly, Hg concentrations in snow were lowest at Mount Everest (<1–3 ng/L) and higher at Mount Nyainqentanglha and Mount Geladaindong, reflecting proximity to arid regions and elevated particulate loads (Loewen et al., 2007).

Total mercury (Hg) concentrations in snow ranged from < 1 to 9 ng/L, with levels increasing northeastward from Mount Everest. Notably, concentrations were higher in snow deposited during the non-monsoon season, primarily driven by atmospheric deposition (Loewen et al., 2007).

5. Underlying drivers of toxic elements accumulation along elevational gradients

Overall, the distribution of toxic elements along elevational gradients is governed by an interplay of climatic, edaphic, and biological factors. For instance, according to the data analysed in this investigation, atmospheric deposition (26.56 %), anthropogenic activities (14.11 %), precipitation (10.37 %), vegetation type (4.56 %) and covers (3.73 %), seasonality and soil properties collectively shape these patterns (Fig. 5 and Table A.2), highlighting the multifaceted drivers underlying toxic element distribution in terrestrial ecosystems.

5.1. Atmospheric deposition, anthropogenic activities, and precipitation

Precipitation plays a critical role in shaping the distribution of toxic elements along terrestrial elevational gradients through atmospheric deposition. At higher elevations, toxic elements were deposited via multiple wet pathways, including rain, snow, fog, frost, and clouds (Liang et al., 2009). Increased precipitation at these altitudes often correlated with higher concentrations of metals such as Pb, Cd, and Zn (Zechmeister, 1995). This trend arises from the cooling of air vapor at

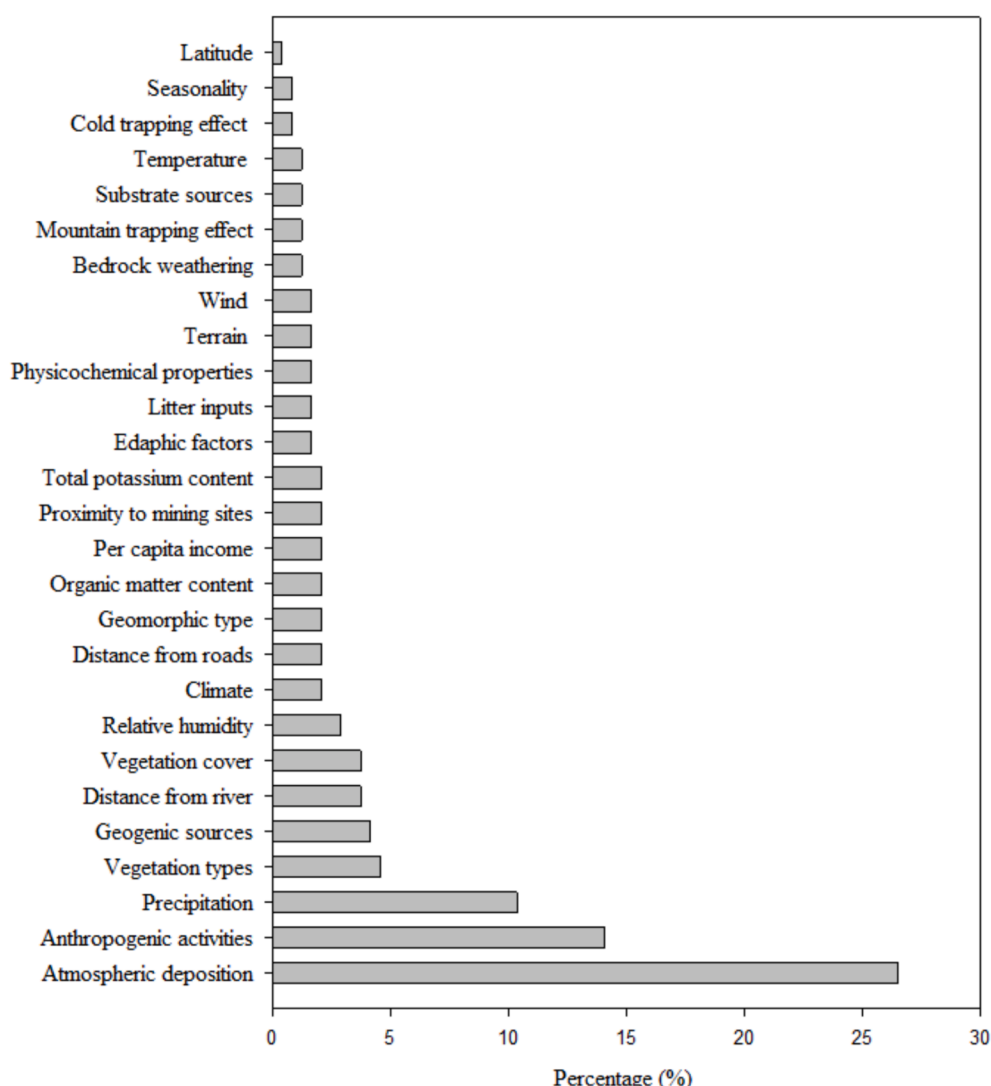


Fig. 5. Drivers of toxic elements along terrestrial elevational gradients.

altitude, which enhances condensation and rainfall, thereby increasing deposition potential (Song et al., 2019). For example, studies in industrial regions like Dzhez-kazgan and Balkhash in Kazakhstan reported elevated concentrations of As, Cu, and Pb due to atmospheric deposition, with mean concentrations of Cd, As, Cu, and Pb at 0.88, 0.96, 16.11, and 3.80 $\mu\text{g/L}$, respectively. In these areas, dry deposition of long-range transboundary pollutants was found to exceed wet deposition by two to five times, particularly under low precipitation conditions that enhance dry deposition (Cherednichenko et al., 2021). Wet deposition and dry deposition pathways differ in their affinity for specific elements based on physicochemical properties. Mercury (Hg), often emitted as volatile gaseous Hg^0 or reactive Hg^{2+} , is highly soluble in water and thus predominantly deposited via wet processes, where precipitation scavenges gaseous or particle-bound Hg (Zhu et al., 2016). In contrast, lead (Pb) and chromium (Cr), typically associated with particulate matter from industrial activities (e.g., smelting, coal combustion), primarily settle through dry deposition due to their adherence to airborne particles (Ati-Hellal and Hellal, 2021; Okerefor et al., 2020). Hg's gaseous phase allows global dispersion, while Pb and Cr bind to coarse particles, limiting their dispersal and favoring localized dry deposition (Shen et al., 2019). Wet deposition efficiently transfers soluble Hg into aquatic systems, whereas dry-deposited Pb/Cr accumulate in soils, degrading fertility and entering food chains via plant uptake (Briffa et al., 2020).

Anthropogenic activities significantly influence precipitation

chemistry, with lower elevations dominated by local emissions and higher elevations more affected by long-range transport (Wang et al., 2017). Consequently, lower elevations experience greater contributions from anthropogenic sources, while higher elevations are primarily impacted by atmospheric deposition (Liu et al., 2019). Different anthropogenic activities may show different effects on toxic element distribution along elevational gradients. For example, coal mining releases airborne particulates enriched with Pb, Cd, and As, which disperse via atmospheric transport and accumulate at higher elevations due to precipitation scavenging and cold trapping (Li et al., 2014). Conversely, textile dyeing discharges Cr and Cu via wastewater, contaminating lowland soils and aquatic systems near industrial zones (Sahu and Poler, 2024). Future research should differentiate the impacts of various anthropogenic sources on the distribution patterns of toxic elements.

Precipitation also indirectly influences toxic element dynamics through ecosystem processes. For instance, increased precipitation was shown to enhance litter biomass production, which facilitates Hg accumulation in forests, as demonstrated on Mt. Ailao ($R^2 = 0.69$, $p < 0.01$) (Wang et al., 2019). Similarly, studies from the southeastern Tibetan Plateau reported positive correlations between precipitation volume and the daily flux of total Hg ($R^2 = 0.42$, $p < 0.001$) and between Hg concentration and daily flux ($R^2 = 0.21$, $p < 0.05$) (Huang et al., 2015). The solubility of toxic elements during precipitation varies with

environmental conditions. Acid precipitation enhanced the solubility of elements such as Cr, Fe, Cu, Ni, and Pb by 20–50 % compared to non-acidic rain, with solubility influenced by factors like pH, precipitation intensity, and duration (Vlasov et al., 2021). These findings underscore precipitation as a key driver in the spatial distribution and accumulation of toxic elements along elevational gradients, mediated by both direct deposition processes and ecosystem interactions.

5.2. Vegetation types and vegetation covers

Vegetation plays a critical role in atmospheric deposition and distribution of toxic elements by intercepting fine particulate matter and aerosols. Forest canopies influence the magnitude and timing of pollutant deposition on forest floors (Xing and Brimblecombe, 2019). Different vegetation types, particularly the structure and density of forest canopies, significantly impact the accumulation and sequestration of toxic elements in terrestrial ecosystems. For instance, spruce-fir forests, characterized by dense coniferous canopies, exhibited a higher capacity to trap atmospheric-bound toxic elements compared to broadleaf forests (Bing et al., 2016; Tan et al., 2019). In boreal forests, forest canopy type and density were primary drivers of atmospheric Hg deposition (Witt et al., 2009). Evidence supports that vegetation sequestration is the dominant pathway for atmospheric Hg deposition, with subtropical mountain forests acting as substantial reservoirs. Net Hg fluxes in these ecosystems ranged from -7.3 to $-1.0 \mu\text{g}/\text{m}^2/\text{month}$ (Wang et al., 2022a).

Vegetation type also influences the soil Hg concentrations across elevations. For instance, surface soil in rainforests contained higher Hg levels than in nebula forests (Drummond et al., 2022). Mixed conifer-broadleaf forests at 1250–2400 m recorded $14.9 \mu\text{g}/\text{m}^2/\text{yr}$ of Hg, whereas evergreen broadleaf forests at 2500–2650 m showed higher amount at $23.1 \mu\text{g}/\text{m}^2/\text{yr}$ (Li et al., 2022). Similarly, annual average Hg^0 input was higher in deciduous forests ($25.1 \mu\text{g}/\text{m}^2$) compared to coniferous forests ($13.4 \mu\text{g}/\text{m}^2$). Coniferous canopies contributed to nocturnal non-stomatal Hg^0 input, capturing 24 % of Hg^0 , while deciduous forest floors accounted for 39 % (Zhou et al., 2023).

Elevational gradients further modulate Hg dynamics through vegetation shifts. Mid-altitude coniferous forests often exhibit higher methylmercury (MeHg) concentrations than higher-elevation alpine ecosystems (Gerson et al., 2017). At Mt. Luoji, coniferous forests displayed lower trace metal concentrations due to their higher absorption capacity and slower litter decomposition rates (Li et al., 2018). Similarly, Coniferous forests showed doubled Hg and Pb concentrations (760–900 m) compared to deciduous forests, with their larger leaf areas enhancing airborne metal capture (Stankwitz et al., 2012). Comparative studies revealed that Balsam fir needles contained significantly higher Hg levels than deciduous leaves, underscoring the role of vegetation type in toxic element accumulation (Rimmer et al., 2010).

Vegetation cover plays a crucial role in controlling the distribution and sequestration of toxic elements across terrestrial ecosystems. Natural and human factors significantly impact vegetation cover. Climate, soil, and topography determine plant distribution, while human activities like deforestation, urbanization, and agriculture cause habitat loss and biodiversity changes (Anees et al., 2024b). The type of vegetation cover significantly influences the accumulation and spatial distribution of these elements due to its impact on canopy structure and related ecological processes. In the Peruvian Amazon, undisturbed forests near gold mines experienced substantial atmospheric Hg deposition, with vegetation cover intercepting gaseous Hg in proportion to leaf area (Gerson et al., 2022). Similarly, on Mt. Luojia in southwestern China, vegetation cover, combined with cold trapping along elevation gradients, shaped the distribution of Pb and Cd in the O horizon, while the A horizon was primarily influenced by vegetation cover. In contrast, Zn distribution was predominantly determined by lithological factors (Li et al., 2018). In the Qinghai-Tibetan Plateau, vegetation cover accounted for a significant proportion of Hg^0 interception, contributing 51 % in

shrublands, 50 % in steppes, and 45 % in meadows (Li et al., 2018).

5.3. Seasonality

Seasonal variations, driven by climatic conditions such as drought and precipitation, play a pivotal role in elevational patterns of toxic elements. For instance, drought conditions can increase Hg concentrations in forest cover through litterfall and total deposition, while winter snowstorms enhanced atmospheric Hg deposition. Seasonality also affected the atmospheric deposition patterns of other toxic elements, with peak deposition typically occurring during summer and winter due to increased atmospheric inputs (Kara et al., 2014). At the onset of the rainy season, concentrations of toxic elements were elevated, as rainfall scavenges accumulated atmospheric dust from the preceding dry season (Al-Khashman et al., 2013). Similarly, peak methylmercury (MeHg) deposition in soil occurs in July (Gerson et al., 2017). In subalpine spruce plantations in Sichuan, Southwest China, seasonal variations also significantly influenced the accumulation and fluxes of toxic elements, including Al, Zn, Fe, Mn, and Cu, with precipitation and temperature being key drivers (Tan et al., 2019). Temperature can influence the biochemical rates of organisms by altering the kinetic and free energies of biochemical reactions. For example, there are two key components to the temperature dependence of reaction rates in enzyme-mediated reactions. Firstly, temperature increases the catalytic rate of an enzyme in its active state by enhancing the kinetic energy of the system. Secondly, temperature affects the probability of the enzyme remaining in its active state, which is typically maximal at an intermediate temperature. At both higher and lower temperatures, this probability declines due to reversible and irreversible enzyme inactivation (Kazmi et al., 2022).

5.4. Other factors

In addition to the major factors mentioned above, the distribution patterns of toxic elements along elevational gradients are also influenced by a complex interplay of climatic, edaphic, and biotic factors. An integrated application of machine learning and remote sensing facilitate the monitoring of terrestrial ecosystems particularly along elevational gradients.

Wind patterns also contribute to the spatial distribution of toxic elements. Increased wind speeds were associated with reduced atmospheric concentrations of these elements due to dilution effects (Zang et al., 2021). Prevailing monsoon winds on the eastern Tibetan Plateau influenced the distribution of Hg and arsenic (As), with windward sloped exhibiting higher litterfall Hg deposition due to enhanced precipitation and litter biomass production (Li et al., 2022). Additionally, wind-transported particles from local soils contributed to the deposition of elements such as Pb, Cd, and Zn in sparsely vegetated regions (Zechmeister, 1995).

Edaphic factors such as soil organic matter, cation exchange capacity, clay minerals, and pH play critical roles in the accumulation, mobility, and distribution of toxic elements (Tack et al., 1997). Anthropogenic activities, including mining and agricultural practices, exacerbate the accumulation and redistribution of these elements through soil erosion, leaching, and dust emissions. At lower elevations, pollution sources such as industrial activities and urban runoff contributed to elevated concentrations of toxic elements, whereas higher elevations were characterized by long-range atmospheric transport (Xiao et al., 2021).

Elevational gradients introduce distinct abiotic and biotic changes, influencing the accumulation and distribution of toxic elements. For example, Hg concentrations in litter and soil at lower elevations often reflected local anthropogenic inputs, while higher elevations exhibit patterns indicative of long-range transport, characterized by depleted $\Delta^{199}\text{Hg}$ values (Wang et al., 2017). These patterns pose ecological risks, such as Hg bioaccumulation in wildlife at higher elevations. Additionally, cold-trapping effects enhanced metal deposition, and bedrock

weathering influenced Zn distribution in high-elevation areas (Li et al., 2018).

Climatic factors, apart from precipitation, temperature accounts for a significant proportion of variations in litter biomass production, which in turn affects toxic element deposition. For instance, temperature was identified as the secondary driver of Hg distribution at Mt. Ailao after precipitation (Wang et al., 2019). Similarly, at Mt. Luoji and Shergyla Mountain, cold trapping and atmospheric uptake of Hg^0 were key factors influencing toxic element distribution (Li et al., 2018). Relative humidity is another significant factor, particularly influencing the accumulation of Cu, Pb, Ni, Cr, Cd, As, and Hg in vegetation (Zang et al., 2021). The distribution of toxic elements such as Cd, Ni, and Pb is further modulated by moss species' bioaccumulation capabilities and growth substrates (Xiao et al., 2021).

6. Effects of toxic elements on biota along elevational gradients

Exposure to high concentrations of toxic elements in terrestrial ecosystems disrupt metabolic activities and increase oxidative stress, leading to tissue injuries and the production of reactive oxygen species (ROS) in plants (Ali et al., 2019). When these toxic elements accumulate in soil organisms, they can cause neurological disorders, acute organ damage, and even mortality (Abdu et al., 2016). The effects of the toxic elements are further illustrated in Fig. 6 for additional clarity (see details in Table A.3, A.4, and A.5). Integrating machine learning and remote sensing can greatly aid in monitoring terrestrial ecosystems across elevations. Remote sensing provides spatial data on vegetation, temperature, and other ecological factors, while machine learning algorithms can analyze this data to identify patterns, assess biodiversity, and track ecosystem changes over time. This integrated approach offers valuable insights to inform sustainable management and conservation of diverse habitats (Anees et al., 2024a).

6.1. Plants

The effects of toxic elements on plants along elevational gradients are significant, as these elements can disrupt nutrient absorption and transport, leading to metabolic disorders and chromosomal aberrations (Cheng, 2003). Plant species display distinct patterns of toxic element accumulation depending on elevation; for example, *Ricinus communis* accumulates cadmium (Cd) in the following order: leaves < stems < roots (Dutta et al., 2019). Although high concentrations of toxic elements typically pose risks, some, like zinc (Zn), can be beneficial at lower levels (Zhang et al., 2021). Mechanistically, toxic elements such as copper (Cu), zinc (Zn), and manganese (Mn) can replace essential ions in proteins and enzymes, triggering oxidative stress through the generation of reactive oxygen species (ROS), which exacerbates metabolic disorders and cellular damage.

(Sanità Di Toppi and Gabbriellini, 1999). For instance, Cd can displace vital cations, such as Fe, thereby eliminating its functions. Similarly, Cd can dislodge Zn, thus disabling finger transcriptional function and ultimately affecting gene expression (Sanità Di Toppi and Gabbriellini, 1999). Growth inhibition and modification of root structure and pigment content were observed after Cd exposure. Accumulation of Cd in plants results in many adverse effects, including biochemical, physiological, and structural changes, which ultimately retards plant growth (Rady and Hemida, 2015; Vatehová et al., 2016). Additionally, toxic elements can compete with essential nutrients for uptake, such as Fe and Mg, disrupting ionic homeostasis (Manna et al., 2023). Some plants develop adaptive mechanisms, such as chelation and compartmentalization, to cope with environmental stresses. For instance, *Senecio coronatus* accumulates nickel (Ni) to deter snail *Helix aspersa*, while hyperaccumulation of Zn by *Thaspi caerulescens* to defend against feeding by slugs, caterpillars, and locusts (Dalcorso et al., 2013).

Elevated concentrations of toxic elements, Pb and Cd, posed potential toxicity risks to plants. Toxic metals such as Pb, Cd and Cr were

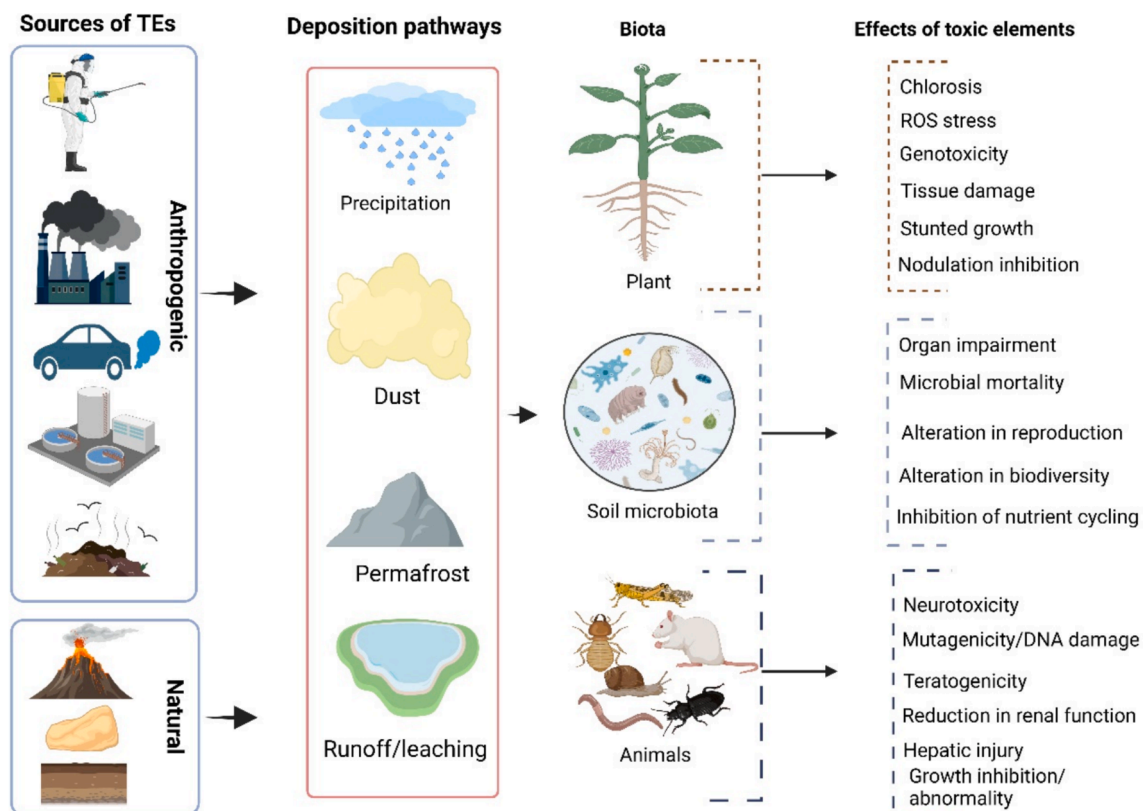


Fig. 6. Transport of toxic elements in terrestrial ecosystems and their effects on biota

found to exhibit immobilisation properties during the decomposition of leaf litter, indicating a potential influence on nutrient cycling and potentially posing a risk to the health and growth of plants in the surrounding environment (Yue et al., 2019). Elevated concentrations of Cd, Cr, Mn, Ni, and Zn in Sudety mountain ferns (*Athyrium distentifolium*) at higher elevations indicate increased pollution impacts on vegetation and potential risks for dependent herbivores (Samecka-Cymerman et al., 2012). In addition to the impacts of toxic elements on plant growth, research has shown that vegetation growth rates are altered by high-elevation terrain (Anees et al., 2025), highlighting the complexities that plants face across elevational gradients within terrestrial ecosystems. Overall, understanding the interplay between toxic element accumulation and plant responses across different elevations is crucial for assessing plant and ecosystem health.

6.2. Microbes

The elevation and bioavailability of toxic elements can significantly alter the phylogenetic composition of bacterial communities in the rhizosphere soil. The availability of Ni in the rhizosphere soil of *Alyssum murale* influenced the diversity of the bacterial community, irrespective of the altitude and physicochemical properties of the soil (Lopez et al., 2017). Soil pH significantly regulated the distribution of As-related functional soil microorganisms in terrestrial ecosystems along the elevational gradients of Taibai Mountain (Bei et al., 2023). The accumulation of Cu, Zn, and Pb along the elevational gradient reduces the abundance of soil microbial communities in the Tianshan Mountains (Yuan et al., 2021). Replacing the rhizosphere microbial communities due to different environmental interactions may distort microbial action mechanisms, ultimately undermining the multifunctional relationship between microbial diversity and soil (Yang et al., 2023).

Microbes are the first responders to toxic elements in the soil, and their metabolic processes can facilitate the speciation of these elements (Palansooriya et al., 2020). Elevated concentrations of toxic elements like cadmium (Cd), copper (Cu), and zinc (Zn) significantly disrupt microbial activity, community structure, diversity, and function, particularly affecting nitrogen cycling processes such as ammonia (NH₃) oxidation (Guo et al., 2017; Rijk et al., 2023). The presence of these toxic elements can entirely inhibit NH₃-oxidizing bacteria, thereby impairing soil microbial communities and their essential functions (Gremion et al., 2004). Additionally, soil contamination alters microbial community composition, as seen in ginseng-growing soils polluted with chromium (Cr), which negatively impacts both bacterial and fungal communities (Sun et al., 2022). Elevation gradients further complicate these dynamics by influencing soil physicochemical properties, such as clay content and moisture levels, as well as cations such as Al, Mn, and Mg, which in turn affect microbial communities (Corneo et al., 2013). The toxicity of elements like Zn and Cu reduces the abundance of beneficial bacteria, such as *Rhizobium leguminosarum*, thereby impacting nutrient cycling and overall soil health (Charlton et al., 2016). Overall, the accumulation of toxic elements in terrestrial ecosystems severely affects soil microbial activity, disrupting nutrient cycling and posing risks to plant growth and ecosystem stability (Bardgett and Van Der Putten, 2014; Wu et al., 2023).

6.3. Animals

Toxic elements in terrestrial ecosystems, such as cadmium (Cd), arsenic (As), mercury (Hg), and lead (Pb), exert lethal and sublethal effects on animals, significantly impacting their immune function, behaviour, and overall health (Boyd, 2009; Larison et al., 2000). Even low concentrations of these elements can alter physiology and species demographics, with invertebrates experiencing reduced immune responses and prolonged development periods (Monchanin et al., 2021). Bioaccumulation of toxic elements varies across trophic levels, with higher concentrations found in carnivores and omnivores due to dietary

habits, leading to biomagnification of elements like copper (Cu) and arsenic (As) (Zhang et al., 2021). For instance, the ingestion of Cd by larvae increases with higher concentrations in plants, while toxic elements like Hg have been detected in various terrestrial animals, indicating industrial contamination's role in their distribution (Dutta et al., 2019; Hsu et al., 2006). Additionally, toxic elements can disrupt the terrestrial food web, as seen in studies showing that exposure to Cu and Zn affects the growth and survival of species like honeybees (*Apis mellifera*) and spined soldier bugs (*Podisus maculiventris*) (Cheruiyot et al., 2013; Di et al., 2020). The complex dynamics of toxic element cycling and their long-term bioaccumulative effects on wildlife, particularly in alpine ecosystems, highlight the need for further research into their ecological impacts (Drummond et al., 2022; Rimmer et al., 2020). The accumulation of toxic elements poses significant risks to animal health across various trophic levels.

6.4. Food webs

Toxic elements have distinct impacts across trophic levels: plants (primary producers) face physiological and biochemical disruptions, such as Cd-induced displacement of essential ions (Fe, Zn, Mg), oxidative stress, and altered root/pigment structures (Sanità Di Toppi and Gabbriellini, 1999; Vatehová et al., 2016). Metal accumulation (e.g., Cd, Cr, Mn in *Athyrium distentifolium* at higher altitudes) may amplify and disrupt nutrient cycling via litter immobilization (Yue et al., 2019) along elevational gradients, though some species adapt via hyper-accumulation (e.g., Zn/Ni in *Thlaspi caerulescens*) to deter herbivory (Dalcorsio et al., 2013). In contrast, microbes (decomposers) experience reduced diversity and functional impairment, as Cu, Zn, and Pb diminish microbial abundance in alpine soils (Yuan et al., 2021), while Cd and Cr disrupt nitrogen cycling (e.g., NH₃-oxidizing bacteria inhibition) and shift community structures in polluted habitats (Guo et al., 2017; Sun et al., 2022), with soil pH and cations (Al, Mn) further modulating responses across elevations (Bei et al., 2023; Corneo et al., 2013). However, animals (consumers) confront direct toxicity (e.g., Cd, As impairing immune function and development in invertebrates; Monchanin et al., 2021) and biomagnification risks, as higher trophic levels accumulate Cu, As, and Hg through dietary transfer (Zhang et al., 2021), with metals propagating through food chains to threaten apex predators and human health (Armid et al., 2021; Ujianti and Androva, 2020). These tiered effects including physiological stress in plants, functional decay in microbes, and bioaccumulative threats in animals, underscore the cascading ecological risks of toxic elements across trophic networks.

Toxic elements, including cadmium, chromium, and lead, can bioaccumulate and transfer through food webs, posing risks to ecological and human health. These contaminants enter ecosystems via water, soil, and air, accumulating in organisms such as fish and transferring to higher trophic levels—evidenced by biomagnification in predatory birds linked to prey exposure (Armid et al., 2021; Ujianti and Androva, 2020). Human-driven contamination of aquatic systems exacerbates metal uptake in fish through sediment and dietary pathways, elevating risks for humans at the food chain apex (Puspitasari et al., 2021). Terrestrial ecosystems are similarly affected, with crops absorbing toxic elements from polluted soils, threatening food safety (Armid et al., 2021). The pervasive presence of these elements in global food chains, driven by industrial and agricultural activities, complicates risk assessments and underscores urgent needs for contamination mitigation (Zhang et al., 2023). Addressing these interconnected pathways is critical to reducing health impacts and safeguarding ecosystem integrity.

The effects of toxic elements also depend on specific habitats, reflecting interactions between environmental conditions and biological processes. In alpine ecosystems, elevated metal accumulation at higher altitudes (e.g., Tianshan Mountains) disrupts microbial communities and nutrient cycling, exacerbating stress on plant-herbivore interactions (Yuan et al., 2021). Polluted mountain regions exhibit distinct contamination profiles, such as ferns in the Sudety Mountains

accumulating Cd, Cr, and Ni at levels detrimental to herbivores, while Taibai Mountain's elevational gradients shape arsenic-microbe dynamics through soil pH variations (Bei et al., 2023). In agricultural soils, chromium contamination in ginseng-growing areas reduces microbial diversity, undermining soil health and productivity (Sun et al., 2022). It is important to consider the critical role of habitat-specific factors in mediating toxic element impacts, necessitating tailored monitoring and mitigation strategies to preserve ecosystem integrity.

7. Effect of toxic elements on ecosystem function along elevational gradients

The accumulation of toxic elements from natural and anthropogenic activities along elevational gradients threatens ecosystem functions such as litter decomposition and nutrient cycling.

7.1. Litter decomposition

The impact of toxic elements on litter decomposition along elevational gradients remains poorly understood. In addition to the risk of higher accumulation of toxic elements, such as Cd, Zn, and Pb, in litter from polluted terrestrial ecosystems, leaf toughness and lignin concentration were also reduced compared with non-contaminated terrestrial ecosystems (Run et al., 2022). The concentrations of toxic elements such as Pb, Cd, and Cr increased during litter decomposition in an alpine forest on the eastern Tibetan Plateau, with elevations ranging from 2458 to 4619 m a.s.l (Yue et al., 2019). The decomposition rate of

contaminated litter was higher than that of non-polluted litter. This indicated that the reduced lignin content and leaf toughness facilitated the decomposition rate. The more significant decomposition potential of toxic element-contaminated litter indicates a rapid nutrient cycling process that promotes effective microbial colonisation (Run et al., 2022). A mixture of Zn and Cu in a controlled laboratory experiment showed potent inhibition of litter decomposition owing to sufficient control of confounding variables (Ferreira et al., 2016).

Fungal necromass, shredder, and microbial communities varied along the toxicity gradient of an agrochemical (fungicide), suggesting that the 40 % decrease in the litter decomposition rate in contaminated terrestrial ecosystems was due to variation in the microbial community (Fernández et al., 2015). Microbially driven organic matter decomposition is drastically hindered in water-inundated soils. Heavy metal contamination (such as Cu and Pb) altered soil pH, enzymatic activities, and bacterial community structures, indicating that such contamination can significantly impact the decomposition process and soil health in forest ecosystems (Xu et al., 2023). Besides affecting microbial communities, increasing heavy metal concentrations (Cd) led to physiological stress in earthworms, reducing their feeding rate and burrowing activity. Consequently, the decomposition rate of leaf litter decreased, and soil nutrient concentrations were adversely affected (Liu et al., 2020).

7.2. Nutrient cycling

Toxic elements can transform and stabilise owing to their non-

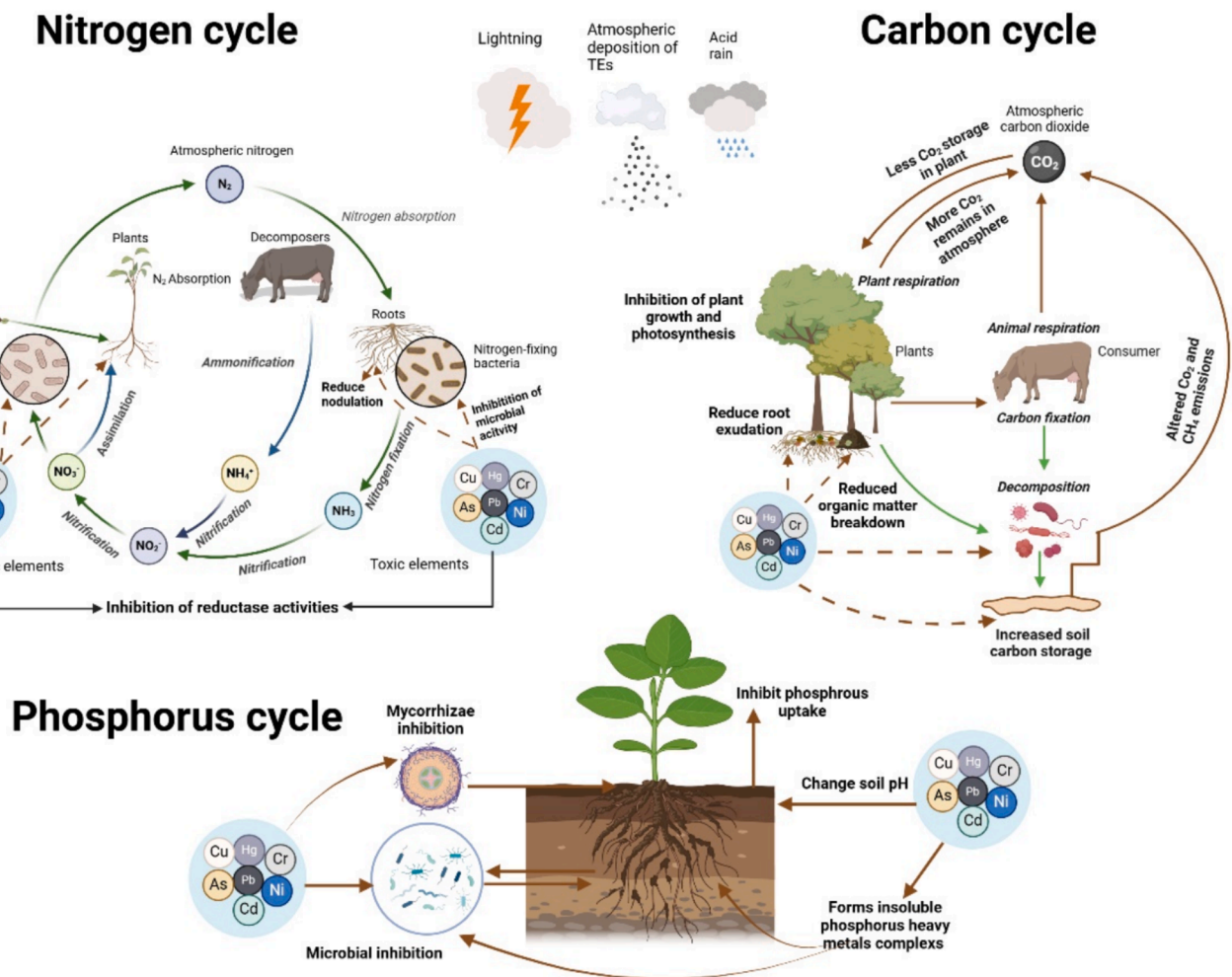


Fig. 7. Schematic illustration of the nutrient cycle under a polluted terrestrial ecosystem.

degradable properties, ultimately leading to their persistence and subsequent accumulation in terrestrial soil (McComb, 2014). Toxic elements in terrestrial ecosystems alter soil nutrient cycling processes by accelerating the release of essential elements from soil leachates and reducing the levels of extractable nutrient pools in terrestrial soils. Plant nutrient assimilation processes are less sensitive to toxic element contamination in terrestrial ecosystems than are soil nutrient cycling processes (Fig. 7). The effects of toxic elements on nutrient cycling depend on contamination level and exposure time. Toxic element contamination significantly degraded soil functions by altering soil communities, particularly fungal diversity and biomass, which are crucial for maintaining soil health and nutrient cycling (Ke et al., 2023).

Toxic elements, particularly heavy metals, disrupt the carbon cycle by impairing plant growth and photosynthesis through cellular damage and metabolic interference, reducing CO₂ absorption (Deng et al., 2025) (Fig. 7). This leads to elevated atmospheric CO₂ levels. Heavy metals also alter root exudation and microbial communities, decreasing carbon availability to soil microbes and slowing organic matter decomposition (Li et al., 2020; Barra Caracciolo and Terenzi, 2021). Reduced microbial activity disrupts carbon fixation and decomposition rates, altering soil CO₂ balance and promoting its release into the atmosphere. Toxic elements may also destabilize carbonate equilibrium and CO₂ exchange (Biedunkova and Kuznietsov, 2024).

Toxic elements inhibit soil enzyme activity and nitrogen-fixing/denitrifying bacteria, reducing nitrogen cycling efficiency (Bai et al., 2023; Wang et al., 2024) (Fig. 7). They impair nodulation and rhizosphere microbial diversity, hampering processes like denitrification and dissimilatory nitrate reduction to ammonia (DNRA) (Tian et al., 2025). Heavy metals suppress soil nitrogen supply, utilization, and retention, particularly in grassland and agroforestry systems (Zhang et al., 2023). However, denitrifying microbes (e.g., *Pseudomonas stutzeri*, *Sphingobium japonicum*) show resilience, dominating > 60 % of microbial abundance in contaminated soils. Elevated heavy metal(loid) concentrations enhance nitrite reductase (Nir) activity via the *nirK* gene, suggesting partial microbial adaptation (Hu et al., 2025).

Toxic elements reduce phosphorus availability by forming insoluble metal-phosphorus complexes and altering soil pH, which affects phosphorus solubility (Tian et al., 2024; Naz et al., 2022) (Fig. 7). Mycorrhizal plants sequester heavy metals in root vesicles and hyphae, limiting phosphorus uptake (Riaz et al., 2021). Heavy metals also disrupt microbial activity and decomposition, further restricting phosphorus mineralization and nutrient release (Barra Caracciolo and Terenzi, 2021). Soil pH shifts impair microbial and mycorrhizal functions, destabilizing phosphorus cycling and exacerbating phosphorus starvation in plants (Naz et al., 2022).

8. Future work and policy implications

A more nuanced understanding is necessary to gain a deeper understanding of the influence of toxic elements on terrestrial ecosystems in the context of changing global climate, thereby strengthening biodiversity conservation strategies, especially in critical areas such as montane ecosystems. Atmospheric deposition of toxic elements from nearby and long-range transboundary sources requires progressive characterisation of their longevity, forms, and solubility in the atmosphere. Preliminary evidence suggests that toxic elements deposited on foliage (leaf) surfaces interfere with the photosynthetic activities of plants. However, further studies are required to elucidate the various mechanisms involved in the stomatal uptake of toxic elements from the atmosphere, given that global emissions of toxic elements and other aerosols continue to rise. The mobility and bioavailability of toxic elements in the soil, particularly from anthropogenic activities, and their effects on soil microbes and ecosystem services, such as net primary productivity, nutrient cycling, and soil organic carbon stocks, require further investigation. Additional investigations are required to understand the mechanisms and potential drivers that influence the

distribution patterns of toxic elements along altitudinal gradients in terrestrial ecosystems. Climatic factors such as temperature affect the orographic effect along the elevational gradient due to temperature variations, future investigations should explore the possible links between temperature dynamics and other drivers in terrestrial ecosystems to better predict the impact of global climate change on ecosystem functions.

Mitigating toxic element contamination in terrestrial ecosystems across elevational gradients requires a policy framework integrating afforestation, pollution control, and phytoremediation. Afforestation should prioritize planting diverse native trees at varying elevations, as they stabilize soil and accumulate contaminants. Targeting contamination-prone areas (e.g., mining zones) maximizes rehabilitation. Concurrently, enforcing strict pollution controls on industrial emissions and agricultural runoff (key contamination sources) is critical. Regular monitoring ensures compliance and protects vulnerable ecosystems. Phytoremediation, using altitude-adapted plants to extract toxins from soil and water, offers targeted remediation. Supporting research on effective plant species and incentivizing community participation enhances scalability and sustainability. Collaborative efforts among local communities, environmental organizations, and governments ensure strategies are tailored to regional ecological conditions while raising public awareness of contamination risks. This integrated approach addresses contamination sources, promotes ecosystem recovery, and safeguards environmental health for future generations.

9. Conclusion

Our study offers one of the first comprehensive analyses of the elevational distribution of toxic elements and the primary drivers behind their accumulation in montane ecosystems, particularly in the context of rapid environmental change. Our findings demonstrate that increasing elevation amplifies the accumulation of toxic elements in terrestrial ecosystems due to enhanced atmospheric deposition. Long-transboundary toxic elements carried by the wind may be deposited on foliage, eventually accumulating in the soil via throughfall and litter decomposition. In addition, variations in climate along elevational gradients create a microclimate that enhances the cold trapping of toxic elements in the atmosphere, thus facilitating wet deposition via precipitation, dew, or frost. A variety of factors, including precipitation, temperature, vegetation cover, vegetation type, and altitude, shape the accumulation patterns of toxic elements in terrestrial ecosystems. Seasonal variability, especially between summer and winter, also modulates the deposition rates (both wet and dry) of toxic elements. Toxic elements pose significant risks to terrestrial biota and may profoundly affect litter decomposition and nutrient cycling. Our findings provide clear empirical insight that changes in elevational gradients driven by shifts in climate and vegetation, play a pivotal role in altering the patterns of toxic elements accumulation in montane ecosystems.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT 4.0 and DeepSeek R1 in order to improve readability and language. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

CRediT authorship contribution statement

Baba Imoro Musah: Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation, Conceptualization. **Jie Yang:** Writing – review & editing, Supervision, Funding acquisition. **Guorui Xu:** Conceptualization, Project administration, Visualization, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2025.113446>.

Data availability

Data are provided in Appendix A.

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