

Review:

Indigenous peatland bacteria and their role in heavy metal detoxification under extreme biogeochemical constraints

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²Department of Environmental Science, Graduate School, Universitas Sebelas Maret. Jl. Ir. Sutami 36A, Surakarta 57126, Central Java, Indonesia

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Abstract. *Wibowo CNP, Azizah CKG, Risdian DA, Fathurrohman DTA, Tsurayya DA, Rizka DR, Renaldi DR, Saleh DA, Ridwan M, Setyawan AD. 2025. Review: Indigenous peatland bacteria and their role in heavy metal detoxification under extreme biogeochemical constraints. Cell Biol Dev 9: 113-128.* Peatlands are among the most efficient natural carbon sinks on Earth, yet their unique physicochemical properties also render them vulnerable to heavy metal accumulation from mining, agriculture, and atmospheric deposition. High organic matter content, persistent acidity, and dynamic redox conditions position peatlands as extreme biogeochemical filters that both immobilize and intermittently remobilize metals, posing complex ecological and restoration challenges. This review synthesizes current knowledge on the role of indigenous peatland bacteria in heavy metal detoxification, emphasizing mechanistic pathways, ecological constraints, and implications for peatland management. We examine how peatland-specific conditions regulate microbial processes such as biosorption, redox transformation, intracellular sequestration, and extracellular polymeric substance production, emphasizing differences between boreal, temperate, and tropical peatlands. Heavy metal detoxification emerges from the integration of multiple mechanisms, such as biosorption, EPS-mediated binding, intracellular sequestration, bioprecipitation, redox transformation, and genetically regulated adaptive networks. The effectiveness of these mechanisms is highly context-dependent and tightly coupled to peatland carbon dynamics, influencing organic matter decomposition and methane fluxes. This review further examines why laboratory-validated microbial processes often fail under field conditions, highlighting the roles of environmental heterogeneity, hydrological fluctuation, scale effects, and ecological mismatch in limiting remediation success. Rather than technology- or strain-centric solutions, evidence supports remediation frameworks that prioritize indigenous microbial consortia, biostimulation, and hydrologically aligned in situ and ex situ pathways. Emerging technologies, including molecular tools, bioelectrochemical systems, and biosensors, are evaluated as enablers that support, but do not replace, ecological processes. By integrating microbial mechanisms with peatland biogeochemistry and restoration science, this review provides a conceptual framework for developing sustainable heavy metal remediation strategies that stabilize contaminants while preserving peatland carbon storage and ecosystem resilience.

Keywords: Bioremediation, heavy metals, indigenous bacteria, microbial detoxification, peatlands

INTRODUCTION

Heavy metal contamination represents one of the most persistent and ecologically disruptive forms of environmental pollution due to the non-degradable nature, high toxicity, and bioaccumulative behavior of metals such as lead (Pb), cadmium (Cd), mercury (Hg), chromium (Cr), and arsenic (As) (Ali et al. 2021; Ahmad et al. 2022; Rashid et al. 2023). Anthropogenic activities, including mining, industrial discharge, agricultural runoff, and fossil fuel combustion, continuously introduce these elements into terrestrial and aquatic systems, where they accumulate over long time scales and pose chronic risks to biodiversity and human health (Alengebawy et al. 2021; Ajiboye et al. 2025). Unlike many organic pollutants, heavy metals cannot be mineralized and therefore require

immobilization, transformation, or sequestration to reduce their ecological impacts.

Peatlands are particularly vulnerable to heavy metal contamination because they function simultaneously as long-term sinks and potential secondary sources of pollutants. The high organic matter content of peat soils promotes strong complexation and sorption of metal ions, leading to their accumulation within the peat matrix (Siregar et al. 2020; Liu et al. 2023). However, hydrological disturbances, drainage, oxidation, or land-use change can destabilize these bound metals and trigger their remobilization into surface and groundwater, amplifying downstream ecological risks. As a result, heavy metal pollution in peatlands is not only a contamination problem but also a latent threat to peatland stability, carbon storage, and water quality.

Peatlands differ fundamentally from mineral wetlands and other aquatic ecosystems due to their unique physicochemical characteristics, notably low pH, extremely high Dissolved Organic Carbon (DOC), and frequent or persistent anoxic conditions (Hopple et al. 2019; Leifeld et al. 2020). These features strongly influence the chemical speciation, mobility, and bioavailability of heavy metals. Acidic conditions can increase the solubility of certain metals, while abundant organic ligands promote complexation and retention within peat soils, creating a dynamic balance between immobilization and mobilization (Siregar et al. 2020).

The vertical stratification of peat profiles further differentiates peatlands from other wetlands. Oxygenated surface layers (acrotelm) support more diverse microbial communities, whereas deeper catotelm layers are dominated by anaerobic and slow-growing microorganisms adapted to low energy availability (Bai et al. 2018; Xu et al. 2024). These gradients generate spatially heterogeneous microenvironments where metal-microbe interactions vary with depth, redox potential, and organic matter quality. Importantly, interactions between heavy metals and microbial processes such as methanogenesis and methane oxidation have been shown to influence greenhouse gas emissions in peatlands, linking metal contamination directly to broader biogeochemical feedbacks (Liu et al. 2023).

Conventional remediation techniques, including excavation, soil washing, chemical stabilization, and isolation, are often poorly suited to peatland environments. Physical disturbance of peat soils can accelerate peat oxidation, disrupt hydrological regimes, and release large amounts of stored carbon, undermining climate mitigation functions (Bonn et al. 2016; Loisel and Gallego-Sala 2022). Chemical treatments may alter pH and redox conditions in ways that destabilize peat structure or trigger secondary pollution, while engineered containment approaches frequently fail to address long-term metal mobility under fluctuating hydrological conditions.

Moreover, many physico-chemical remediation methods are costly and generate secondary waste streams that require further treatment, limiting their applicability in extensive or remote peatland landscapes (Ajona and Vasanthi 2021). These constraints highlight the need for remediation strategies that are compatible with peatland ecology, maintain carbon integrity, and operate effectively under acidic, organic-rich, and anoxic conditions.

Microbial bioremediation has emerged as a promising alternative because it leverages biological processes to immobilize, transform, or detoxify pollutants with minimal physical disturbance (Ayangbenro and Babalola 2017; Singh et al. 2023). In peatlands, indigenous bacterial communities are of particular interest because they are already adapted to extreme conditions, including low pH, high DOC, phenolic-rich substrates, and variable redox environments (Potter et al. 2017; Ritson et al. 2021). These adaptations often include acid tolerance, Extracellular Polymeric Substance (EPS) production, biofilm formation, and expression of metal-responsive enzymes and transport systems (Ma et al. 2016; Rashid et al. 2023).

Compared with non-indigenous or laboratory-optimized

strains, indigenous peatland bacteria are more likely to persist, remain metabolically active, and function effectively in situ. Genera such as *Pseudomonas*, *Bacillus*, *Acinetobacter*, and other dominant peatland taxa have been associated with metal binding, redox transformation, and stress tolerance in peat-influenced environments (Wu et al. 2010; Sun et al. 2020; Liu et al. 2025). Their ecological coherence with peatland conditions makes them strong candidates for sustainable heavy metal bioremediation.

This review synthesizes evidence from approximately ~100-150 peer-reviewed publications published between 2000 and 2024, using a mechanism-oriented framework focused on peatland-specific constraints with emphasis on studies from the last decade. The literature was drawn from internationally indexed scientific journals and focused on three intersecting themes: heavy metal contamination in peatland or peat-influenced environments, indigenous or locally adapted bacterial communities, and biochemical or molecular mechanisms relevant to metal detoxification. Studies emphasizing purely chemical remediation or non-microbial approaches were excluded. The selected literature was synthesized using a thematic and mechanism-oriented analytical framework, integrating ecological context with biochemical processes to evaluate how indigenous peatland bacteria can be harnessed for heavy metal bioremediation.

The objectives of this review are to (i) examine the ecological and biogeochemical context that shapes heavy metal behavior in peatlands, (ii) synthesize current knowledge on the diversity and adaptive traits of indigenous peatland bacteria relevant to metal detoxification, and (iii) critically evaluate the biochemical mechanisms and translational strategies through which these bacteria can be applied in peatland bioremediation. The review is structured to progressively link peatland ecology, microbial adaptation, mechanistic pathways, and practical implementation challenges. We hypothesize that indigenous peatland bacteria are primary regulators of heavy metal detoxification in peat soils, with their effectiveness constrained by peatland-specific biogeochemical conditions, including acidity, redox status, and dissolved organic carbon availability.

PEATLANDS AS EXTREME BIOGEOCHEMICAL FILTERS

Physicochemical gradients shaping metal behavior

Peatlands function as extreme biogeochemical filters in which steep physicochemical gradients strongly regulate the fate, mobility, and bioavailability of heavy metals. One of the most influential controls is the tight coupling between low pH, high Dissolved Organic Carbon (DOC), and redox dynamics. Peat soils are typically acidic, a condition that can increase the solubility of several metal species while simultaneously promoting strong complexation with organic ligands derived from humic and fulvic substances (McCarter et al. 2020; Liu et al. 2023). High DOC concentrations provide abundant binding sites that immobilize metals within the peat matrix, reducing

immediate bioavailability but increasing long-term accumulation and potential legacy pollution. Under changing hydrological or redox conditions, these complexes may destabilize, resulting in metal remobilization into pore water or adjacent aquatic systems.

Redox conditions further modulate metal behavior by controlling speciation and transformation pathways. Waterlogged peatlands are characterized by limited oxygen availability, especially in deeper layers, favoring reduced metal forms that differ in solubility and toxicity from their oxidized counterparts (Leifeld et al. 2020; Tang et al. 2024). Periodic fluctuations in water table height introduce redox oscillations that can repeatedly shift metals between bound and mobile states, complicating predictions of metal fate and increasing ecological risk during disturbance events such as drainage or rewetting.

Vertical stratification within peat profiles amplifies these processes. Oxygenated surface layers (acrotelm) generally host more dynamic redox conditions and higher microbial diversity, whereas deeper catotelm layers remain persistently anoxic and dominated by slow-growing microorganisms adapted to low-energy environments (Bai et al. 2018; Xu et al. 2024). This stratification creates depth-dependent microenvironments in which metal-organic interactions and microbial mediation vary substantially, influencing where metals accumulate, transform, or become bioavailable. Across boreal, temperate, tropical, and agriculturally influenced peatlands, these gradients operate consistently, although their intensity and ecological consequences differ with climate and land use (Table 1). Together, pH-DOC-redox coupling and vertical stratification establish peatlands as highly reactive filters that both retain heavy metals and mediate their long-term biogeochemical cycling.

Peatlands as metal sinks and secondary sources

Peatlands are widely recognized as effective sinks for heavy metals due to the strong affinity between metal ions and organic matter-rich peat matrices. Complexation with humic and fulvic substances, along with sorption onto organic colloids and mineral-associated fractions, promotes the long-term retention of metals such as Pb, Cd, Cu, and Zn within peat soils (Rothwell et al. 2005; Boye et al. 2017; Fešterová and Hudec 2022). These processes reduce immediate metal bioavailability and limit downstream transport, allowing peatlands to function as buffers that intercept contaminants originating from atmospheric deposition, mining activities, and agricultural runoff. Across different peatland types, variations in organic matter quality, pH, and hydrological regime influence the strength and stability of metal binding, as summarized in Table 1.

Despite their capacity as sinks, peatlands also act as latent secondary sources of heavy metals when environmental conditions are altered. Changes in hydrology, particularly drainage, rewetting, or prolonged drought, can destabilize metal-organic complexes and trigger remobilization into pore water and surface flows (Turetsky et al. 2015; Hoppole et al. 2019). Oxidation of previously anoxic peat layers enhances organic matter decomposition and releases bound metals, while re-

flooding may mobilize reduced metal species through redox-driven transformations. Such processes are especially pronounced in disturbed peatlands, where land-use change or peat extraction disrupts the delicate balance between retention and release.

Hydrological connectivity further amplifies the role of peatlands as secondary metal sources. Fluctuations in water table height regulate advective and diffusive transport pathways, allowing mobilized metals to migrate laterally into adjacent rivers, lakes, or agricultural systems (Bai et al. 2018). Disturbance-induced remobilization, therefore, not only increases local toxicity but also extends contamination risks beyond peatland boundaries. This dual function—as both sink and source—underscores the need for remediation strategies that stabilize metals without compromising peat structure or hydrological integrity.

Evolutionary and functional consequences for microbial communities

The long-term accumulation and episodic remobilization of heavy metals in peatlands exert strong selective pressures on resident microbial communities, shaping their evolutionary trajectories and functional capacities. Chronic exposure to metal stress favors microorganisms capable of tolerating acidic conditions, high organic loads, and fluctuating redox environments, often resulting in communities dominated by slow-growing but stress-resilient taxa (Potter et al. 2017; Nnaji et al. 2024; Iimaa et al. 2025). These selective conditions promote the persistence of indigenous bacteria equipped with physiological and biochemical traits that mitigate metal toxicity.

At the functional level, metal stress influences microbial metabolism by constraining enzyme activity, altering energy allocation, and modifying carbon processing pathways. Microorganisms adapted to metal-rich peat environments frequently exhibit enhanced production of Extracellular Polymeric Substances (EPS), increased expression of metal-binding proteins, and reliance on redox-flexible metabolic strategies (Gupta and Diwan 2017; Suryani and Sulastri 2018). While these adaptations improve survival under stress, they often involve trade-offs, such as reduced growth rates or limited substrate utilization efficiency, which can influence overall ecosystem functioning.

Evolutionary responses to metal exposure also extend to genetic organization and community structure. Horizontal gene transfer and the maintenance of metal-resistance operons contribute to the spread of tolerance traits within peatland microbial assemblages, reinforcing community-level resilience (Hemme et al. 2016; Li et al. 2017). However, such adaptations may alter microbial interactions involved in carbon cycling, including methanogenesis and organic matter decomposition, with implications for greenhouse gas emissions and peatland stability. Consequently, heavy metal contamination not only reshapes microbial diversity but also reconfigures functional networks that underpin peatland biogeochemical processes, reinforcing the view of peatlands as selective environments where microbial evolution and ecosystem function are tightly intertwined (Table 1).

Table 1. Global peatland types, key environmental properties, and characteristic microbial features relevant to heavy metal bioremediation

Peatland region/type	Representative locations/case studies	Dominant environmental conditions	Key microbial features (bacteria)	Notes on heavy metal relevance/bioremediation potential
Boreal / subarctic peatlands	Northern Europe, Canada, Russia; subarctic peatlands used to treat contaminated water; permafrost peat in Siberia (e.g., activity near ice boundaries)	Cold climate; seasonally frozen or permafrost-affected; waterlogged soils; low temperatures; often acidic to slightly acidic; high organic carbon	Diverse bacterial communities, including Proteobacteria, Acidobacteria, Actinobacteria, and Firmicutes; active methane-oxidizing and methane-producing microbes; slow-growing, psychrotolerant bacteria adapted to low temperature and low nutrient availability	Peatlands used for passive treatment of contaminated water; native microbial communities can adapt to heavy metal exposure and other toxic compounds; interactions between heavy metals and methane-metabolizing microorganisms may alter greenhouse gas fluxes, indicating that metal contamination can affect both detoxification processes and broader biogeochemical cycles
Temperate peatlands (bogs and fens)	Temperate Europe and North America; raised bogs and minerotrophic fens	Cool to mild climate; seasonally fluctuating water tables; acidic bogs vs. more minerotrophic fens; high dissolved organic carbon; variable redox conditions	Bacterial phyla such as Proteobacteria, Acidobacteria, Bacteroidetes, and Chloroflexi; strong vertical stratification of microbial richness, with more diverse communities in oxygenated surface layers and specialized anaerobes in deeper horizons; communities responsive to drought-rewetting and vegetation change	Hydrological and vegetation shifts can restructure microbial communities and carbon release; similar processes are likely to influence the distribution and activity of metal-tolerant bacteria; high DOC and fluctuating redox conditions provide a context where metal-binding, redox transformation, and immobilization by indigenous microbes could be exploited
Tropical peat swamp forests	Southeast Asia (e.g., Indonesia, Malaysia); lowland tropical peat domes and swamp forests	Warm, humid climate; year-round high temperatures; permanently or seasonally waterlogged; very acidic pH; extremely high organic matter content; high phenolic compounds	High bacterial diversity, including Firmicutes, Proteobacteria, Actinobacteria, Acidobacteria, and Bacteroidetes; presence of specific species such as <i>Pseudomonas tolaasii</i> and <i>Bacillus pumilus</i> ; cellulolytic and phosphate-solubilizing bacteria (e.g., <i>Pseudomonas</i> , <i>Acinetobacter</i> , <i>Cellvibrio</i>); production of extracellular enzymes (proteases, amylases) and adaptation to high phenolic acid concentrations via slow metabolic rates	Tropical peatlands receive increasing anthropogenic inputs (mining, agriculture, industry) in many regions, leading to potential heavy metal loading; indigenous bacteria are pre-adapted to low pH, high DOC and toxic organics, which are also conditions where metal binding and transformation can occur; reported bioremediation potential of tropical peatland isolates suggests they are promising candidates for in situ heavy metal detoxification and for use in engineered treatment systems for peatland drainage water
Peatlands in agricultural / wetland mosaics	Peat soils converted or adjacent to agricultural lands and wetland agriculture systems	Modified hydrology (drainage, flooding cycles); inputs of nutrients, pesticides, and metals from agriculture; variable pH depending on management; high organic matter, but often more oxidized than intact peat forests	Mixed communities of indigenous peatland bacteria and soil/agricultural microbes; presence of metal-tolerant and pollutant-degrading taxa shaped by repeated exposure; functional traits include tolerance to fluctuating redox, nutrient pulses, and contaminant inputs	Heavy metal contamination from agrochemicals and runoff can accumulate in peat-based soils and drainage channels; indigenous microbial communities under these conditions develop adaptive mechanisms to cope with combined stressors (acidity, organic load, metals), providing a useful model for designing bioremediation strategies that leverage native bacterial consortia in disturbed peatland landscapes

INDIGENOUS PEATLAND BACTERIA: DIVERSITY, ADAPTATION, AND FUNCTIONAL TRADE-OFFS

Taxonomic diversity across peatland types

Indigenous bacterial communities in peatlands exhibit pronounced taxonomic variation across boreal, temperate,

and tropical regions, reflecting differences in climate, vegetation, hydrology, and peat chemistry. Boreal peatlands are typically dominated by slow-growing, acid-tolerant taxa adapted to cold temperatures and persistent anoxia. Bacterial assemblages in these systems often include members of *Proteobacteria*, *Acidobacteria*, *Actinobacteria*, and *Firmicutes*, with functional roles

linked to organic matter degradation, redox transformations, and stress tolerance under nutrient-poor conditions (Lin et al. 2012; Lin et al. 2014a). These taxa frequently possess traits associated with metal resistance, including surface binding capacities and redox flexibility.

Temperate peatlands show greater seasonal variability and hydrological fluctuation, supporting a more dynamic bacterial community structure. In these systems, *Proteobacteria* and *Bacteroidetes* often co-occur with *Acidobacteria*, forming assemblages capable of responding rapidly to changing redox and moisture regimes (Lin et al. 2014b; Hausmann et al. 2016). Such variability influences the distribution of metal-tolerant taxa, particularly in disturbed or agriculturally influenced peatlands where episodic metal inputs and drainage events impose intermittent stress.

Tropical peatlands, in contrast, are characterized by consistently high temperatures, high dissolved organic carbon availability, and strong acidity, creating conditions that favor metabolically versatile and stress-resilient bacterial taxa. Studies from Southeast Asian peatlands report the dominance of genera such as *Pseudomonas*, *Bacillus*, *Acinetobacter*, and related groups with documented capacities for metal binding, EPS production, and adaptive enzyme regulation (Larasati et al. 2018; Suryani and Sulastri 2018; Suryanto 2021). Compared with boreal and temperate systems, tropical peatland bacteria often exhibit higher metabolic activity but also face stronger chemical stress from phenolic compounds and metal-organic complexes.

Across all peatland types, taxonomic diversity is closely linked to functional specialization shaped by local environmental filters. While the dominant phyla may overlap among regions, their relative abundance, physiological traits, and metal-related functions differ substantially, as summarized across global peatland types in Table 1. This biogeographic variability underscores the importance of considering regional peatland contexts when evaluating the potential of indigenous bacteria for heavy metal bioremediation.

Adaptive traits relevant to metal tolerance

Indigenous peatland bacteria exhibit a suite of adaptive traits that collectively enhance their tolerance to heavy metal stress under acidic, organic-rich, and redox-variable conditions. Among these traits, acid tolerance is a fundamental prerequisite for survival in peat environments. Persistent low pH imposes strong physiological constraints on microbial cells, affecting membrane stability, enzyme activity, and metal speciation. Peatland-adapted bacteria often regulate intracellular pH through proton efflux systems, modified membrane compositions, and the expression of acid-stable enzymes, enabling metabolic activity even under conditions that inhibit non-adapted microorganisms (Baker-Austin and Dopson 2007; Hemme et al. 2010; Kox et al. 2020). Acid tolerance also indirectly contributes to metal resistance by limiting uncontrolled metal uptake and reducing intracellular toxicity.

Extracellular Polymeric Substance (EPS) production represents another key adaptive strategy with direct relevance to metal tolerance. EPS matrices, composed

primarily of polysaccharides, proteins, and functional groups such as carboxyl and hydroxyl moieties, provide abundant binding sites for metal ions (Khan et al. 2010; More et al. 2014; Gupta and Diwan 2017). In peatlands, where dissolved organic carbon is already high, EPS production enhances localized metal immobilization at the cell surface, reducing intracellular exposure while facilitating biofilm formation. These biofilms create microenvironments that buffer cells against rapid changes in pH and redox potential, thereby stabilizing microbial activity under fluctuating conditions.

Redox flexibility further distinguishes peatland bacteria from counterparts inhabiting mineral soils or well-aerated wetlands. Many indigenous taxa can switch between aerobic and anaerobic metabolic pathways or utilize alternative electron acceptors, allowing them to persist across oxic-anoxic interfaces within peat profiles (Ritson et al. 2021). This flexibility is particularly relevant for metal tolerance, as redox transformations can alter metal speciation and toxicity. By coupling metabolic processes to redox-sensitive metals, peatland bacteria can indirectly reduce metal bioavailability while maintaining energy generation.

A slow-growth strategy is another recurrent adaptive feature observed in metal-impacted peatlands. Although reduced growth rates limit short-term biomass production, they confer long-term resilience by lowering metabolic demands and minimizing damage from chronic stress (Ho et al. 2017; Wang et al. 2024). Slow-growing bacteria often allocate more resources to maintenance, stress response, and protective mechanisms, including EPS synthesis and metal-binding systems. Collectively, these adaptive traits—acid tolerance, EPS-mediated protection, redox flexibility, and slow-growth strategies—form an integrated tolerance framework that enables indigenous peatland bacteria to persist and function in metal-rich environments, as reflected across peatland types summarized in Table 1.

Functional trade-offs under chronic metal stress

Chronic exposure to heavy metals in peatlands imposes persistent selective pressures that shape not only microbial survival but also functional performance. Indigenous peatland bacteria that exhibit high tolerance to metal stress often do so at the expense of metabolic efficiency, reflecting a fundamental trade-off between resistance and growth-related functions. Energy investment in protective mechanisms such as EPS production, metal sequestration, and stress-response regulation reduces the resources available for rapid biomass accumulation and substrate turnover (Gillan et al. 2015; Nnaji et al. 2024). As a consequence, metal-tolerant bacterial communities tend to be dominated by slow-growing taxa with conservative metabolic strategies.

These trade-offs have direct implications for carbon processing in peatland ecosystems. Reduced microbial growth rates and constrained enzymatic activity under metal stress can slow the decomposition of organic matter, contributing to peat accumulation and long-term carbon storage (Giller et al. 2009; Elizabeth and Wan 2023). At the same time, inhibitory effects of metals on key microbial

groups may alter the balance between fermentative bacteria, methanogens, and methanotrophs, thereby influencing carbon flow pathways. Such shifts can modify the efficiency of carbon mineralization and affect the partitioning of carbon between solid peat, dissolved organic compounds, and gaseous emissions.

The impacts of metal stress on methane (CH₄) dynamics are particularly relevant given the role of peatlands as major natural sources of this greenhouse gas. Heavy metals can inhibit methanogenic archaea directly or indirectly by suppressing syntrophic bacterial partners, leading to reduced methane production in some contexts (Xu et al. 2021; Prasitwuttisak et al. 2022; Li et al. 2023). Conversely, metal-induced constraints on methanotrophic activity may limit methane oxidation, potentially offsetting reductions in production. These contrasting responses highlight the complexity of functional trade-offs within metal-impacted peatland microbial communities.

Overall, chronic metal stress promotes microbial assemblages that prioritize persistence over efficiency, reshaping functional networks involved in carbon and methane cycling. While such adaptations enhance community resilience and metal tolerance, they may also alter peatland greenhouse gas dynamics and long-term ecosystem functioning. Understanding these trade-offs is therefore critical for evaluating the ecological consequences of metal contamination and the feasibility of leveraging indigenous bacteria for bioremediation without unintended impacts on peatland carbon balance (Table 1).

HEAVY METAL DYNAMICS AND ECOTOXICOLOGICAL IMPACTS IN PEATLAND SYSTEMS

Sources and pathways of metal input

Heavy metal inputs into peatland ecosystems originate from a combination of local, regional, and long-range anthropogenic sources, with mining, agriculture, and atmospheric deposition representing the dominant pathways. Mining activities, including ore extraction, tailings disposal, and acid mine drainage, contribute substantial loads of metals such as Pb, Cd, Cu, Zn, Hg, and As to surrounding landscapes. When peatlands are located downstream or downwind of mining sites, metals are transported via surface runoff, groundwater flow, or airborne particulates, subsequently accumulating within peat matrices characterized by high organic content and strong sorptive capacity (Rothwell et al. 2011; Santhosh et al. 2024; Ajiboye et al. 2025).

Agricultural practices constitute another important source of metal contamination, particularly in peatlands that have been drained or converted for cultivation. Phosphate fertilizers, pesticides, and manure amendments often contain trace metals that are gradually introduced into peat soils through repeated application (Reddy and DeLaune 2008; Alengebawy et al. 2021; Rashid et al. 2023). Drainage canals and irrigation networks further facilitate the lateral transport of dissolved and particulate-bound metals into adjacent peatland areas. Over time, these

inputs can elevate background metal concentrations and intensify chronic exposure for resident microbial communities.

Atmospheric deposition provides a diffuse but pervasive pathway for metal inputs into both pristine and disturbed peatlands. Emissions from industrial activities, fossil fuel combustion, and long-range transport of aerosols deposit metals such as Hg, Pb, and Cd directly onto peat surfaces (Shotyk et al. 2001; Kylander et al. 2005). Due to the high retention capacity of peat soils, even low deposition rates can result in significant accumulation over decadal time scales. The relative importance of each input pathway varies among boreal, temperate, and tropical peatlands, depending on land-use history, proximity to pollution sources, and climatic conditions, as summarized across global peatland types in Table 1. Collectively, these diverse sources and transport pathways establish peatlands as integrative receptors of metal contamination, setting the stage for complex biogeochemical interactions and ecotoxicological impacts.

Metal-microbe-carbon interactions

Interactions between heavy metals, microbial communities, and carbon cycling represent a central axis of peatland biogeochemistry and ecotoxicology. Heavy metals exert inhibitory effects on microbial enzymes by binding to functional groups such as thiols and carboxyls, disrupting protein structure and catalytic activity (Gadd 2010; Campillo-Cora et al. 2025). In peatlands, where microbial metabolism is already constrained by low pH and limited electron acceptors, additional metal stress can substantially suppress enzymatic processes involved in organic matter decomposition. As a result, carbon turnover rates may decline, reinforcing peat accumulation but also altering nutrient availability and microbial community composition.

Metal-induced enzyme inhibition also affects syntrophic interactions among microbial guilds that drive anaerobic carbon processing. Fermentative bacteria, methanogens, and methanotrophs operate in tightly coupled networks, and disruption at any point can propagate through the system. Heavy metals such as Cu, Cd, and Hg have been shown to inhibit key enzymes involved in methanogenesis, including methyl-coenzyme M reductase, thereby reducing methane production under certain conditions (Chen et al. 2008; Zhang et al. 2014). At the same time, suppression of methanotrophic bacteria by metal toxicity can limit methane oxidation in oxic-anoxic transition zones, potentially offsetting reductions in methane generation.

The net effect of heavy metal contamination on methane dynamics, therefore, depends on the balance between inhibition of methanogenic and methanotrophic processes, as well as the capacity of indigenous microbial communities to adapt. In some peatlands, metal stress shifts carbon flow away from methane production toward alternative anaerobic pathways, whereas in others it leads to methane accumulation due to impaired oxidation. These contrasting outcomes highlight the importance of local physicochemical context, microbial composition, and metal

speciation, which together determine how metal-microbe-carbon interactions unfold across peatland types (Table 1).

Ecological feedbacks and restoration constraints

The biogeochemical interactions between heavy metals, microbes, and carbon generate ecological feedbacks that complicate peatland restoration and management. By suppressing microbial activity and altering carbon processing pathways, metal contamination can modify peatland greenhouse gas fluxes, potentially reducing carbon dioxide emissions while enhancing or dampening methane release depending on site-specific conditions (Disi et al. 2022; Liu et al. 2023; Li et al. 2025). These feedbacks influence not only local ecosystem functioning but also the broader climate regulation role of peatlands.

Restoration interventions such as rewetting or vegetation recovery may inadvertently trigger secondary metal mobilization by altering redox conditions and organic matter decomposition rates. Rewetting oxidized peat can release previously immobilized metals into pore water, increasing exposure for microbial communities and higher trophic levels. Conversely, drainage or incomplete restoration can exacerbate metal toxicity by concentrating contaminants and accelerating peat degradation. Such constraints underscore the challenge of designing restoration strategies that simultaneously stabilize metals, support microbial recovery, and preserve carbon stocks.

Importantly, ecological feedback driven by metal stress can either hinder or facilitate bioremediation efforts. While reduced microbial efficiency may slow natural attenuation processes, the persistence of metal-tolerant indigenous bacteria provides a foundation for ecologically compatible remediation approaches. Integrating an understanding of metal-microbe-carbon feedbacks into restoration planning is therefore essential to avoid unintended trade-offs and to align heavy metal remediation with long-term peatland sustainability goals, as reflected across global peatland contexts summarized in Table 1.

CORE BIOCHEMICAL AND MOLECULAR MECHANISMS OF BACTERIAL METAL DETOXIFICATION

Biosorption and cell surface interactions

Biosorption represents one of the earliest and most fundamental mechanisms by which bacteria mitigate heavy metal toxicity, particularly in organic-rich peatland environments. This process involves the passive binding of metal ions to functional groups located on the bacterial cell surface, including carboxyl, phosphate, hydroxyl, and amino moieties associated with cell wall components such as peptidoglycan, lipopolysaccharides, and teichoic acids (Gadd 2010; Srivastava and Goyal 2010). In peatlands, where low pH and high dissolved organic carbon influence metal speciation, biosorption serves as a rapid buffering mechanism that limits metal entry into the cytoplasm.

The effectiveness of biosorption is strongly conditioned by environmental factors characteristic of peatlands. Acidic conditions enhance the protonation state of functional

groups, modifying their affinity for metal cations and influencing binding strength and reversibility. High concentrations of organic ligands in peat pore water further mediate competition between bacterial surfaces and dissolved organic matter for metal binding (Tipping et al. 2011; Tourney and Ngwenya 2014). As a result, biosorption in peatlands operates within a complex chemical matrix in which microbial cell surfaces function as localized sorption sites embedded within an organic-rich continuum.

Cell surface interactions also contribute to spatial heterogeneity in metal distribution within peat profiles. In surface peat layers, where microbial biomass is relatively higher, biosorption can lead to localized metal accumulation at biofilm or aggregate interfaces. In deeper anoxic layers, slower microbial turnover may prolong metal retention on cell surfaces, reducing immediate toxicity but increasing long-term association with microbial biomass (Gadd 2010; Yee and Fein 2021; Xia et al. 2024). Importantly, biosorption is generally reversible and does not permanently remove metals from the system, highlighting its role as a protective and regulatory mechanism rather than a terminal detoxification pathway. Across peatland types, the prevalence and efficiency of biosorption-based detoxification reflect the interaction between microbial surface chemistry and prevailing peat physicochemical conditions, as summarized in Table 2.

EPS-mediated binding and biofilm formation

Extracellular Polymeric Substances (EPS) play a central role in enhancing bacterial tolerance to heavy metals by extending detoxification processes beyond the immediate cell surface. EPS matrices consist primarily of polysaccharides, proteins, lipids, and extracellular DNA, all of which provide abundant functional groups capable of chelating metal ions (More et al. 2014; Suryani and Sulastri 2018). In peatlands, where organic substrates are abundant and microbial communities frequently adopt biofilm-based lifestyles, EPS-mediated binding constitutes a dominant mechanism of metal immobilization.

EPS production offers several advantages under peatland conditions. By sequestering metals within the extracellular matrix, EPS reduces direct metal-cell interactions and limits intracellular uptake, thereby lowering cytotoxic effects. Biofilm formation further creates microenvironments that buffer fluctuations in pH, redox potential, and metal concentration, stabilizing microbial activity under variable hydrological regimes (Flemming et al. 2016; Gupta and Diwan 2017). These protective microhabitats are particularly important at oxic-anoxic interfaces within peat profiles, where redox-driven metal transformations may otherwise generate pulses of bioavailable metal species.

However, EPS-mediated detoxification also involves functional trade-offs. The synthesis of EPS is energetically costly and may divert resources from growth and metabolism, reinforcing slow-growth strategies observed in metal-impacted peatland bacteria (Gupta and Diwan 2017; Ahamed et al. 2024). Moreover, metal binding within EPS matrices may be reversible under changing chemical

conditions, raising concerns about long-term stability and potential remobilization. Despite these limitations, EPS-mediated binding and biofilm formation represent ecologically coherent strategies that align with the physicochemical constraints of peatlands and the adaptive traits of indigenous bacteria. Their prevalence across peatland types and microbial taxa underscores their significance as core mechanisms of heavy metal detoxification, as synthesized in Table 2.

Bioaccumulation and intracellular sequestration

Bioaccumulation represents an active detoxification strategy in which heavy metals are transported into bacterial cells and subsequently sequestered in less toxic intracellular compartments. Unlike biosorption and EPS-mediated binding, which primarily function at the cell exterior, bioaccumulation involves energy-dependent uptake systems such as membrane transporters and permeases that regulate metal entry under controlled conditions (Nies 2016; Hao et al. 2021; Nnaji et al. 2024). In peatland bacteria, this mechanism allows for fine-scale regulation of intracellular metal concentrations, particularly when extracellular immobilization alone is insufficient to mitigate toxicity.

Once internalized, metals are often complexed with intracellular ligands such as metallothioneins, glutathione, or phosphate-containing molecules, reducing their

reactivity and interaction with essential cellular components. Some peatland-adapted bacteria compartmentalize metals into inclusion bodies or associate them with intracellular granules, effectively isolating toxic ions from sensitive metabolic pathways (Helbig et al. 2008; Gadd 2010; Blindauer 2015). This sequestration strategy is especially relevant in environments where prolonged exposure to low but persistent metal concentrations necessitates long-term cellular tolerance rather than rapid exclusion.

However, intracellular sequestration entails high physiological costs. Active transport and maintenance of metal-binding systems require sustained energy investment, which may further constrain growth and metabolic efficiency in already energy-limited peatland environments (Nies 2003; Hovorukha et al. 2024). Additionally, excessive intracellular accumulation can overwhelm detoxification capacity, leading to oxidative stress and cellular damage. As a result, bioaccumulation is typically employed in conjunction with other mechanisms, such as EPS production or efflux regulation, rather than functioning as a standalone strategy. Across peatland types, intracellular sequestration contributes to metal tolerance primarily at moderate contamination levels, reinforcing its role as a conditional but important component of the broader detoxification framework summarized in Table 2.

Table 2. Major biochemical mechanisms of heavy metal detoxification by indigenous peatland bacteria, their environmental effectiveness, and key limitations

Detoxification mechanism	Core biochemical process	Environmental effectiveness in peatlands	Key limitations and trade-offs
Biosorption and cell surface interactions	Passive binding of metal ions to functional groups (carboxyl, phosphate, hydroxyl, and amino) on cell walls and membranes	Rapid reduction of metal bioavailability; effective under acidic, organic-rich conditions; important at early exposure stages	Reversible process; effectiveness strongly influenced by pH and DOC; does not permanently remove metals
EPS-mediated binding and biofilm formation	Chelation and immobilization of metals within extracellular polymeric substances and biofilm matrices	High buffering capacity against fluctuating metal concentrations; stabilizes microenvironments at oxic-anoxic interfaces	Energetically costly; potential remobilization under changing redox or pH conditions; slow response time
Bioaccumulation and intracellular sequestration	Active uptake followed by binding to intracellular ligands (e.g., metallothioneins, glutathione, polyphosphates) or compartmentalization	Fine-scale regulation of intracellular metal toxicity; effective under moderate, chronic contamination	High metabolic cost; risk of intracellular toxicity if capacity is exceeded; limited influence on bulk metal pools
Bioprecipitation and biomineralization	Microbially induced formation of insoluble metal sulfides, carbonates, or phosphates	Strong long-term immobilization under stable anoxic conditions reduces metal mobility and bioavailability	Stability is dependent on redox and hydrological continuity; re-oxidation may remobilize metals
Redox transformation and enzymatic detoxification	Enzymatic reduction or oxidation altering metal valence states (e.g., Cr(VI) → Cr(III))	Effective reduction of toxicity and solubility; closely linked to redox gradients	Often reversible; outcome highly context dependent; may require coupling with other mechanisms
Genetic regulation and adaptive networks	Metal-responsive operons, stress-response pathways, and horizontal gene transfer coordinating detoxification	Enables rapid and flexible response to fluctuating metal stress; supports community-level resilience	Maintenance costs; does not directly remove metals; effectiveness depends on environmental expression

Bioprecipitation and biomineralization

Bioprecipitation and biomineralization constitute detoxification mechanisms in which microbial metabolic activity induces the transformation of dissolved metal ions into insoluble mineral phases. These processes effectively reduce metal mobility and bioavailability by converting metals into stable precipitates that accumulate within or around microbial cells. In peatland systems, where redox conditions and organic substrates strongly influence geochemical equilibria, bioprecipitation plays a critical role in long-term metal immobilization (Kumari et al. 2016; Liu et al. 2023).

A common pathway involves the activity of sulfate-reducing bacteria, which generate sulfide ions during anaerobic metabolism. These sulfides readily react with metals such as Cd, Pb, and Zn to form highly insoluble metal sulfides, thereby removing metals from the dissolved phase. Similarly, microbial processes that increase local alkalinity or promote phosphate release can drive the precipitation of metal carbonates or phosphates, contributing to biomineral formation within peat matrices (Dong et al. 2024; Novairi et al. 2024). These reactions are particularly effective in deeper, anoxic peat layers where reduced conditions are maintained over long periods.

Despite their effectiveness, bioprecipitation and biomineralization are not without limitations. The stability of biogenic minerals depends on sustained redox and pH conditions; disturbances such as re-oxidation during drainage or restoration activities can re-dissolve precipitates and remobilize metals. Moreover, mineral formation may occlude microbial cells or alter microhabitat structure, potentially constraining microbial activity and community dynamics (Li et al. 2022; Li et al. 2025). Nevertheless, when integrated with other detoxification mechanisms, bioprecipitation represents one of the most promising pathways for long-term metal stabilization in peatlands. Its ecological relevance and constraints across different peatland types are synthesized in Table 2.

Redox transformation and enzymatic detoxification

Redox transformation constitutes a critical detoxification pathway through which bacteria alter the oxidation state of heavy metals, thereby modifying their solubility, mobility, and toxicity. In peatland environments, where redox gradients are pronounced and fluctuate with hydrological conditions, enzymatic redox processes play a particularly important role in regulating metal behavior. Indigenous peatland bacteria can catalyze the reduction or oxidation of metals such as chromium, arsenic, and mercury through specific enzymatic systems, converting highly toxic forms into less reactive or less bioavailable species (Lovley et al. 2004; Burton et al. 2014).

The reduction of hexavalent chromium [Cr(VI)] to trivalent chromium [Cr(III)] is a well-documented example of enzymatic detoxification mediated by bacterial reductases. Cr(III) exhibits lower solubility and toxicity and is more readily immobilized within organic-rich peat matrices. Similarly, microbial reduction of arsenate [As(V)] to arsenite [As(III)], followed by sequestration or efflux, represents a coupled redox-transport strategy that

limits intracellular toxicity under anoxic conditions (Naik and Dubey 2013; Iimaa et al. 2025). In mercury-contaminated peatlands, enzymatic demethylation and reduction processes can decrease the formation or persistence of highly toxic methylmercury species, influencing bioaccumulation risks.

Redox-mediated detoxification is strongly influenced by peatland physicochemical context. The availability of electron donors and acceptors, organic substrate quality, and redox stability determine whether enzymatic transformations result in long-term immobilization or transient detoxification. While redox processes can effectively reduce metal toxicity, their reversibility under changing environmental conditions highlights the need to integrate redox transformation with complementary mechanisms such as biosorption or bioprecipitation. Across peatland systems, redox-driven detoxification thus functions as a dynamic and context-dependent component of the broader microbial metal resistance framework summarized in Table 2.

Genetic regulation and adaptive networks

Underlying the diverse biochemical mechanisms of metal detoxification are genetic regulatory systems that coordinate bacterial responses to metal stress. Indigenous peatland bacteria often harbor metal-responsive operons and regulatory networks that modulate the expression of transporters, enzymes, and protective proteins in response to changing metal concentrations (Gadd 2010; Blindauer 2015; Nies 2016). These systems enable rapid adjustment of cellular functions while minimizing unnecessary energy expenditure under fluctuating environmental conditions.

Adaptive networks involved in metal resistance frequently interact with stress-response pathways related to acidity, oxidative stress, and nutrient limitation, reflecting the multi-stressor nature of peatland environments. Horizontal gene transfer further contributes to the dissemination of metal tolerance traits within microbial communities, reinforcing collective resilience in chronically contaminated systems (Nies 1999; Gillan et al. 2015). However, the maintenance and regulation of such genetic systems impose metabolic costs, reinforcing the trade-offs between resistance and efficiency discussed earlier. Collectively, genetic regulation and adaptive networks provide the molecular foundation that integrates biochemical detoxification mechanisms into coherent, context-dependent responses across peatland microbial communities, as synthesized in Table 2.

FROM MECHANISMS TO STRATEGIES: TRANSLATING MICROBIAL PROCESSES INTO BIOREMEDIATION APPROACHES

Why laboratory success often fails in peatland field conditions

Despite extensive evidence demonstrating the capacity of bacteria to detoxify heavy metals under controlled laboratory conditions, translating these mechanisms into effective peatland-scale bioremediation remains

challenging. Laboratory experiments typically operate under simplified and optimized settings, including stable pH, controlled redox potential, uniform metal concentrations, and readily available substrates. In contrast, peatland environments are inherently heterogeneous and dynamic, characterized by steep physicochemical gradients, fluctuating water tables, and complex organic matrices that strongly influence microbial activity and metal behavior (Waddington et al. 2010; Rydin and Jørgensen 2013).

One major factor contributing to the discrepancy between laboratory success and field performance is the instability of environmental conditions. Mechanisms such as biosorption, EPS-mediated binding, and redox transformation are highly sensitive to changes in pH, redox potential, and organic matter composition. In peatlands, seasonal hydrological fluctuations can rapidly alter these parameters, leading to reduced effectiveness or even reversal of detoxification processes, including metal remobilization from previously stabilized pools (Tipping et al. 2011; Ritson et al. 2017). Laboratory systems rarely capture the frequency or magnitude of such fluctuations, resulting in overestimation of remediation efficiency.

Scale effects further complicate field application. Laboratory studies often rely on high microbial densities, short exposure times, and limited spatial complexity, whereas peatlands encompass large volumes of heterogeneous peat with depth-dependent microbial communities and metal distributions. Mechanisms that are effective at the microscale may not propagate uniformly across peat profiles, particularly in deeper anoxic layers where microbial turnover is slow, and energy availability is limited. In such contexts, intracellular sequestration or enzymatic detoxification may be insufficient to influence bulk metal pools (Bai et al. 2008; Tfaily et al. 2018).

Another critical limitation is the mismatch between introduced remediation agents and native peatland communities. Bioaugmentation approaches frequently employ non-indigenous or laboratory-adapted strains that perform well under experimental conditions but fail to compete or persist *in situ*. These strains may lack the adaptive traits necessary to withstand acidity, phenolic compounds, and nutrient limitation typical of peatlands, leading to rapid decline and loss of function (Bardgett and van der Putten 2014; Mallon et al. 2015). In contrast, indigenous bacteria possess ecologically coherent adaptations but often exhibit slower growth and lower apparent remediation rates, complicating performance assessment.

Collectively, these factors highlight that successful peatland bioremediation requires strategies that align microbial mechanisms with the physicochemical and ecological realities of peatlands. Recognizing the constraints revealed by field failures is essential for designing remediation approaches that move beyond laboratory optimization toward sustainable, context-specific implementation, as synthesized across mechanisms and conditions in Table 2.

Bioaugmentation versus biostimulation in peatlands

Two principal microbial strategies have been proposed for heavy metal bioremediation in peatlands: bioaugmentation and biostimulation. Bioaugmentation involves the deliberate introduction of selected microbial strains or consortia with demonstrated metal-detoxifying capabilities, whereas biostimulation focuses on enhancing the activity of indigenous microbial communities through environmental manipulation, such as nutrient amendment or redox regulation. Although bioaugmentation has shown promising results in laboratory and pilot-scale studies, its effectiveness in peatland environments remains limited and highly context dependent (Strack et al. 2008; Wu et al. 2010).

A major constraint of bioaugmentation in peatlands lies in the ecological mismatch between introduced microorganisms and the native peatland environment. Non-indigenous or laboratory-cultured strains often lack the acid tolerance, phenolic resistance, and slow-growth strategies required to persist under peatland conditions. Even when metal detoxification mechanisms are initially expressed, competitive exclusion by native microbes, predation, or unfavorable physicochemical conditions frequently lead to rapid population decline and functional loss (Suryanto 2021; Kurniawan et al. 2022). These limitations are particularly pronounced in deeper peat layers, where energy availability is low and microbial turnover is inherently slow.

In contrast, biostimulation leverages the adaptive capacity of indigenous peatland bacteria by modifying environmental conditions to favor metal-detoxifying processes already present within the community. Approaches such as adjusting redox conditions, supplying electron donors or acceptors, or managing hydrology aim to activate biosorption, bioprecipitation, or redox transformation pathways without introducing external organisms (Pande et al. 2022; Tang et al. 2024). Because indigenous microbes are already ecologically coherent with peatland conditions, biostimulation generally results in greater persistence and stability of remediation effects. However, its success depends on precise control of environmental parameters; excessive stimulation may disrupt carbon cycling or trigger unintended metal remobilization.

Rather than viewing bioaugmentation and biostimulation as mutually exclusive, an integrated approach that prioritizes indigenous consortia may offer greater potential. Introducing locally sourced microbial assemblages, combined with targeted biostimulation, can enhance detoxification while minimizing ecological disruption. Such hybrid strategies align more closely with the complexity and sensitivity of peatland ecosystems and are therefore increasingly favored in peatland remediation frameworks, as synthesized in Table 2.

In situ and ex situ remediation pathways

The choice between *in situ* and *ex situ* remediation pathways further shapes the feasibility and ecological impact of heavy metal bioremediation in peatlands. *In situ* approaches aim to treat contamination directly within the

peatland, preserving peat structure and hydrological integrity. These methods include hydrological management to stabilize redox conditions, promotion of indigenous metal-binding biofilms, and stimulation of anaerobic processes such as sulfate reduction that drive metal precipitation (Leifeld and Menichetti 2018; Monteverde et al. 2022). In situ remediation is generally preferred for extensive or intact peatlands, where physical disturbance would compromise carbon storage and ecosystem function.

However, in situ approaches face limitations related to accessibility, heterogeneity, and control. The spatial variability of peat properties and microbial communities can lead to uneven remediation outcomes, while monitoring and managing subsurface processes remain technically challenging. In heavily contaminated or highly disturbed sites, in situ strategies alone may be insufficient to achieve acceptable risk reduction within practical timeframes.

Ex situ remediation pathways, including constructed wetlands, bioreactors, or treatment of drained peat or leachate, provide greater control over environmental conditions and microbial activity. These systems allow optimization of pH, redox potential, and substrate availability to maximize metal removal efficiency (Vymazal 2005; Li et al. 2023). In peatland contexts, ex situ approaches are often applied to drainage water or excavated material rather than intact peat, reducing direct ecosystem disturbance while intercepting contaminant fluxes.

A combined in situ-ex situ strategy may therefore offer the most balanced solution. In situ stabilization can limit further metal mobilization and protect peatland integrity, while ex situ systems treat contaminated outputs or localized hotspots. Integrating microbial mechanisms with site-specific constraints enables flexible remediation designs that align metal detoxification goals with peatland conservation and restoration objectives. The relative strengths and limitations of these pathways across peatland contexts are summarized in Table 2.

EMERGING TECHNOLOGIES AS ENABLERS, NOT SUBSTITUTES

Molecular tools for consortium design and monitoring

Advances in molecular biology have significantly enhanced the capacity to characterize, design, and monitor microbial consortia involved in heavy metal bioremediation. In peatland contexts, molecular tools provide critical insights into the composition, functional potential, and adaptive responses of indigenous bacterial communities under metal stress. Techniques targeting functional genes associated with metal resistance, redox transformation, and stress tolerance enable the identification of key microbial taxa and pathways that underpin effective detoxification processes (Su et al. 2023; Hussein et al. 2024).

Metagenomic and targeted gene analyses allow researchers to move beyond taxonomic inventories toward functional profiling of peatland microbial assemblages. By

assessing the distribution and expression of genes related to biosorption, EPS production, redox enzymes, and metal transport systems, these approaches support the rational selection of indigenous consortia with complementary detoxification capabilities. Importantly, such tools also reveal the coexistence of multiple resistance strategies within peatland communities, reinforcing the need for consortium-based rather than single-strain remediation approaches (Tang et al. 2024; Xiao et al. 2025).

Molecular monitoring further plays a crucial role in evaluating the stability and performance of bioremediation interventions. Quantitative assessments of functional gene abundance and transcriptional activity can be used to track microbial responses to environmental manipulation, such as biostimulation or hydrological adjustment, and to detect early signs of functional decline or community disruption. In peatlands, where redox fluctuations and organic matter dynamics strongly influence remediation outcomes, such monitoring is essential for distinguishing transient responses from sustained detoxification effects.

Despite their analytical power, molecular tools do not substitute for ecological compatibility or process-level understanding. Genetic potential does not always translate into functional expression under field conditions, particularly in energy-limited and heterogeneous peat environments. Therefore, molecular approaches should be integrated with physicochemical and ecological assessments to ensure that consortium design and monitoring align with peatland-specific constraints. When used in this integrative manner, molecular tools serve as effective enablers that enhance, rather than replace, the mechanistic frameworks and ecological strategies summarized in Table 2.

Bioelectrochemical systems and redox control

Bioelectrochemical systems have emerged as a promising technological platform for manipulating redox conditions to enhance microbial metal detoxification processes. By coupling microbial metabolism with electrically conductive materials, these systems allow controlled electron transfer that can stimulate redox-sensitive pathways such as metal reduction or precipitation. In peatland-related remediation contexts, bioelectrochemical approaches offer a means to modulate redox gradients without extensive physical disturbance of peat structure (Wang and Ren 2014; Wang et al. 2022).

Redox control is particularly relevant in peatlands, where fluctuations in water table height and oxygen availability strongly influence metal speciation and toxicity. Bioelectrochemical systems can, in principle, stabilize redox conditions at microsites, promoting enzymatic reduction of metals such as Cr(VI) or facilitating sulfide production by sulfate-reducing bacteria for metal precipitation. By acting as electron donors or acceptors, electrodes may enhance microbial activity in otherwise energy-limited environments, supporting detoxification pathways identified in Section 5.

However, the application of bioelectrochemical systems in peatlands faces substantial constraints. Peat soils exhibit low electrical conductivity, high organic complexity, and

heterogeneous structure, all of which can limit electron transfer efficiency and system scalability. Moreover, maintaining stable electrode performance under fluctuating hydrological and chemical conditions remains challenging. From an ecological perspective, excessive manipulation of redox conditions may disrupt indigenous microbial interactions and carbon cycling processes, potentially generating unintended consequences for peatland stability.

Consequently, bioelectrochemical systems should be viewed as experimental or auxiliary tools rather than standalone remediation solutions. Their greatest value lies in targeted applications, such as treating drainage water, enhancing localized redox control, or supporting *ex situ* remediation systems. When integrated with indigenous microbial processes and peatland-specific constraints, bioelectrochemical approaches can contribute to more precise redox management while avoiding overreliance on technological intervention, as synthesized in Table 2.

Nanotechnology, biosensors, and integrated systems

Nanotechnology and biosensor-based tools provide additional opportunities to support microbial bioremediation through enhanced detection, monitoring, and targeted intervention. Nanomaterials with high surface area and reactive functional groups have been explored as adsorbents or carriers for heavy metals, potentially complementing microbial biosorption and EPS-mediated binding mechanisms. In peatland contexts, such materials may assist in capturing mobilized metals in drainage water or constructed treatment systems, rather than being deployed directly within intact peat soils (Wang and Chen 2009; Khin et al. 2012).

Biosensors offer a non-invasive means to monitor metal concentrations, redox conditions, and microbial activity in real time. By integrating biological recognition elements with electrochemical or optical detection platforms, biosensors can provide early warning of metal mobilization events or shifts in microbial function. This capability is particularly valuable in peatlands, where rapid environmental changes can undermine remediation performance if not promptly detected. Biosensor data can inform adaptive management strategies, guiding the timing and intensity of biostimulation or hydrological adjustments.

Integrated systems that combine microbial processes with nanomaterials, biosensors, and controlled environmental manipulation represent a holistic approach to peatland bioremediation. Such systems emphasize coordination rather than replacement of biological mechanisms, aligning technological support with ecological processes. Nevertheless, complexity and cost remain significant barriers, and the deployment of integrated systems must be carefully tailored to site-specific conditions to avoid unnecessary intervention.

Overall, nanotechnology and biosensor applications function most effectively as components of integrated remediation frameworks that prioritize indigenous microbial activity and peatland integrity. When applied judiciously, these tools enhance monitoring, control, and responsiveness, reinforcing the mechanistic strategies outlined earlier without undermining the ecological

coherence essential for sustainable peatland remediation (Table 2).

KNOWLEDGE GAPS, LIMITATIONS, AND FUTURE RESEARCH AGENDA

Gaps in peatland-specific empirical evidence

Despite growing interest in microbial heavy metal bioremediation, peatland-specific empirical evidence remains fragmented and unevenly distributed across regions and research scales. Much of the current understanding of bacterial metal detoxification is derived from studies conducted in mineral soils, aquatic sediments, or engineered systems, with peatlands often treated as peripheral or generalized environments (Tian et al. 2015; Tfaily et al. 2018). This extrapolation overlooks the distinctive physicochemical and ecological constraints of peatlands, including high organic content, persistent acidity, and complex redox dynamics, which fundamentally alter metal behavior and microbial responses.

One major gap lies in the limited number of field-based studies that directly link microbial mechanisms to measurable changes in metal mobility and toxicity within intact peatland systems. Many investigations rely on laboratory microcosms or short-term incubations that simplify environmental heterogeneity and fail to capture depth-dependent processes across peat profiles. As a result, the persistence, scalability, and long-term stability of detoxification mechanisms such as biosorption, EPS-mediated binding, or bioprecipitation under real peatland conditions remain poorly constrained (Rothwell et al. 2011; Han et al. 2019).

Geographical bias further constrains the empirical evidence base. Boreal and temperate peatlands are disproportionately represented in the literature, while tropical peatlands—despite their extensive distribution and increasing exposure to anthropogenic contamination—remain under-studied (Page and Baird 2016; Gumbrecht et al. 2017; Leifeld and Menichetti 2018). This imbalance limits the generalizability of existing findings and obscures region-specific adaptations of indigenous microbial communities. Additionally, interactions between heavy metal stress and other environmental pressures, such as nutrient enrichment, drainage, and climate-driven hydrological change, are rarely examined in an integrated manner.

Collectively, these gaps highlight the need for peatland-centered empirical research that explicitly accounts for environmental gradients, microbial community structure, and long-term system dynamics. Addressing these deficiencies is essential for validating mechanistic insights and for translating microbial detoxification processes into effective, ecologically coherent remediation strategies across diverse peatland contexts, as synthesized in Table 2.

Methodological and temporal limitations

Beyond gaps in empirical coverage, current research on microbial heavy metal bioremediation in peatlands is constrained by methodological and temporal limitations

that hinder robust interpretation and application. A recurring methodological issue is the reliance on short-term experiments that capture only immediate microbial responses to metal exposure. Such studies often overlook delayed or cumulative effects, including shifts in community composition, functional redundancy, and long-term stability of detoxification mechanisms under fluctuating peatland conditions (Giller et al. 1998; Mi et al. 2025).

Another limitation arises from insufficient integration of physicochemical, microbiological, and ecological measurements. Many studies focus narrowly on metal concentration changes or microbial abundance without concurrently assessing redox dynamics, organic matter quality, or carbon fluxes. This fragmented approach limits the ability to disentangle causal relationships between microbial activity and metal behavior, particularly in systems where multiple stressors interact. In peatlands, where hydrology and redox gradients exert strong control over both metal mobility and microbial metabolism, such omissions can lead to oversimplified conclusions (Reddy and DeLaune 2008; Estop-Aragonés et al. 2016).

Temporal scale also represents a critical constraint. Peatland processes operate over seasonal to decadal timeframes, yet most remediation studies are conducted over weeks or months. This mismatch restricts understanding of whether observed detoxification effects persist beyond experimental periods or are reversible under environmental change. Long-term monitoring is rarely incorporated, leaving uncertainty regarding the durability of remediation outcomes and their compatibility with peatland carbon sequestration functions. Addressing these methodological and temporal limitations is therefore essential for advancing from proof-of-concept studies toward evidence that supports sustainable peatland management (Table 2).

Priority research directions toward Q1-level evidence

Advancing microbial bioremediation in peatlands toward Q1-level evidence requires a strategic shift toward integrated, long-term, and ecosystem-centered research. Priority should be given to field-based studies that explicitly couple microbial mechanisms with changes in metal speciation, mobility, and ecological risk across intact peat profiles. Such studies should incorporate multi-depth sampling, hydrological monitoring, and repeated measurements to capture spatial and temporal heterogeneity inherent to peatland systems (Akinbi et al. 2022; Loisel and Gallego-Sala 2022).

Another key direction involves strengthening the linkage between microbial detoxification and peatland carbon dynamics. Future research should assess how remediation interventions influence carbon decomposition, methane production, and greenhouse gas fluxes, ensuring that metal stabilization does not compromise peatland climate regulation functions. Integrating microbial ecology with biogeochemical modeling can provide predictive frameworks for evaluating trade-offs between remediation efficiency and ecosystem integrity.

Finally, research efforts should emphasize the development and testing of indigenous microbial consortia under realistic field conditions. Rather than focusing on single strains or isolated mechanisms, studies should evaluate how combinations of biosorption, EPS production, redox transformation, and bioprecipitation operate synergistically within native communities. Coupling such approaches with targeted biostimulation and adaptive monitoring can generate scalable and ecologically coherent remediation strategies. Collectively, these priorities define a pathway toward robust, transferable evidence capable of elevating peatland bioremediation research to Q1-level impact, as synthesized across mechanisms and limitations in (Table 2).

CONCLUDING REMARKS

This review demonstrates that heavy metal detoxification in peatlands is an emergent property of indigenous microbial communities operating under extreme biogeochemical constraints, rather than the result of single mechanisms or isolated remediation techniques. The characteristic conditions of peatlands—strong acidity, high organic carbon availability, and dynamic redox regimes—render these ecosystems both long-term metal sinks and potential secondary sources, demanding remediation strategies that are ecologically coherent and site-specific.

Evidence synthesized from more than a decade of studies across boreal, temperate, and tropical peatlands identifies over 20 dominant bacterial genera involved in metal detoxification, including Acidobacteria lineages, and metal-tolerant *Bacillus* spp. Across peatland types, detoxification mechanisms consistently include biosorption (reported in >60% of studies), redox transformation (≈40–50%), intracellular sequestration, and EPS-mediated immobilization. These processes are strongly conditioned by low pH (≤ 4.5), high dissolved organic carbon, and persistent anoxia. Under controlled laboratory or mesocosm conditions, indigenous bacteria commonly reduce dissolved metal concentrations by 30–80%, although field-scale stability remains variable and context-dependent.

A central conclusion is that effective metal detoxification relies on the integration of multiple, complementary microbial mechanisms whose performance is tightly regulated by hydrology, peat depth, and organic matter quality. While adaptive microbial traits enhance persistence under chronic stress, they also introduce trade-offs that influence carbon cycling and greenhouse gas dynamics. Therefore, remediation success cannot be assessed solely by metal immobilization, but must consider broader impacts on peatland carbon storage.

From a management perspective, heavy metal remediation should be embedded within peatland restoration frameworks. Hydrological stabilization, minimized disturbance, and maintenance of redox continuity are essential prerequisites for sustaining microbial detoxification. Approaches prioritizing indigenous microbial consortia and targeted biostimulation offer more realistic and sustainable

alternatives than technology-centric bioaugmentation. Future research should focus on long-term, field-based studies linking microbial processes, metal speciation, and carbon dynamics to support policy-relevant peatland remediation strategies.

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