frontiers | Frontiers in Environmental Science

TYPE Review
PUBLISHED 18 July 2025
DOI 10.3389/fenvs.2025.1610193

OPEN ACCESS

EDITED BY
Can Wang,
Southwest Jiaotong University, China

REVIEWED BY
Chen Zhang,
Institute of Loess Plateau, Shanxi University, China
Qiming Mao,
Central South University, China

*CORRESPONDENCE
Wei Zhou,
46752711@qq.com
Longzao Luo,
luolongzao@sru.edu.cn

†These authors have contributed equally to this work and share first authorship

RECEIVED 11 April 2025
ACCEPTED 09 July 2025
PUBLISHED 18 July 2025

CITATION
Qiao Z, Lin X, Zhang T, Luo S, Wang C, Zhou W and Luo L (2025) A review of research progress on the application of bryophytes in the ecological restoration of mining areas of China. *Front. Environ. Sci.* 13:1610193.
doi: 10.3389/fenvs.2025.1610193

A review of research progress on the application of bryophytes in the ecological restoration of mining areas of China

Zhanrui Qiao[1,2†], Xiaoai Lin[3†], Tao Zhang[1,4], Shuigen Luo[5], Cunbao Wang[1,4], Wei Zhou[1,4]* and Longzao Luo[5]*

[1]Technology Innovation Center for Land Spatial Ecological Protection and Restoration in Great Lakes Basin, Ministry of Natural Resources of the People's Republic of China, Nanchang, Jiangxi, China, [2]The Eight Geological Team of Jiangxi Geological Bureau Shangrao, Shangrao, Jiangxi, China, [3]College of Life Science, Shangrao Normal University, Shangrao, China, [4]Jiangxi Provincial Institute of Land and Space Survey and Planning, Nanchang, Jiangxi, China, [5]School of Chemistry and Environmental Science, Shangrao Normal University, Shangrao, Jiangxi, China

The process of mining is invariably associated with ecological and environmental challenges within the mining region, making ecological restoration efforts in these areas especially crucial. Bryophytes, acting as key pioneer species, exhibit distinctive advantages and potential for application in the ecological restoration of mining sites. This study offered a concise overview of the fundamental traits of bryophytes, as well as their classification and distribution in mining regions across China using literature synthesis and field surveys. It primarily explored the role bryophytes played in the ecological restoration of such areas, the selection of appropriate bryophyte species, and cultivation techniques through systematic analysis. Additionally, the case studies of bryophytes' applications in ecological restoration within mining regions were analyzed. Results indicated that bryophytes in China's mining areas were diverse and widely distributed. Notably, bryophytes contributed to soil improvement, vegetation recovery, and the monitoring and indication of heavy metal pollution, with most demonstrating a robust tolerance to these contaminants. Future research should focus on screening suitable bryophytes, refining cultivation methods, and investigating their interactions with soil microorganisms.

KEYWORDS

bryophyte, mining area, ecological restoration, bryophyte ecological restoration, rapid cultivation

1 Introduction

Mining activities have significantly contributed to the economic development of mining regions and adjacent areas, but the detrimental impacts on the ecological environment cannot be underestimated. Prolonged mineral extraction has led to the destruction of surface vegetation, exacerbating soil erosion and degradation (Figure 1). These processes have reduced soil fertility and hinder vegetation recovery and growth (Chen et al., 2023). Furthermore, waste residues and effluents generated during mining operations have caused severe contamination of soil and water resources, posing threats to both the local ecosystem and public health (Feng et al., 2025). The resulting environmental degradation has also triggered a decline in biodiversity, disrupted ecological equilibrium, and destabilized the

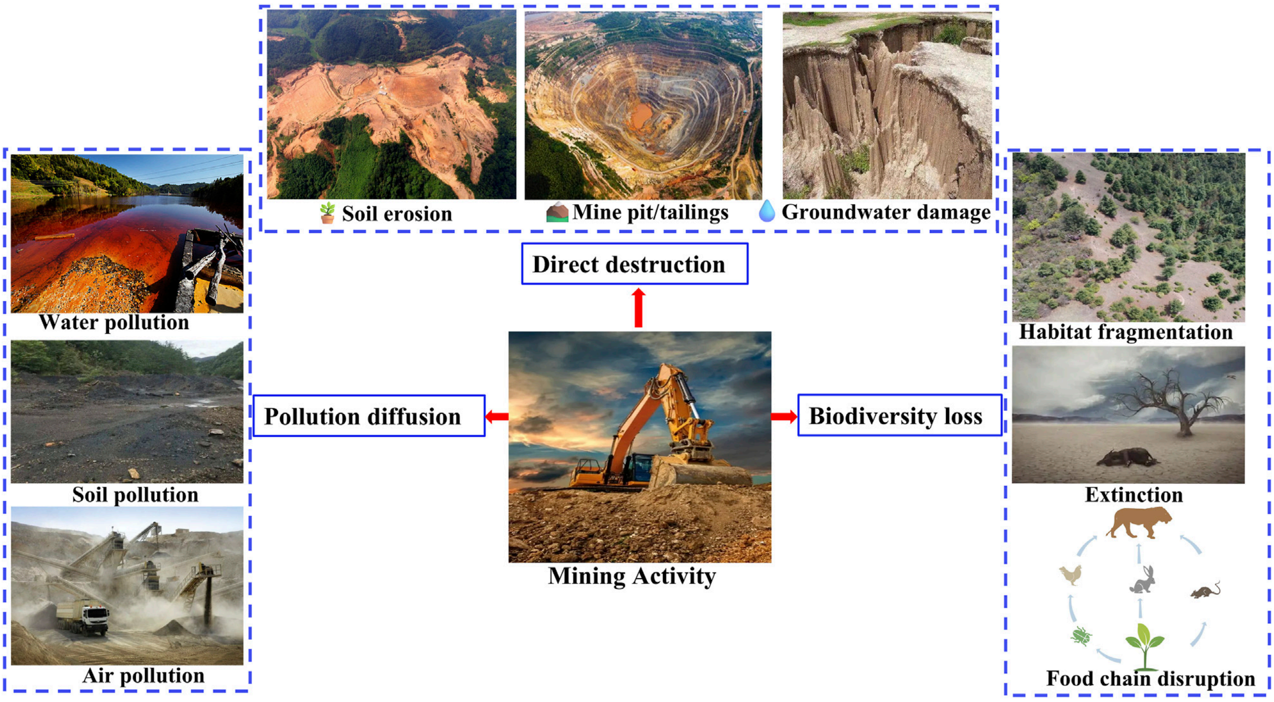

FIGURE 1
Impacts of mining activities on the ecological environment.

broader ecosystem (Chen et al., 2023). To mitigate these challenges, ecological restoration in mining areas is imperative. Effective strategies include vegetation rehabilitation, soil amelioration, water resource conservation, and heavy metal pollution remediation. These measures enhance environmental quality, conserve biodiversity, create sustainable economic opportunities, and ultimately advance the goals of ecological civilization and long-term sustainability (Feng et al., 2025). Given the severe ecological damage caused by mining activities, exploring effective ecological restoration strategies is imperative. Among these strategies, bryophytes offer unique advantages and potential, as detailed in the following sections.

Bryophytes act as pioneer species in ecological restoration, contributing to soil improvement and vegetation recovery through strong adaptability and tolerance to harsh environments. Although bryophytes possess a simple structure without true roots, stems, or leaves, these organisms thrive in harsh environments and are therefore regarded as pioneer species in vegetation restoration. Bryophytes demonstrate extraordinary vitality, capable of surviving in extreme environments such as barrenness, drought, and acidity. Additionally, these plants exhibit excellent soil-binding and water-retaining abilities, which effectively control soil erosion and improve soil structure (Cao et al., 2020). Unlike conventional methods (e.g., vascular plant seeding, chemical stabilization), bryophytes establish on degraded slopes without soil replacement/amendment, reducing long-term maintenance costs through minimized reseeding or chemical applications. Furthermore, bryophytes can absorb carbon dioxide and release oxygen through photosynthesis, improving air quality and creating favorable conditions for the growth of other organisms. Bryophytes assimilate atmospheric carbon dioxide via photosynthesis and convert it into organic carbon stored within biomass, thereby contributing to long-term carbon sequestration. This process holds substantial relevance for advancing China's "dual carbon" goals. Bryophytes regulate net carbon dioxide emissions via litter input, photosynthesis, and respiration (Elbert et al., 2012). For example, *Sphagnum* contributes more than half of the world's peat, accounting for 10%–15% of terrestrial carbon storage (Zhu, 2022). Therefore, bryophytes are ideal materials for ecological restoration and have shown great potential in the ecological restoration of mining areas.

In recent years, extensive research has been conducted globally on the application of bryophytes in ecological restoration of mining areas. Internationally, universities and research institutions have validated the efficacy of bryophytes under diverse environmental conditions through experimental studies. Notable examples include investigations in Ukraine (Lobachevska et al., 2019), Canada (Liu et al., 2024), Slovakia (Širka et al., 2018), the United States (Stern et al., 2016), Turkey (Karakaya et al., 2015), Portugal (Anawar et al., 2013), Poland (Rola and Osyczka, 2018), and Japan (Suzuki et al., 2016), which collectively highlight the adaptability of bryophytes in varying mining contexts. In China, significant advancements have also been achieved. For example, researchers from Sichuan University showed that bryophyte mats not only significantly reduced rainfall-induced heavy metal migration (particularly Cd and Cu) but also improved critical soil characteristics including pH regulation, cation exchange capacity, and bulk density optimization. These improvements further stimulated microbial community diversity and abundance in pyritic tailings (Lin K. K. et al., 2024). Investigations by research groups from Wuhan City and Guizhou Province characterized bryophyte assemblages in mining

TABLE 1 Morphological and structural characteristics of bryophytes.

Characteristic	Specific manifestation	Ecological significance
Morphological structure	Absence of vascular tissues, rhizoids composed of uniseriate cells (not unicellular)	Reduced metabolic consumption; adaptation to nutrient-poor substrates
Water metabolism	Direct water absorption through leaves, low transpiration rate (0.5–2.0 mmol m^{-2} s^{-1})	Drought tolerance, maintenance of microhabitat humidity
Reproductive strategy	High spore production (>10^6 per plant), regenerative capacity of vegetative propagules (<2 mm)	Rapid colonization, facilitation of community succession

areas through community architecture (Pengpeng et al., 2023; Han et al., 2022; Huang and Zhang, 2017; Ji and Zhang, 2015; Jiang and Zhang, 2012; Pan and Zhang, 2011), metallophyte adaptation (Pengpeng et al., 2023; Ma et al., 2023), life history strategies (Liao et al., 2024), and restoration ecology applications (Ren et al., 2021). Furthermore, scholars explored bryophyte community dynamics and artificial cultivation techniques in rare earth mining regions of southern Jiangxi Province, providing critical insights for region-specific restoration practices (Kong et al., 2023; Shen et al., 2022).

Despite the significant potential of bryophytes in ecological restoration of mining areas, practical application of bryophytes in ecological restoration faces persistent challenges. Key issues include the selection of species adapted to site-specific environmental conditions, optimization of planting techniques and management protocols, and the development of robust evaluation frameworks to assess restoration efficacy. These challenges demand immediate attention, as unresolved limitations may hinder the scalability and long-term success of bryophyte-based restoration strategies. Consequently, advancing research on the mechanistic roles of bryophytes and refining technical methodologies is critical for enhancing restoration technologies and accelerating ecological recovery. Through a systematic review and meta-analysis of global case studies, this work evaluated the practical viability of bryophytes in mining area restoration, aiming to bridge knowledge gaps and inform future scientific and engineering endeavors.

2 Biological characteristics and ecological functions of bryophytes

2.1 Morphological characteristics and adaptive traits

Bryophytes, classified as non-vascular plants, lack true roots and vascular tissues. The morphology is typically characterized by small stature, green leaf-like structures, and simple thalloid or foliose gametophytes, accompanied by distinct reproductive organs (Table 1). Reproduction occurs through sexual (spore dispersal) and asexual strategies (vegetative fragmentation, stem segment regeneration, and clonal colonization via specialized structures like gemmae) (Wang et al., 2022). Notably, bryophytes exhibit exceptional environmental adaptability, thriving under extreme conditions such as drought, low temperatures, nutrient-poor substrates, and limited light availability (Wang et al., 2022). Additionally, bryophytes demonstrate remarkable tolerance to abiotic stressors, including high salinity, acidic pH, and elevated heavy metal concentrations (Lin X. et al., 2024; Guan and Zhang, 2020). These adaptive traits underpin their ecological resilience in mining areas, where harsh environments (e.g., metal-contaminated soils, unstable substrates) necessitate robust survival mechanisms. Consequently, bryophytes serve as pivotal agents in mining area restoration by stabilizing substrates, enhancing microhabitat conditions, and facilitating secondary succession.

2.2 Role of bryophytes in ecological restoration in mining areas

Bryophytes play a pivotal role in ecological restoration within mining areas, particularly through capacity to rehabilitate degraded soils (Figure 2). During growth, bryophytes accumulate substantial organic matter, which enhances soil structure and fertility, thereby establishing a nutrient-rich foundation for subsequent vegetation recovery (Chun et al., 2021). The water absorption capability of bryophytes reduce soil moisture evaporation, improving water-holding capacity and creating optimal hydration conditions for plant regeneration (Chun et al., 2021). Furthermore, bryophytes secrete organic acids that chelate mineral ions, forming insoluble complexes. These complexes, combined with bryophyte detritus, facilitate the accumulation of soil organic matter, ultimately elevating nutrient availability and promoting vascular plant establishment (Feng et al., 2022). Empirical validation from the Shengli Coal Mine reclamation project in Inner Mongolia confirmed fundamental bryophyte-soil synergies, with statistical analyses demonstrating significant positive correlations between bryophyte colonization density and critical soil nutrient parameters including total nitrogen content and phosphorus availability across rehabilitation chrono sequences. Bryophyte distribution patterns further aligned with microscale improvements in organic matter stabilization and biogeochemical cycling efficiency, establishing these non-vascular plants as both biomarkers and active mediators of pedogenic recovery in post-mining ecosystems (Chun et al., 2021). Similarly, long-term studies on a potassium-magnesium salt tailings pond in Sweden revealed that natural succession over decades led to the formation of resilient biological soil crusts dominated by bryophytes, lichens, and cyanobacteria. These crusts demonstrated high tolerance to heavy metals (e.g., Cd, Pb) and effectively restored soil functionality by stabilizing substrates and enhancing microbial activity (Lobachevska et al., 2019). Complementary research by Ren et al. in manganese slag areas further highlighted the role of bryophytes in enriching bioavailable nutrients and diversifying soil microbial communities, which collectively primed the environment for vascular plant

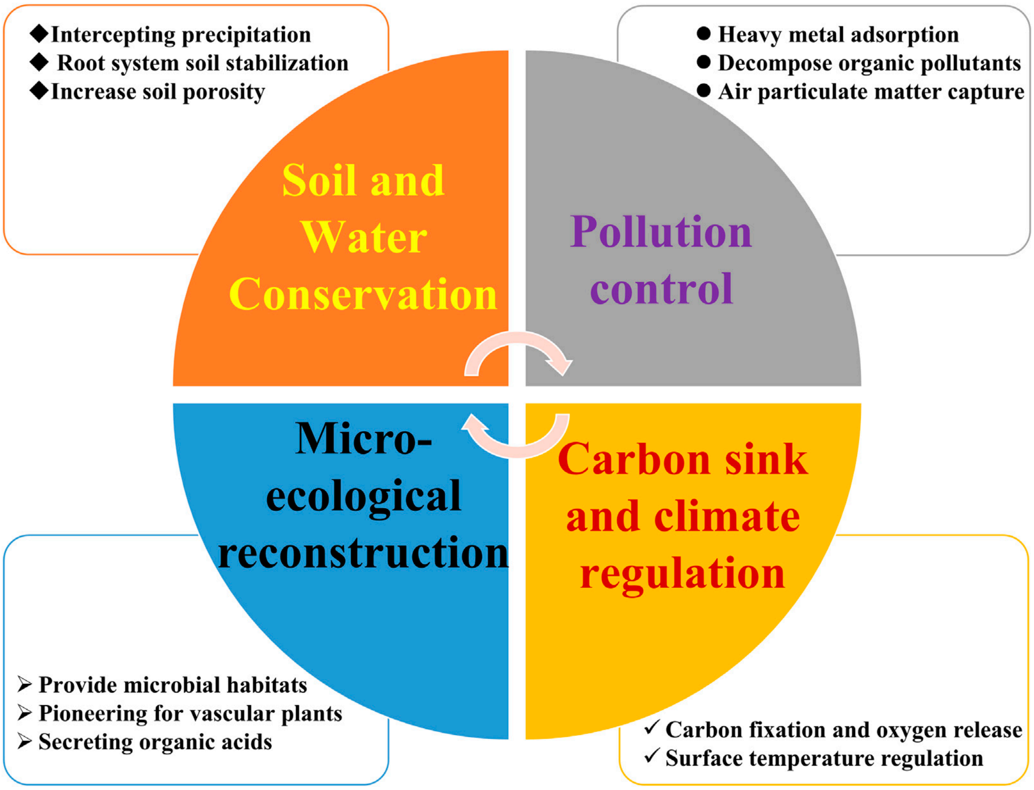

FIGURE 2
Ecological functions of bryophytes.

colonization (Ren et al., 2021). These findings underscore the pivotal role of bryophytes in initiating ecological succession, which is further explored in the following section on species screening.

As pioneer species in mining area restoration, bryophytes colonize exposed slag surfaces, creating foundational soil and moisture conditions for subsequent vegetation establishment (Chun et al., 2021). The collaborative interactions with algae, lichens, bacteria, and fungi drive the formation of biological soil crusts (BSCs). BSCs stabilize substrates, mitigate erosion, and shield emerging plant communities during early succession (Song et al., 2018). Beyond physical protection, bryophytes regulate soil microenvironments by modulating temperature fluctuations and enhancing moisture retention, thereby optimizing conditions for vascular plant recruitment (Gao et al., 2017). Field investigations in rare earth tailing ecosystems revealed the crucial ecological functions of bryophytes. Shen et al. recognized T*richostomum brachydontium*, *T. involutum*, *Anoectangium stracheyanum*, and *Brachymenium exile* as stress-adapted bryophyte species that can expedite revegetation via rapid substrate stabilization (Shen et al., 2022). Similarly, Širka et al. measured the contributions of bryophytes to biodiversity restoration in Central Slovakian mercury and copper slag heaps. Total of 83 and 76 bryophyte taxa were reported respectively. These bryophytes together increased species richness and promoted successional paths (Širka et al., 2018).

Bryophytes act as potent bioindicators in mining areas due to high heavy metal capability. Quantifying metal concentrations in bryophyte tissues (e.g., Cu, Pb, Cd) provides a reliable proxy for assessing soil pollution levels, with elevated values directly correlating to anthropogenic mining impacts (Ren et al., 2020). Moreover, changes in bryophyte communities, particularly increases in the number of species and their diversity, can be used to measure the success of ecological restoration. This is because a greater variety of species often indicates better habitat conditions (Feng et al., 2022). Field investigations in Wanshan mercury mining district in Guizhou Province demonstrated that mercury speciation analysis (total Hg and methyl-Hg concentrations) in seven bryophyte species effectively tracked atmospheric Hg pollution sources and quantified spatiotemporal dispersion gradients. This biomonitoring approach revealed distinct species-specific accumulation patterns correlated with industrial emission profiles and microclimatic deposition dynamics (Cao et al., 2016). Although lichens and bryophytes are well-known for indicating air quality, their potential for diagnosing soil pollution is not fully used. Notably, Rola and Osyczka documented that lichen-bryophyte consortia in southern Poland's Zn-Pb mining zones exhibited high sensitivity to soil metal gradients, enabling quantitative estimation of contamination severity (Rola and Osyczka, 2018). Similarly, in Turkey's Giresun sulfide deposits, *Rhabdoweisia crispata*, *Pohlia nutans*, and *Pohlia elongata* showed remarkable metal accumulation capabilities, which could be ascribed to the absence of cuticles and cation-exchangeable cell walls (Karakaya et al., 2015). Japanese researchers further identified *Scopelophila cataractae* as a dual Cu-As hyperaccumulator in aquatic systems

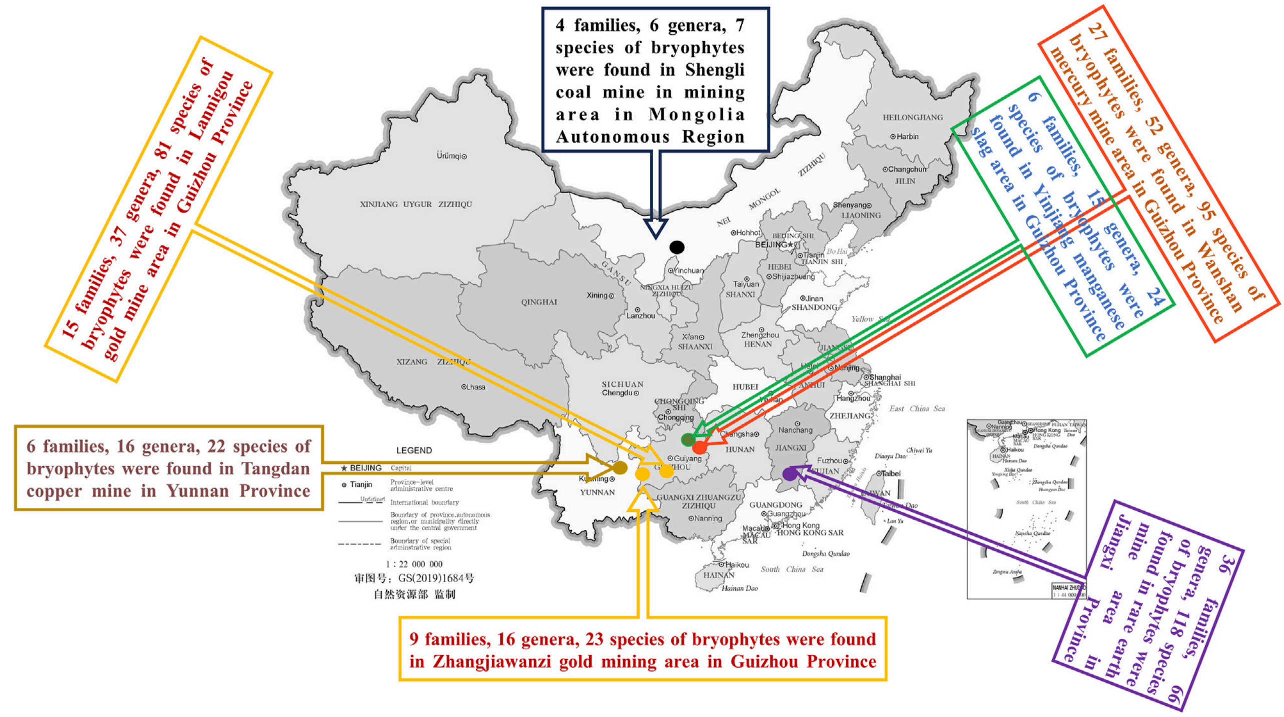

FIGURE 3
Distribution of bryophyte species in different types of mines in China.

TABLE 2 Comparison of species diversity and heavy metal enrichment characteristics of bryophytes in Chinese mining areas.

Mine type	Representative mine	Number of moss species	Dominant families	Heavy metal enrichment ability	Typical data source
Copper mine	Tangdan Copper Mine in Yunnan Province	22 species	*Pottiaceae*	68% of species inhabited patinated cupreous rocks and 32% cupreous soil	Zhou and Zhang (2007)
Gold mine	Guizhou Zhangjiawanzi Gold Mine	23 species	*Pottiaceae* and *Bryaceae*	Gymnostomum subrigidulum has a strong ability to enrich Cd, with an enrichment coefficient of 5.58 for Cd	Bing and Zhaohui (2008)
Mercury Mine	Guizhou Wanshan Mercury Mining Area	95 species	*Hypnaceae*, *Thuidiaceae* and *Brachytheciaceae*	With total mercury contents of 120–450 mg kg^{-1}, methylmercury contents of 0.8–3.2 mg kg^{-1}	(Pan and Zhang (2011), Cao et al. (2016)
Manganese Mine	Guizhou Yinjiang Manganese Slag Area	24 species	*Pottiaceae* and *Bryaceae*	Mn enrichment coefficient of 0.009–0.212, Cd enrichment coefficient of 0.754–5.360	Ren et al. (2021)
Rare Earth Mine	Jiangxi South rare earth ion-type mine	118 species	*Polytrichaceae*, *Dicranales*, *Fissidentales* and *Pottiales*	—	Kong et al. (2023), Cai et al. (2023)
Coal Mine	Inner Mongolia Shengli Coal Mine	7 species	*Ditrichaceae*, *Bryaceae*, *Funariaceae* and *Pottiaceae*	—	Feng et al. (2022)

near copper tailings, demonstrating bryophytes' niche-specific adaptation to polymetallic stress (Suzuki et al., 2016).

2.3 Distribution characteristics of bryophytes in mining areas of China

There are approximately 3,108 bryophyte species spanning 160 families and 632 genera in mining areas of China, demonstrating exceptional diversity and stress adaptation (Zhu et al., 2022). Recent research prioritizes the spatial heterogeneity and metal hyperaccumulation capacities, particularly regarding bioremediation mechanisms in post-mining ecosystems. Figure 3; Table 2 systematically presented the bryophyte species and the heavy metal enrichment characteristics in copper, gold, manganese, rare earth, and coal mining areas in China.

2.3.1 Copper mines

The Tangdan Copper Mine in Yunnan Province's metallogenic belt exemplified extreme edaphic constraints on bryophyte colonization, sustaining merely six families (e.g., *Pottiaceae*, *Mniaceae*) with 68% of observed species selectively inhabiting Cu-oxide encrustations rather than Cu-saturated soils. This niche partitioning showed specialized substrate optimization. Protonemal attachment and exocellular metal exclusion strategies allowed survival in Cu-rich environments (Zhou and Zhang, 2007).

2.3.2 Gold mines

The Zhangjiawanzi and Lanni Gou gold mines in Guizhou Province exhibited striking bryophyte community contrasts driven by microenvironmental heterogeneity. At Zhangjiawanzi, 23 species (16 genera, 9 families) demonstrated extreme oligotrophic adaptation. The families *Polytrichaceae* and *Bryaceae* were particularly dominant, indicating a preference for the nutrient-poor, acidic soils often found in gold mine environments. In contrast, the nearby Lanni Gou Gold Mine boasted a richer bryophyte community, with 81 species spread across 37 genera and 15 families, pointing to a greater ecological complexity and a higher level of biodiversity in this area (Bing and Zhaohui, 2008).

2.3.3 Mercury mines

The Wanshan Mercury Mine in Guizhou Province presented a striking contrast to typical mining environments, with a notable diversity of 95 bryophyte species spanning 52 genera and 27 families. This remarkable biodiversity might stem from the unique ecological niches formed by mercury extraction activities, which created heterogeneous microhabitats. A parallel example from Yunchangping Town, also in Guizhou Province, documented 62 bryophyte species over a 1-year period. These findings underscored the resilience and adaptability of bryophyte communities in heavily contaminated environments, suggesting high dynamic capacity to colonize and thrive under persistent heavy metal stress (Pan and Zhang, 2011).

2.3.4 Manganese mines

A 50-year-old manganese slag heap in Guizhou Province has developed into a distinct bryophyte refuge, supporting 20 taxa dominated by the structurally resilient families *Bryaceae* and *Polytrichaceae*. In the manganese slag area of Yinjiang County, 24 bryophyte species were found. *Gymnostomum subrigidulum*, *Pohlia gedeana*, and *Bryum atrovirens* were the most common, probably because they can tolerate high levels of metals. By contrast, the electrolytic manganese slag area in Songtao County hosted a depauperate bryophyte community of just six species, reflecting harsher edaphic or microclimatic conditions. Strikingly, *B. atrovirens* populations in both regions exhibit dual hyperaccumulation of manganese and cadmium. This remarkable ability of *B. atrovirens* to bind metals makes it a prime candidate for phytostabilization efforts in ecosystems contaminated with heavy metals (Ren et al., 2021).

2.3.5 Rare earth mines

In Jiangxi Province, ion-adsorption rare earth mines presented a unique ecological scenario where bryophyte biocrusts played a crucial role in shaping microbial community diversity and structure. Land-use intensity and anthropogenic disturbances strongly mediated bryophyte distribution patterns, with soil moisture regimes and substrate stability identified as key determinants of habitat suitability. Erect-growing forms were the most common in these groups, a trait that likely helps them retain moisture and stabilize soil in damaged areas. This ecological specialization positioned bryophytes as pivotal agents for post-mining revegetation, offering a natural template for restoring biogeochemical cycles in leached soils (Kong et al., 2023). Building on this, Cai et al. demonstrated that targeted bryophyte cultivation could accelerate ecosystem recovery pathways, leveraging dual role in microbial habitat provisioning and physical substrate rehabilitation (Cai et al., 2023).

2.3.6 Coal mines

In the semi-arid steppes of Inner Mongolia Autonomous Region, the Shengli Coal Mine was a key test site for studying how bryophytes adapt to post-industrial environments. Bryophyte assemblages here were tightly mediated by soil edaphic filters, particularly pH gradients and silt content, which served as deterministic forces structuring community composition. Only 7 bryophyte species were observed in the Shengli Coal Mine, likely due to aridity and alkaline soils limiting diversity. These findings revealed that the physical and chemical characteristics of the soil play a pivotal role in determining the species composition and distribution of bryophytes in coal mine environments (Feng et al., 2022).

Together, these studies delineated bryophytes as biodiversity hotspots within China's mining regions, showcasing not only wide biogeographic range but also evolutionarily refined heavy metal detoxification pathways. The capacity to dominate oligotrophic, metal-laden substrates underscored the dual ecological role as pioneers in primary succession and engineers of microhabitat amelioration. This dominance is further underpinned by critical interactions with soil microbiomes, including the secretion of organic acids (e.g., oxalate) for nutrient solubilization and metal bioavailability control, as well as stress-alleviating fungal symbioses that form nutrient-sharing networks analogous to mycorrhizae. Crucially, this functional resilience positioned bryophytes as keystone species for phytostabilization protocols and bioindicator frameworks. These distribution patterns further exemplify niche partitioning theory, with species like *B. atrovirens* (Mn-Cd hyperaccumulator) and *G. subrigidulum* occupying distinct ecological niches. Metal toxicity and edaphic filters shape these niches, driving community assembly through resource-use differentiation (Table 2).

3 Mine-adapted bryophytes screening

Screening aimed to identify bryophyte species with high adaptability to the harsh environmental conditions of mining areas, such as heavy metal contamination, soil erosion, and extreme pH levels. The selection of bryophyte species suitable for mining ecosystem rehabilitation was guided by a multi-criteria screening framework that integrates environmental tolerance, functional performance, and ecological benefits (Figure 4). The screening criteria encompassed five key parameters: (1) Tolerance to Heavy Metals, defined as the ability to survive and proliferate in soils contaminated with elevated concentrations of toxic elements, (2) Soil Adaptation, reflecting the capacity to establish in nutrient-poor substrates characterized by low organic matter and extreme pH ranges, (3) Drought Resistance, quantified through survival rates under prolonged water scarcity and post-dehydration recovery

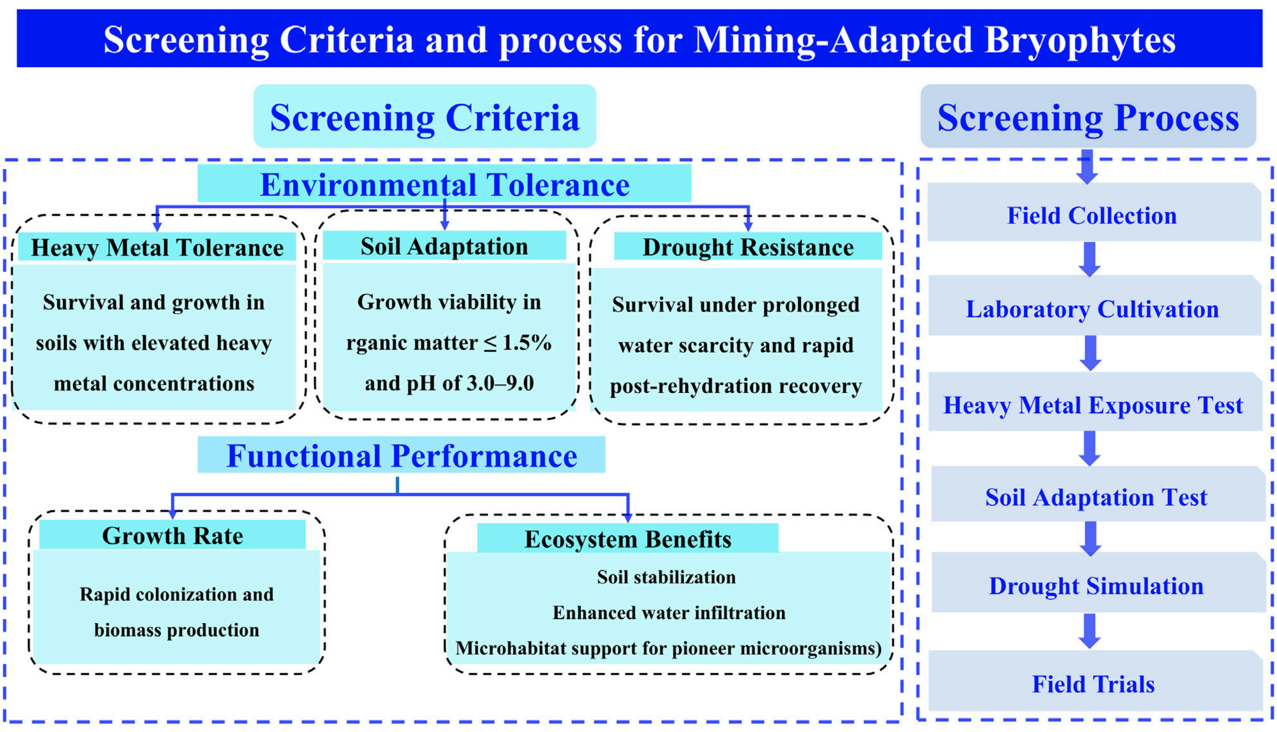

FIGURE 4
screening criteria and process for mining-adapted.

efficiency, (4) Growth Rate, prioritizing species with rapid colonization and high biomass accumulation, and (5) Ecosystem Benefits, including soil stabilization via rhizoid networks, enhanced water infiltration capacity, and facilitation of microbial symbionts.

The screening process followed a sequential experimental protocol (Figure 4). Initially, bryophyte samples were collected from naturally occurring populations in mining-impacted zones or analogous degraded ecosystems. These specimens underwent laboratory cultivation under controlled light, temperature, and humidity to assess baseline growth dynamics and stress resilience. Subsequent heavy metal exposure tests employed dose-response assays to evaluate metal tolerance thresholds and bioaccumulation potential. Concurrently, soil adaptation tests measure establishment successed in mining-derived substrates, with performance metrics including shoot elongation rate and biomass partitioning. Drought simulation experiments utilized osmotic stress gradients to quantify desiccation tolerance and rehydration recovery kinetics. Finally, candidate species demonstrating robust laboratory performance were subjected to field trials involving transplantation to target mining sites, where long-term viability, ecological integration, and functional efficacy were monitored over ≥2 growing seasons. This systematic approach ensured the identification of bryophyte species that align with site-specific rehabilitation goals while minimizing ecological risks.

Researchers systematically evaluated bryophyte species to identify candidates with high adaptability, rapid growth rates, and multifunctional ecological benefits for mining area restoration. Selected species exhibited exceptional survival rates and restoration efficacy under harsh mining conditions. Early research emphasized the pioneering role of bryophytes in ecological restoration, particularly the drought tolerance (xerophytic adaptation), resilience to nutrient-poor substrates, and prolific reproductive strategies, which collectively prime degraded sites for subsequent vegetation recovery (Sun et al., 2004; Zuo et al., 2006). For instance, Sun et al. assessed the feasibility of bryophyte-mediated restoration in Jiuzhaigou Valley's post-disaster landscapes, identifying key constraints (e.g., substrate instability) requiring mitigation in practical applications (Sun et al., 2004). Subsequent studies shifted focus to drought resistance screening. Through controlled drought simulations, Li et al. identified three hyper-tolerant bryophyte species (e.g., *Bryum argenteum*) in northern Hebei Province and optimized the cultivation protocols for slope stabilization (Li, 2017). Following the Jiuzhaigou earthquake, Xia et al. developed an Analytic Hierarchy Process (AHP)-based evaluation framework to prioritize bryophyte species for revegetating exposed slopes. Criteria included stress tolerance, propagule availability, ecological functionality, reproductive capacity, biomass yield, and aesthetic value. This approach selected five species—*Racomitrium japonicum*, *Hypnum plumaeforme*, *Eurohypnum leptothallum*, *Plagiomnium acutum*, and *Brachythecium rutabulum*—for targeted slope greening (Xia et al., 2023).

4 Cultivation of bryophytes

Figure 5 outlined a standardized *in vitro* protocol for bryophyte rapid propagation, integrating surface sterilization, hormone-

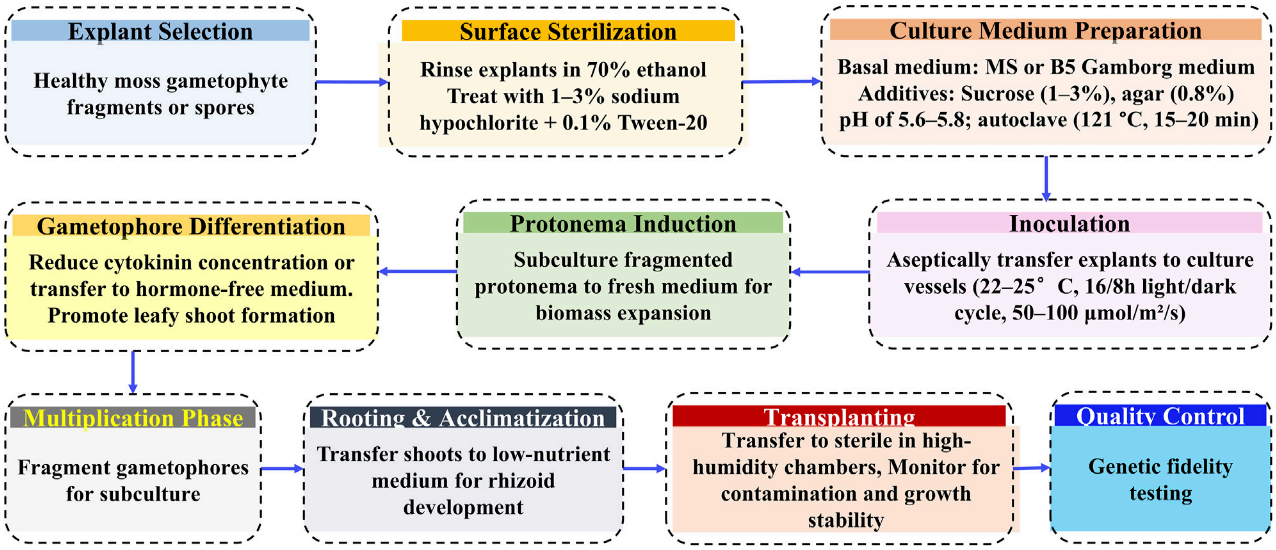

FIGURE 5
Rapid propagation scheme for bryophytes.

regulated differentiation, and cyclic subcultures to achieve high-efficiency biomass production while maintaining genetic uniformity and pathogen-free status. This optimized protocol enabled rapid clonal propagation of bryophyte species (e.g., *Physcomitrium* patens) through surface-sterilized gametophyte explants cultured on hormone-supplemented media (MS/B5) under controlled light and temperature. Protonema induction, cytokinin-mediated gametophore differentiation, and cyclic subcultures ensured scalable biomass production, followed by acclimatization on low-nutrient substrates. Genetic fidelity and contamination-free status were validated via molecular assays, supporting applications in research and ecological restoration.

Common methods for bryophyte cultivation include stem cutting propagation and tissue culture rapid propagation. Stem cutting propagation technology can rapidly propagate certain bryophyte species and adapt to artificial environmental control. For example, Chen et al. successfully identified the suitable environmental conditions and propagation factors for the feather bryophyte in artificial culture through stem cutting propagation experiments, providing an efficient rapid propagation method for stone slope greening and ecological restoration (Chen et al., 2022). Additionally, the application of tissue culture technology has made rapid propagation of bryophytes possible while ensuring the genetic stability of the seed sources (Zhang X. et al., 2023). Taking Yue's research as an example, rapid propagation of bryophytes was achieved by inducing callus formation, adventitious buds, and adventitious roots (Huanli, 2009). Huang et al. used four wild bryophyte species from a uranium tailings area as materials to explore the effects of different pH, temperature, cultivation substrates, and plant growth regulators on bryophyte growth and established the rapid propagation techniques for the grey bryophyte, large grey bryophyte, sharp-leafed creeping light bryophyte, and scale bryophyte (Huang et al., 2019). Although bryophyte cultivation techniques have made some progress, there are still some challenges. The application scalability of bryophytes is compromised by poikilohydric constraints, particularly slow biomass accrual rates and multi-year reproductive maturation periods, requiring targeted culturing innovations to overcome these physiological barriers. Spore propagation is greatly influenced by environmental factors, and its germination rate and survival rate are usually low. Moreover, bryophytes have strict requirements for the growth environment, necessitating precise control of light, water, temperature, and other conditions, which can lead to relatively high cultivation costs.

In recent years, important research achievements have been made in the field of bryophyte cultivation techniques. Studies indicate that bryophyte species possess different preferences for cultivation substrates. Common cultivation substrates like peat, perlite, and vermiculite demonstrate high compatibility with multiple bryophyte species. This was exemplified by a Canadian case study on lithium mine waste rock revegetation in Quebec, where bryophyte regeneration success rates showed significant variation depending on substrate composition and microenvironmental conditions (Liu et al., 2024). Meanwhile, special substrates such as volcanic rock and forest humus have a significant promotional effect on the growth of certain bryophyte species (Shi et al., 2022). Through proportional experiments with different substrates, researchers can select the most suitable ratio for the growth of specific bryophytes. For example, a volume ratio of peat to vermiculite of 2:1 is most beneficial for the growth of short-toothed bryophyte (Yu et al., 2024). In terms of environmental factors, light intensity is a key factor affecting bryophyte growth. Studies have shown that moderate shading helps the growth of certain bryophyte species (Fazan et al., 2022). Water and temperature are also limiting factors for bryophyte growth. Appropriate watering and a suitable temperature range can promote bryophyte growth, while excessive watering or extreme temperatures can inhibit bryophyte growth (Slate et al., 2024; Zhang Y. et al., 2023).

5 Application cases of bryophytes in mine ecological restoration

5.1 Application of bryophytes in ecological restoration of limestone mine slopes in northern Guangxi Province

Guangxi Province is one of China's representative regions for karst landscapes, rich in limestone resources. In the past, simple open-pit mining methods severely damaged the landforms and vegetation in mining areas, making ecological restoration research critical. Li conducted a case study at the Tieshan Quarry (Qixing District, Guilin City, Guangxi Province) to investigate bryophyte-based ecological restoration on limestone mine slopes. The mining area located in a subtropical monsoon climate zone with brown-gray limestone soil. Open-pit mining has damaged the land, vegetation, mountain structures, and rock and soil exposures. By integrating drone surveys with ground-based observations, a 3D terrain model was developed and six bryophyte species across five families and six genera were identified, with *Barbula unguiculata* as the dominant taxon. The study revealed that climatic temperature-humidity fluctuations critically regulate bryophyte colonization, while an optimized protocol combining crushed bark inoculation, Hoagland solution application, and intermittent misting achieved a coverage of 7.18% within 20 days, which was much higher than the control treatment (0.17%) (Li, 2023).

5.2 Application of bryophytes in semi-underground space ecological restoration of a 100-m deep mining pit

In karst areas, abandoned mining pits often have complex geological conditions due to post-mining changes like increased karstification and more fissures in rock walls. This makes it hard for plants to grow and difficult to redevelop the land. In the ecological restoration of Xinsheng Cement Plant's abandoned mining pit (Changsha City, Hunan Province), a novel rapid greening technology was developed using cold-tolerant bryophytes and biodegradable bio-glue for concrete and rock wall stabilization (Li et al., 2021). Through rigorous species screening, xerophytic mosses with 99.5% survival rates under high solar irradiance and drought stress were selected. This approach significantly accelerated plant community succession, transforming the degraded site into the "Joyful Paradise" landscape within 12 months. This ecological engineering approach created synergistic value chains where bryophyte-mediated slope stabilization enhanced biodiversity, which in turn attracted nature-based tourism while empowering local stakeholders through hands-on restoration workshops.

These applications operationalize ecological succession theory. Bryophytes act as early-successional engineers that accelerate trajectory shifts from degraded to functional states. Bryophyte restoration helps achieve UN Sustainable Development Goals by naturally repairing damaged land. Bryophytes act as pioneer species that form erosion-proof living crusts on degraded sites like mines, supporting SDG 15 for terrestrial ecosystems. These organisms capture carbon three to five times more effectively than regular plants, directly advancing climate action under SDG 13, with peat mosses alone locking away 10%–15% of the world's land-based carbon. Dense mats of bryophytes also filter toxic metals from runoff, protecting water quality for SDG 6. Unlike traditional methods that often need chemicals or repeated planting, bryophyte solutions eliminate pollution while cutting long-term costs. By creating self-sustaining microhabitats that boost biodiversity, bryophytes offer a practical nature-based path to meet global sustainability targets in challenging environments.

6 Conclusion

Bryophytes are emerging as pivotal agents in mining ecosystem restoration, bridging applied remediation needs with fundamental ecological research due to strong adaptability, soil-binding ability, and heavy metal enrichment capacity. While substantial progress has been made in laboratory settings, field implementation challenges persist, particularly regarding scaling propagation protocols and ensuring survivability in oligotrophic substrates or metal-contaminated environments. Notably, tolerant species immobilize contaminants through exclusion/detoxification mechanisms, enabling phytostabilization, whereas hyperaccumulators actively concentrate metals in harvestable tissues for phytoextraction, which requires distinct deployment strategies to avoid ecological risks. Moreover, overcoming key practical barriers, notably high propagation costs, slow growth rates, and the logistical complexity of large-scale deployment, remains critical for enhancing the scalability and economic feasibility of bryophyte-based restoration as a transformative ecological strategy. Future research should prioritize three interconnected fronts: 1) conducting long-term monitoring studies on bryophyte-based restoration projects, 2) exploring the combined use of bryophytes with other plant species for enhanced restoration outcomes, and 3) refining species-specific cultivation matrices through machine learning optimization, deciphering bryophyte-microbiome synergies governing metal (loid) sequestration, and mapping epigenetic adaptation pathways under climate fluctuation scenarios. These investigations will catalyze next-generation phytostabilization technologies while advancing ecological theory on pioneer species' roles in anthropogenic landscape rehabilitation.

Author contributions

ZQ: Conceptualization, Writing – original draft, Data curation, Methodology. XL: Formal Analysis, Writing – original draft. TZ: Writing – original draft, Methodology, Validation, Investigation. SL: Writing – review and editing, Conceptualization, Resources. CW: Writing – review and editing, Writing – original draft, Formal Analysis. WZ: Formal Analysis, Writing – review and editing. LL: Supervision, Writing – review and editing, Investigation, Project administration.

Funding

The author(s) declare that financial support was received for the research and/or publication of this article. This work was funded by the Open Project of Technology Innovation Center for Land Spatial Ecological Protection and Restoration in Great Lakes Basin, MNR, grant number No. JXCXZX2024007.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that Generative AI was used in the creation of this manuscript. Generative AI was used to grammar, spelling errors, etc.

Publisher's note

References

Anawar, H. M., Canha, N., Santa-Regina, I., and Freitas, M. C. (2013). Adaptation, tolerance, and evolution of plant species in a pyrite mine in response to contamination level and properties of mine tailings: sustainable rehabilitation. *J. Soils Sediments* 13, 730–741. doi:10.1007/s11368-012-0641-7

Bing, L., and Zhaohui, Z. (2008). Studies on the bryophytes and analysis of ecological restore potential in the lannigou gold deposit, Guizhou province. *J. Trop. Subtropical Bot.* 16, 511–515. doi:10.3969/j.issn.1005-3395.2008.6.2047

Cai, Q. Y., Li, B., Cai, M. T., Liu, Y. Z., Wu, L., and Ge, G. (2023). Diversity and distribution of bryophytes in ion-type rare Earth mines in southern Jiangxi province, southeast China, and the implications for vegetation restoration. *Plant Soil* 484, 79–94. doi:10.1007/s11104-022-05771-0

Cao, A., Ao, M., Liang, L., Xu, X., Qiu, G., and Chen, Z. (2016). Mercury concentration in epilithic mosses and its bio-indication of atmospheric Mercury pollution. *Huanjing Huaxue-Environmental Chem.* 35, 2204–2210. doi:10.7524/j.issn.0254-6108.2016.10.2016022505

Cao, W., Xiong, Y. X., Zhao, D. G., Tan, H. Y., and Qu, J. J. (2020). Bryophytes and the symbiotic microorganisms, the pioneers of vegetation restoration in karst rocky desertification areas in Southwestern China. *Appl. Microbiol. Biotechnol.* 104, 873–891. doi:10.1007/s00253-019-10235-0

Chen, J., Jiskani, I. M., and Li, G. (2023). Ecological restoration of coalmine-degraded lands: influence of plant species and revegetation on soil development. *Sustainability* 15, 13772. doi:10.3390/su151813772

Chen, X., Bu, C., Wang, C., Mo, Q., and Wang, H. (2022). Propagation by cutting stems of Brachythecium plumosum and its growth factors. *J. Central South Univ. For.* 42, 117–126. doi:10.14067/j.cnki.1673-923x.2022.06.013

Chun, F., Yu, S., Zhang, W., and Sai, X. (2021). Variability of aboveground biomass and interspecific compensatory effect of grassland communities in baiyinhua mining Area,Inner Mogolia,China. *Acta Agrestia Sin.* 29, 1533–1539. doi:10.11733/j.issn.1007-0435.2021.07.020

Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andreae, M. O., et al. (2012). Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nat. Geosci.* 5, 459–462. doi:10.1038/ngeo1486

Fazan, L., Gwiazdowicz, D. J., Fragniere, Y., Faltynowicz, W., Ghosn, D., Remoundou, I., et al. (2022). Factors influencing the diversity and distribution of epiphytic lichens and bryophytes on the relict tree *Zelkova abelicea* (lam.) boiss. (*ulmaceae*). *Lichenologist* 54, 195–212. doi:10.1017/s0024282922000159

Feng, C., Gan, Y., He, X., Lei, S., Cheng, W., Huang, J., et al. (2022). Bryophyte diversity of a grassland mining area and its relationship with soil physical and chemical properties. *J. East China Normal Univ. Nat. Sci.*, 76–84. doi:10.3969/j.issn.1000-5641.2022.01.010

Feng, S., Li, Z., Zhang, C., Qi, R., and Yang, L. (2025). Ecological restoration in high-altitude mining areas: evaluation soil reconstruction and vegetation recovery in the jiangcang coal mining area on the Qinghai-Tibet Plateau. *Front. Environ. Sci.* 12, 1538243. doi:10.3389/fenvs.2024.1538243

Gao, Y., Ding, C., Ren, D., and Bai, X. (2017). Impacts of ree's enrichment on growth and anatomy of eight common mosses from baiyun obo. *Acta Bot. Boreali-Occidentalia Sin.* 37, 23–31. doi:10.7606/j.issn.1000-4025.2017.01.0023

Guan, Q., and Zhang, R. (2020). Study on the arsenic release characteristics of bryophytes in acid high-arsenic coal mine. *Environ. Sci. Technol.* 43, 6–10. doi:10.19672/j.cnki.1003-6504.2020.04.002

Han, J.-H., Wang, Z.-H., and Zhang, Z.-H. (2022). Moss biomonitors for heavy metal pollution in soils of manganese carbonate mine across ecological succession stages. 67, 83–92.

Huang, H., and Zhang, Z.-H. (2017). Diversity characteristics of bryophytes in different succession stages on the karst bauxite tailing piles. *Plant Sci. J.* 35, 807–814. doi:10.11913/psj.2095-0837.2017.60807

Huang, Q., Luo, X., Tang, W., Zhao, J., and Liang, Z. (2019). Effects of different cultivation substrates on the growth of three bryophytes. *Guangdong Agric. Sci.* 46, 56–62. doi:10.16768/j.issn.1004-874X.2019.09.008

Huanli, Y. (2009). *The investigation in application and selection of bryophyte to roadside ecological restoration*. Beijing: Beijing Forestry University.

Ji, Y., and Zhang, Z. (2015). Biodiversity of bryophytes and their characteristics of ecological distribution in the second lindai karst bauxite area. *Carsologica Sin.* 34, 599–606. doi:10.11932/karst20150609

Jiang, H., and Zhang, Z. (2012). Comparative study on bryophytes between laterite gold deposit southwest Guizhou and Tuobuka-boka gold mine in Yunnan province. *Guangdong Agric. Sci.* 39, 179–182. doi:10.16768/j.issn.1004-874x.2012.23.003

Karakaya, M. Ç., Karakaya, N., Küpeli, Ş., Karadağ, M. M., and Kırmacı, M. (2015). Potential bioaccumulator mosses around massive sulfide deposits in the vicinity of the Giresun area. *Northeast Turk.* 43, 27–37. doi:10.1002/clen.201200651

Kong, Z., Zhong, H., Jin, X., Cai, Q., Zou, Z., Ge, G., et al. (2023). Linking microbial community structure to function underneath moss-dominated biocrusts in rare Earth elements mine areas under a subtropical climate. *Land Degrad. and Dev.* 34, 4057–4069. doi:10.1002/ldr.4737

Li, J., He, C., and Zeng, B. (2021). Research on ecological restoration and utilization technology of semi-underground space in 100-meter mine pit. *Constr. Technol.* 50, 20–22. doi:10.7672/sgjs2021020020

Li, S. (2023). *Application of bryophytes in the ecological restoration of limestone mine slopes in northern guilin-tie Shan quarry in guilin as an example*. Guilin City: Guilin University of Technology.

Li, T. (2017). *Study on the selection of bryophytes for side-slope rehabilitation in northern Hebei Province*. Beijing: Beijing Forestry University.

Liao, K., Tao, Y., Zeng, Y., Tu, J., She, S., Fu, Y., et al. (2024). A feasible method of induced biological soil crust propagation through the inoculation of moss and addition of soil amendments in a Pb-Zn tailing pond. *Sci. Total Environ.* 910, 168569. doi:10.1016/j.scitotenv.2023.168569

Lin, K. K., Jian, J. N., Zhang, Y. M., Liu, Y. K., Li, S. Y., Zhao, Y., et al. (2024a). Study on plant-blanket to reduce heavy metal migration caused by precipitation and to improve the soil environment of pyritic tailings. *Sci. Total Environ.* 939, 173376. doi:10.1016/j.scitotenv.2024.173376

Lin, X., Zhuo, Y., Liu, L., Shi, X., and Zhuo, L. (2024b). Membrane stability of the desert moss Syntrichia caninervis mitt. During NaCl stress. *Acta Ecol. Sin.* 44, 3483–3491. doi:10.20103/j.stxb.202306161284

Liu, C., Pouliot, K., Roy, S., and Rochefort, L. (2024). Moss regeneration for lithium mine waste rock revegetation in Québec, Canada. *Botany* 102, 26–40. doi:10.1139/cjb-2023-0110

Lobachevska, O. V., Kyyak, N. Y., and Rabyk, I. V. (2019). Ecological and physiological peculiarities of bryophytes on a post-technogenic salinized territory. *Biosyst. Divers.* 27, 342–348. doi:10.15421/011945

Ma, Y., Zhang, Z., and Wang, Z. (2023). Response of mosses and their rhizobial bacterial communities to heavy metal pollution in manganese mining areas of south China. *Water, Air, and Soil Pollut.* 235, 28. doi:10.1007/s11270-023-06834-3

Pan, S., and Zhang, Z.-H. (2011). Bryophyte communities from abandoned mercury mine in eastern Guizhou province. *Bull. Botanical Res.* 31, 241–248. doi:10.7525/j.issn. 1673-5102.2011.02.020

Pengpeng, C., Zhihui, W., and Zhaohui, Z. (2023). Dynamic characteristics of soil heavy metals and microbial communities under moss cover at different successional stages in a manganese mining area. *Environ. Geochem. Health* 45, 7711–7726. doi:10. 1007/s10653-023-01681-x

Ren, J., Liu, F., Luo, Y., Zhu, J., Luo, X., and Liu, R. (2021). The pioneering role of bryophytes in ecological restoration of manganese waste residue areas. *Southwest. China* 2021, 9969253. doi:10.1155/2021/9969253

Ren, J., Liu, F., Zhu, J., Luo, Y., Li, S., and Zhong, X. (2020). Diversity of the bryophytes and heavy metal pollution monitoring in manganese ore waste area. *J. Saf. Environ.* 20, 2398–2407. doi:10.13637/j.issn.1009-6094.2019.1335

Rola, K., and Osyczka, P. (2018). Cryptogamic communities as a useful bioindication tool for estimating the degree of soil pollution with heavy metals. *Ecol. Indic.* 88, 454–464. doi:10.1016/j.ecolind.2018.01.013

Shen, F., Zheng, T., Duan, J., Hu, R., and Yu, R. (2022). Feasibility on artificial cultivation of bryophytes in rare Earth tailings in southern Jiangxi. *Sci. Soil Water Conservation* 20, 136–144. doi:10.16843/j.sswc.2022.04.017

Shi, B., Wang, X., Chen, H., and Yang, S. (2022). Growth and physiological responses of Plagiomnium acutum to different cultivation substrates. *Acta Bot. Boreali-Occidentalia Sin.* 42, 1208–1218. doi:10.7606/j.issn.1000-4025.2022.07.1208

Širka, P., Bittnerová, S., and Turisová, I. (2018). Succession pattern at two mineralogically different spoil heaps in central Slovakia. *Biologia* 73, 809–820. doi:10.2478/s11756-018-0095-5

Slate, M. L., Antoninka, A., Bailey, L., Berdugo, M. B., Callaghan, D. A., Cárdenas, M., et al. (2024). Impact of changing climate on bryophyte contributions to terrestrial water, carbon, and nitrogen cycles. *New Phytol.* 242, 2411–2429. doi:10.1111/nph.19772

Song, L., Bai, Z., Fan, X., Sun, P., and Wei, Y. (2018). Effect of biological soil crust on photographically measured value of vegetation coverage. *Acta Ecol. Sin.* 38, 1272–1283. doi:10.5846/stxb201612312723

Stern, M., Medeiros, I. D., Negoita, L., and Rajakaruna, N. (2016). Limestone flora of the simonton corner quarry preserve, rockport, Maine, USA. *Rhodora* 118, 206–226. doi:10.3119/15-23

Sun, J., Chen, Q., Wang, Y., and Yang, J. (2004). Application of bryophytes in vegetation restoration project of jiuzhaigou valley scenic and historic interest area scenic spot.

Suzuki, Y., Takenaka, C., Tomioka, R., Tsubota, H., Takasaki, Y., and Umemura, T. (2016). Accumulation of arsenic and copper by bryophytes growing in an aquatic environment near copper mine tailings. *Mine Water Environ.* 35, 265–272. doi:10.1007/ s10230-015-0335-7

Wang, Y., Zheng, J., and Peng, X. (2022). A review on ecological functions of bryophytes in extreme environments. *Plant Physiology J.* 58, 101–108. doi:10.13592/ j.cnki.ppj.2021.0223

Xia, H., Liu, L., Zhou, X., Chen, K., Li, Y., Kuang, P., et al. (2023). Selection of suitable mosses for bare rock and steep slope greening after jiuzhaigou earthquake based on the analytic hierarchy process. *Bull. Botanical Res.* 43, 540–549. doi:10.7525/j.issn.1673-5102.2023.04.007

Yu, W., He, X., Lei, S., Kou, J., and Feng, C. (2024). Effects of different substrate compositions and concentrations on the growth of didymodon tectorus. *J. Nanjing For. Univ. Nat. Sci. Ed.* 48, 184–190. doi:10.12302/j.issn.1000-2006.202207003

Zhang, X., Yu, W., Xue, Y., Hu, D., and Feng, C. (2023a). Tissue culture of seven typical xerophytic mosses. *J. North-East For. Univ.* 51, 23–28. doi:10.13759/j.cnki.dlxb. 2023.08.008

Zhang, Y., He, N., and Liu, Y. (2023b). Temperature factors are a primary driver of the forest bryophyte diversity and distribution in the southeast Qinghai-Tibet Plateau. *For. Ecol. Manag.* 527, 120610. doi:10.1016/j.foreco.2022.120610

Zhou, L., and Zhang, Z. (2007). Bryophytes in tangdan copper mine site in Yunnan province. *J. Trop. Subtropical Bot.* 15, 82–85. doi:10.3969/j.issn.1005-3395.2007.01.014

Zhu, R. (2022). Peat mosses (sphagnum): ecologically, economically, and scientifically important group of carbon sequestration plants. *Chin. Bull. Bot.* 57, 559–578. doi:10. 11983/CBB22031

Zhu, R., Ma, X., Cao, C., and Cao, Z. (2022). Advances in research on bryophyte diversity in China. *Biodivers. Sci.* 30, 22378. doi:10.17520/biods.2022378

Zuo, Y., Gu, B., and Ai, Y. (2006). Investigation of application of bryophyte to road side ecological restoration. *Sci. Soil Water Conservation* 4, 122–125. doi:10.16843/j.sswc. 2006.s1.028