



Microbial Community Diversity Dynamics in Acid Mine Drainage and Acid Mine Drainage-Polluted Soils: Implication on Mining Water Irrigation Agricultural Sustainability

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Environmental degradation related to mining-generated acid mine drainage (AMD) is a major global concern, contaminating surface and groundwater sources, including agricultural land. In the last two decades, many developing countries are expanding agricultural productivity in mine-impacted soils to meet food demand for their rapidly growing population. Further, the practice of AMD water (treated or untreated) irrigated agriculture is on the increase, particularly in water-stressed nations around the world. For sustainable agricultural production systems, optimal microbial diversity, and functioning is critical for soil health and plant productivity. Thus, this review presents up-to-date knowledge on the microbial structure and functional dynamics of AMD habitats and AMD-impacted agricultural soils. The long-term effects of AMD water such as soil acidification, heavy metals (HM), iron and sulfate pollution, greatly reduces microbial biomass, richness, and diversity, impairing soil health plant growth and productivity, and impacts food safety negatively. Despite these drawbacks, AMD-impacted habitats are unique ecological niches for novel acidophilic, HM, and sulfate-adapted microbial phylotypes that might be beneficial to optimal plant growth and productivity and bioremediation of polluted agricultural soils. This review has also highlighted the impact active and passive treatment technologies on AMD microbial diversity, further extending the discussion on the interrelated microbial diversity, and beneficial functions such as metal bioremediation, acidity neutralization, symbiotic rhizomicrobiome assembly, and plant growth promotion, sulfates/iron reduction, and biogeochemical N and C recycling under AMD-impacted environment. The significance of sulfur-reducing bacteria (SRB), iron-oxidizing bacteria (FeOB), and plant growth promoting rhizobacteria (PGPRs) as key players in many passive and active systems dedicated to bioremediation and microbe-assisted phytoremediation is also elucidated

and discussed. Finally, new perspectives on the need for future studies, integrating meta-omics and process engineering on AMD-impacted microbiomes, key to designing and optimizing of robust active and passive bioremediation of AMD-water before application to agricultural production is proposed.

Keywords: acid mine drainage, heavy metal bioremediation, active and passive technologies, plant growth promoting rhizobacteria, sulfate-reducing bacteria, agricultural sustainability

INTRODUCTION

Globally, large-scale commercial mining operations and other related industries generate various waste streams, that constitute one of the major anthropogenic sources of environmental pollution. Mining is associated with significant production of large volumes of toxic acidic water with elevated heavy metals (HM) and sulfates known as acid mine drainage (AMD) (Rambabu et al., 2020). Acid mine drainage has become a serious global issue in recent times owing to its hazardous impact on the environment and living organisms (Kefeni et al., 2017; Grande et al., 2018; Steyn et al., 2019; Rezaie and Anderson, 2020). In the mining regions of Australia (Lei et al., 2010), Brazil (Galhardi and Bonotto, 2016), Canada (Sracek et al., 2004), England, Wales, Spain, Norway (Hallberg, 2010; Romero et al., 2011), Morocco (Boularbah et al., 2006), South Africa (Ochieng et al., 2010), China (Wu et al., 2009; Wang et al., 2021b), and United States of America (Blowes et al., 2005; Acharya and Kharel, 2020) concern over AMD pollution has been reported, with inactive and abandoned mines generating huge quantities of AMD that contaminates both terrestrial and aquatic systems including agricultural soils, ground-, and surface-water sources (Rezaie and Anderson, 2020). The negative effects of phytotoxicity-related AMD acidity and HM contamination of agricultural soil and crops have been documented (Netto et al., 2013; Liao et al., 2016), the HM entering the food chain through the food crop uptake posing a potential health risk to human population (Kumar et al., 2020; Massányi et al., 2020).

With an increased public health concern and ecological awareness, stricter legislative control on mine water/waste management and remediation strategies are being implemented in many countries to counter the environmental hazards posed by AMD. Furthermore, the increased interest in the beneficial use of mine-impacted water for irrigation, especially in water-stressed regions in the world, imply remediation to meet the set water quality regulatory standard is key for long term sustainable application of the AMD wastewater in agricultural production (Annandale et al., 2006). Toward this, various treatment methods that cut across active and passive treatment methods have been adopted by many countries in the treatment of AMD. These range from conventional active treatment methods employing various physical and chemical approaches such as neutralization, adsorption, ion exchange, membrane technology, and electrochemical approaches. The active treatment of AMD is based on the principle of increasing the pH to precipitation of HM and sulfates before discharging into environment. In contrast, passive treatment involves biological treatment under

natural or constructed wetlands through the aid of both plants, aerobic and anaerobic microorganisms, algae strains, and other macroorganisms (Bwapwa et al., 2017; Park et al., 2019; Rambabu et al., 2020) to accelerate conversion HM and sulfates to an acceptable form with least or null environmental impact.

Detailed reports of AMD origin and different processes contributing to AMD generation, including the role of iron- and/or sulfur-oxidizing microbes are available in literature (Baker and Banfield, 2003; Hallberg, 2010; Chen et al., 2016). In many AMD sites, oxidation is primarily catalyzed by naturally occurring bacteria called *Acidithiobacillus ferrooxidans* (Chen et al., 2015; Mesa et al., 2017; Bomberg et al., 2019; Wang et al., 2019b) and these bacteria accelerate the oxidation reactions for sulfides of most HM (Akcil and Koldas, 2006). According to Edwards et al. (2000), about 75% of AMD produced results from microbial activity. Under the extremophilic AMD environment, acidophilic microbial communities belonging to Bacteria, Archaea, and Eukarya domains dominates, with members of phylum Proteobacteria, Nitrospira, Actinobacteria, Firmicutes, and Acidobacteria being the dominant bacterial taxa (Mesa et al., 2017; Lukhele et al., 2019; Distaso et al., 2020), as well as iron/sulfur-oxidizing microbes such *Leptospirillum ferrooxidans*, *Ferroplasma*, *Acidithiobacillus* occurring in an environmentally dependent biogeographic pattern (Kuang et al., 2013, 2016; Wang et al., 2019b). In addition, a large number of rare taxa constituting a “rare biosphere” in the microbial community that may perform crucial function in AMD ecosystems have been reported (Luo et al., 2020b). Collectively, AMD environments are unique ecological niches with significantly reduced species richness and diversity, but enriched with sulfate-, acid-, and toxic-metals-adapted microorganisms. However, remediation treatments of AMD targeting increasing pH, HM, and sulfate removal is associated with shifts in microbial diversity and structure from acidophilic microbial communities to a more metabolically diverse set of taxa and from a less sulfur-reducing bacteria (SRB) to a more SRB.

In the last few decades significant efforts have been made to increase agricultural productivity to meet food security for the ever increasing global population. In water stressed mining nations, where the pressures on agricultural lands and water resources are extremely great amid rapid population growth, the use of AMD water and AMD-affected streams for irrigated agriculture and expansion of agriculture on mining impacted land is common (Jovanovic et al., 1998; Lin et al., 2005; Vicente-Beckett et al., 2016; Musvoto and de Lange, 2019). This implies that the application of AMD water for irrigated agriculture have the potential to alter the soil microbiome which could negatively

impact soil health, plant growth and productivity of the crops. This review provides an overview of the microbial community structure and diversity of AMD wastewater, highlighting the potential positive and negative roles associated microbiome may play under AMD-irrigated agricultural production. Furthermore, the understanding of the enriched microbial groups in the treated AMD that could give an insight into their roles and potential application in the bioremediation of polluted agricultural land and possibly enhance sustainable agricultural productivity are discussed.

ENVIRONMENTAL AND HEALTH IMPACTS OF AMD POLLUTION

Acid mine drainage (AMD) is a global environmental issue negatively impacting many mining-associated ecological system, including prokaryotic and eukaryotic life. From the standpoint of global food security, mining activities, and its associated AMD pollution is causing massive disturbances of aquatic resources and land-use changes that are significantly altering agricultural productivity and food quality (Choudhury et al., 2017). Generally, AMD threat to ecological systems, agricultural land, and human health is attributable to its high acidity and non-biodegradable HM contamination in living organisms and food chains. For example, small-scale mining site in Ghana caused Pb, Hg, Cd, and K pollution of rivers used in crop irrigations (Nukpezah et al., 2017). In Portugal, AMD contributes to higher levels of SO_4^{2-} , Fe, Al, as well as Cu, Pb, Zn, Cd, and As pollution of irrigation water sources in Lousal area (Luís et al., 2009). Downstream water sources and agricultural land laden with high concentration of Pb, Cu, and Zn as impacted by AMD has also been reported in China (Wu et al., 2009; Cao et al., 2019; Luo et al., 2020a), India (Sahoo et al., 2017; Mohanty et al., 2018; Dutta et al., 2020), and USA (Acharya and Kharel, 2020).

Acid mine drainage also severely affects aquatic and terrestrial life ecosystem. Specifically, contaminations of the aquatic systems by HM can stimulate the production of reactive oxygen species (ROS) that can damage fishes, aquatic macroinvertebrates, and other organisms (Jennings et al., 2008; Gomez Isaza et al., 2020). Furthermore, acidification affects the structure and functioning of ecosystems (Carlson, 2013; Bonilla et al., 2018; Simate, 2021). Bioaccumulation and biotransformation of toxic HM and metalloids (e.g., As, Pb, Cr, Cd, and Hg) along the food chains that may constitute a serious public health risk associated with AMD pollution have also been reported in literature (Emmanuel et al., 2018; Darko et al., 2019; Gwenzi, 2020; Chan et al., 2021; Yang et al., 2021). The main effects of HM on human health range from bronchitis, skin and bladder cancer, liver and kidney failure, to mental retardation in children (Rambabu et al., 2020).

In the latter subsections, we focus on the prokaryotic structure and functioning providing a comprehensive assessment of the main implications and challenges of using untreated AMD wastewater for irrigated agricultural production. The discussion is further extended to the impact of active and passive treatment systems on the microbial community composition and function

that may beneficial in the use AMD wastewater for agricultural production and bioremediation.

MICROBIAL COMMUNITY DIVERSITY UNDER AMD HABITATS

In the last three decades, advances in 16S rRNA gene and metagenomics based molecular analyses in combination with culture-dependent approaches has drastically enlarged knowledge on the microbial diversity and functioning of AMD microenvironments as shaped by environmental factors such as very low pH, high concentrations of dissolved HM and other solutes, low total organic carbon (TOC), and dissolved oxygen (DO). There are excellent articles that has thoroughly reviewed AMD ecosystems as extreme habitats that provides multiple niches for distinct bacterial, archaeal, and eukaryotic microbiomes (Baker and Banfield, 2003; Méndez-García et al., 2015; Chen et al., 2016; Mesa et al., 2017; Lukhele et al., 2020). In these reports, the dominance of members of Eukarya domain, including fungal and algal taxa has been reported in diverse AMD sites across the globe (Baker et al., 2009). For example, members of *Stramenopiles*, *Alveolata*, *Rhizaria*, and *Opisthokonta* was also observed as the dominating microbes in abandoned mercury mine at Los Ruedos (NW Spain) (Mesa et al., 2017). *Acidea extrema*, *Acidiella bohémica*, *Acidiella uranophila*, *Acidomyces acidophilus*, *Acidomyces acidothermus*, *Acidothrix acidophila*, *Coniochaeta fodinicola*, *Hortaea acidophila*, and *Soosiella minima* are fungal species has reported to be enriched in acidic habitat (Selbmann et al., 2008; Vázquez-Campos et al., 2014). Most recently, Kalu et al. (2021) revealed Ascomycota and Basidiomycota as the dominant phyla in two gold mining sites in Gauteng Province of South Africa using high-throughput sequencing technology. Prasanna et al. (2011) also reported the enrichment of AMD with algal communities such as *Euglena* sp. and *Ulothrix* sp. as well as unicellular microalgae such as *Chlorella*, *Cylindrocystis*, *Botryococcus*, and *Navicula* and several filamentous forms identified as *Microspora*, *Cladophora*, and *Binuclearia*. These studies indicates that diversity of organisms within the Eukarya domain is dependent on the AMD from different mining sites.

Similarly, different studies have unveiled the diversity of bacterial and archaeal communities that are enriched in AMD sites. Collated information of the bacterial communities dominating diverse AMD polluted environment show that Proteobacteria, Nitrospirae, Acidobacteria, Chloroflexi, and Actinobacteria are the dominant phyla (Kuang et al., 2013; Méndez-García et al., 2015; Lukhele et al., 2019; Wang et al., 2019b). Among the key dominant bacteria taxa, acidophilic proteobacterial taxa such as *Acidithiobacillus* spp, *Leptospirillum* spp., *Acidiphilum* spp., and *Ferroplasma* spp, play important role chemolithotrophic metabolism of iron and sulfur under AMD environment (Kuang et al., 2013; Méndez-García et al., 2015; Wang et al., 2019b). However, there is evidence of uniqueness of the mines with respect to the bacterial diversities and functioning capabilities of autochthonous taxa related to biogeochemical recycling of iron, sulfur, nitrogen, carbon, and oxygen. In Yunfu sulfide mine in

Guangdong province, China, Nitrospira, Alphaproteobacteria, Betaproteobacteria, and Gammaproteobacteria bacterial families as well as *Acidithiobacillus* and *Gallionella* genera were identified as the major dominating bacterial communities (He et al., 2007). *Acidiphilium* spp. in pyrite mine tailings and AMD lake in Anhui Province, China (Hao et al., 2010; Xin et al., 2021), Proteobacteria, Firmicutes, and Planctomycetes including *Marinobacteria* spp. and *Anabaena* spp. in deep mines, tailings and mine-water from AMD dams in South Africa (Keshri et al., 2015; Lukhele et al., 2019; Sibanda et al., 2021). Novel species belonging to *Leptospirillum* spp., *Acidiphilium* spp., *Acidithiobacillus* spp., and *Ferrovum* spp., including other members of Alphaproteobacteria, Euryarchaeota, Gammaproteobacteria, and Nitrospira in AMD sites across Southeast China has been reported (Kuang et al., 2013, 2016). The dominance of *Acidithiobacillus ferrivorans*, Acidobacteria, Actinobacteria, and Chloroflexi in Svalbard (García-Moyano et al., 2015). In contrast, members of phylum Crenarchaeota and Thaumarchaeota are the important archaeal taxa with Thermoplasmatales and *Ferroplasma* playing key roles in metabolism and element cycling in a number of AMD systems. For example, Thermoplasmatales dominates AMD from Dabaoshan Mine (Guangdong Province, China) (Lu et al., 2010). Ditaso et al. (2020) and Korzhenkov et al. (2019) also recently reported higher representation of archaea Thermoplasmatales across all depths in oxic and low-pH sediment layers underlying an acidic stream in Parys Mountain (Mynydd Parys) AMD habitat in the UK, indicating contribution of these organisms to carbon, and probably to iron and sulfur cycles in this ecosystem. Gupta et al. (2021) also reported the dominant archaeal communities in AMD sediment of Malanjkhand Copper Project, India as *Thermoplasmata*, *Nitrososphaeria*, *Bathymarchaeia*, *Hydrothermarchaeota*, *Methanomassiliicoccales*, *Methanobacteriaceae*, *Methanocellaceae*, *Haloferaceae*, *Methanosaetaceae*, and *Methanoregulaceae*. In this study, members of the *Thermoplasmata* present in Malanjkhand AMD were reported to be mostly involved in chemoheterotrophy, Fe/S redox cycling, and with HM resistance, while the *Nitrososphaeria* members participate in ammonia oxidation and fixation at low pH and oligotrophic environment and subsequently play an important role in nitrification process in AMD sediment. **Table 1** summarizes various microbial communities associated with diverse AMD systems in different countries.

AMD REMEDIATION TECHNOLOGIES AND MICROBIAL COMMUNITY STRUCTURE

Due to its detrimental toxicological impact to environments, several AMD remediation technologies have been proposed or are being used for remediation of AMD water and AMD-polluted soils. This includes an assortment of passive treatment technologies involving processes that combine geochemical and biological activities in the remediation of AMD wastewater as well as mine waters to improve the water quality are being applied across the globe (Rambabu et al., 2020). In contrast, active treatment processes involving the use alkaline reagents

to precipitate metals, adsorption, ion exchange, and systems with membranes in constructed plant to remediate contaminated AMD water (RoyChowdhury et al., 2015; Rodríguez-Galán et al., 2019). Comparatively, a high quality of treated effluent can be considered as a great advantage of active treatment over passive treatments, however, passive treatment technologies have found wider use due to low operational and labor costs, easy process design and control, and with better sulfate and metal recovery (Rambabu et al., 2020).

The key goal for both remediation systems is to remove HM and sulfates from the acidic AMD and to increase pH level. To date, some of the used methods range from limestone, lime, flyash neutralization (Watten et al., 2005; Tolonen et al., 2014; Iakovleva et al., 2015), phytoremediation and use of wetlands (RoyChowdhury et al., 2015; Ding and Sun, 2021), adsorption (Gitari, 2014; Kim et al., 2021), permeable reactive barriers (Obiri-Nyarko et al., 2014) sulfidogenic bioreactors (Panda et al., 2016; Aoyagi et al., 2018), among others. Each of these technologies are characterized by pros and cons based on running cost, efficiencies, and generation of effluent sludge. Furthermore, the effectiveness of these technologies/systems are influenced by the types of pollution, amounts of pollutants, and activities of microorganisms and the aquatic plants that present in the AMD sites. More importantly, removal of HM and sulfates and neutralization of acidity by the treatment technologies may be associated with perturbations of the autochthonous AMD microbial structural diversity and functioning dependent on the type of treatment method applied. Despite limited data on the impacts of AMD treatment systems on the microbial communities, accumulating evidence indicates a general shift from acidophilic and less sulfur-reducing microbial communities upon treatment to a more metabolically diverse and SRB and iron-reducing (FeOB) bacteria set of taxa being reported (Müller et al., 2015; Aoyagi et al., 2018; Dutta et al., 2020). **Table 2** below summarizes the microbial diversity of AMD sites and agricultural soils treated using passive and active technologies.

In passive successive alkalinity-producing system (SAPS) AMD treatment, enrichment of *Dsr-AB* type dissimilatory reductase based bacteria comprising Clostridia and Deltaproteobacteria as well as Bacilli, Nitrospirae, and Thermodesulfobacteria, with higher levels acidity and metals SAPS bioreactor having a more diverse (i.e., higher Shannon, Shannon, and inverse Simpson indices), and evenly distributed bacterial community (i.e., higher ACE and Chao indices) (Jung et al., 2014). Passive treatment of As-rich AMD via iron biological oxidation showed that the biogenic precipitate formed is dominated by iron-oxidizing bacteria (FeOB) such as *Gallionella*, *Ferrovum*, *Leptospirillum*, *Acidithiobacillus*, and *Ferritrophicum*, and arsenite-oxidizing *Thiomonas* spp. (Laroche et al., 2018). Similarly, passive bioremediation system enriched with *Ignavibacterium*, *Pelotomaculum*, and *Petrimonas* and species known to catalyse the dissimilatory reduction of ferric iron (*Geobacter psychrophilus*), oxidation of sulfur (*Polaromonas hydrogenivorans*, *Flavobacterium johnsoniae*, *Dechloromonas aromatica*, *Novosphingobium sediminicola*, *Clostridium saccharobutylicum*, and *Pseudomonas extremaustralis*), and reduction of nitrate (*Sulfuricella*

TABLE 1 | Microbial diversities associated with selected AMD sites across the world.

AMD sites	Sample type	Identification methods	Dominant microbial taxa	References
Richmond Mine at Iron Mountain, Northern California, USA	AMD water	18S rRNA metagenomic, beta-tubulin gene phylogenies, and Fluorescent <i>in situ</i> hybridization (FISH),	Rhodophyta (red algae) lineage, Vahlkampfiidae family, Dothideomycetes, and Eurotiomycetes	Baker et al., 2004, 2009
	Biofilms	Fluorescent <i>in situ</i> hybridization (FISH), 16S rRNA metagenomic, and proteomics	Class Thermoplasmata, ARMAN nanoarchaeal lineage, <i>Ferroplasma</i> and <i>Aplasma</i> , Thermoplasmatales group, <i>Leptospirillum</i> , <i>Sulfobacillus</i> , <i>Acidiphilium</i> , <i>Acidimicrobium</i> , d-Proteobacteria taxa	Baker and Banfield, 2003; Justice et al., 2012
Cae Coch Pyrite Mine, North Wales	Biofilms	Cultivation, 16S rRNA genes Metagenomics, FISH, and T-RFLP	Psychrotolerant iron/sulfur-oxidizing <i>Acidithiobacillus ferrovarans</i> , <i>Leptospirillum ferrooxidans</i> , <i>Ferrovum myxofaciens</i> , <i>Gallionella ferruginea</i> , <i>Sphingomonas</i> sp. <i>Ralstonia pickettii</i>	Kimura et al., 2011
Los Ruedos abandoned mercury underground mine, NW Spain	AMD water and biofilms	16S rRNA genes Metagenomics	Clades SAR (Stramenopiles + Alveolata + Rhizaria), <i>Opisthokonta</i> (Fungi), <i>Gonostomum</i> , <i>Oxytricha</i> , <i>Paramicrosporidium</i> spp., unclassified microbial <i>Helotiales</i> . Nitrospirae (<i>L. ferrodiazotrophum</i>), Acidithiobacillales (<i>At. ferrovarans</i> ; RCP1-48), β -Proteobacteria (<i>Ferrovum myxofaciens</i>), ARMAN-related Euryarchaeota	Mesa et al., 2017
Rio Tinto, Iberian Peninsula, Spain	Floating macroscopic filaments, AMD water	Denaturing gradient gel electrophoresis (DGGE), 16S rRNA genes metagenomics, and FISH	<i>Acidithiobacillus ferrooxidans</i> , <i>Leptospirillum ferrooxidans</i> , <i>Acidiphilium</i> spp., <i>Ferroplasma acidiphilum</i> , <i>Ferrimicrobium acidiphilum</i> , <i>Aeromonas</i> , <i>Desulfosporosinus</i> , <i>Clostridium</i> , <i>Mycobacterium</i> , and <i>Acinetobacter</i>	García-Moyano et al., 2007; Santofimia et al., 2013
Abandoned mines, Svalbard high Arctic	Surface run-off, iron stalks	Cloning, 16S rRNA genes metagenomic survey, quantitative PCR (qPCR)	Algal-dominated microbial mats, <i>Acidithiobacillus ferrovarans</i> , <i>Acidobacteria</i> , and <i>Actinobacteria Saccharibacteria</i> , Gallionellaceae	García-Moyano et al., 2015
Copper, lead–zinc, pyrite, and polymetallic mines, South East China	AMD water, river sediments, mine tailings	16S rRNA metagenomic	<i>Acidithiobacillus</i> (<i>A. ferrooxidans</i> and <i>A. caldus</i>), <i>Ferrovum</i> spp., <i>Leptospirillum</i> (<i>L. ferrodiazotrophum</i> , <i>L. ferrooxidans</i> , and <i>L. ferriphilum</i>) <i>Acidiphilium</i> (<i>Ac. Cryptum</i>), <i>Nitrospira Acidocella</i> , <i>Acidiphilium</i> , <i>Lactobacillus</i> , <i>Gallionella</i> , <i>Propionicimonas</i> , <i>Rhodococcus</i> , <i>Caloramator</i> , <i>Paenibacillus</i> , <i>Mycobacterium</i> , <i>Streptomyces</i> , and <i>Desulfosporosinus</i> , <i>Idiomarina</i> , <i>Halomonas</i> , <i>Comamonas</i> , and <i>Flavobacterium</i> , <i>Arthronema</i> , <i>Hydrogenophaga</i> , <i>Sediminibacterium</i> , <i>Rhodoplanes</i> , <i>Opitutus</i> , <i>Methylobacterium</i> , <i>Leptolyngbya</i> , <i>Pseudanabaena</i> . candidate phylum Parvarchaeota	Kuang et al., 2013, 2016; Zhang et al., 2019; Luo et al., 2020b; Bao et al., 2021
Yunfu sulfide mine, China	AMD water	PCR-based cloning approach metagenomics	Nitrospira, Alphaproteobacteria, Betaproteobacteria, and Gammaproteobacteria	He et al., 2007
Pyrite mine Anhui Province, China	Mine tailing AMD water	16S rRNA and 18S rRNA PCR-based cloning and metagenomics approach	Alphaproteobacteria (<i>RCP2-17</i> , Rickettsiaceae family), Betaproteobacteria (<i>Ferrovum myxofaciens</i>), Gammaproteobacteria (<i>Legionella</i> spp.), Actinobacteria (<i>Ferritrix thermotolerans</i>), Firmicutes (<i>Alicyclobacillus</i> , uncultured bacterium clone <i>SBNB5C11</i>), phylum Crenarchaeota, phylum Alveolata (<i>Oxytricha</i> sp., <i>Nuclearia</i>)	Hao et al., 2010; Xin et al., 2021
Pary Mountain (Mynydd Parys), UK	AMD water and sediments	16S rRNA metagenomics	<i>Metallibacterium</i> , <i>Acidithiobacillus</i> (family Acidithiobacillaceae), <i>Acidiphilium</i> (family Acetobacteraceae), <i>Leptospirillum</i> spp. (Nitrospirae), <i>Ferrimicrobium</i> spp. (Actinobacteria), archaea Euryarchaeota (Thermoplasmatales)	Korzhnev et al., 2019; Distaso et al., 2020
Malanjkhand Copper Project, India	AMD sediments	16S rRNA metagenomics	Archaea <i>Thermoplasmata</i> (BSLdp215, uncultured <i>Thermoplasmata</i> , and <i>Thermoplasmataceae</i>) and <i>Nitrososphaeria</i> (Nitrosotaleaceae)	Gupta et al., 2021

(Continued)

TABLE 1 | Continued

AMD sites	Sample type	Identification methods	Dominant microbial taxa	References
Deep shaft mine tailings dam, South Africa	AMD water, sediments, mine tailings	16S rRNA and 18S rRNA metagenomics	<i>Acidiphilium</i> spp., <i>Acidibacillus</i> , <i>Acidibacter</i> , <i>Acidobacterium</i> , <i>Acidothermus</i> , <i>Legionella</i> , <i>Metallibacterium</i> , <i>Mycobacterium</i> , <i>Saccharibacteria</i> , ca. TM6_(<i>Dependentiae</i>) and ca. JG37-AG-4, <i>Aspergillus</i> , <i>Penicillium</i> , <i>Candida</i> , and unclassified <i>Saccharomycetales</i>	Keshri et al., 2015; Lukhele et al., 2019; Sibanda et al., 2019; Kalu et al., 2021
Pyhäsalmi mine, Finland	AMD water	16S rRNA metagenomics, qPCR	<i>Leptospirillum</i> , <i>Acidiphilium</i> , <i>Acidithiobacillus</i> , <i>Ferroplasma</i> , and <i>Thermoplasma</i> , Fungal <i>Ascomycetes</i>	Bomberg et al., 2019
San Domingos, Portugal	Polluted river Sediment	16S rRNA metagenomics	Bacterial genera <i>Acidiphilium</i> , <i>Acidibacter</i> , <i>Acidobacterium</i> , and <i>Acidocella</i> , family RCP1-48, archaeal class <i>Thermoplasmata</i>	Carrier et al., 2020
Kahramanmaraş, Turkey	AMD water	Cloning, 16S rRNA metagenomics	<i>Acidiphilium</i> , <i>Metallibacterium</i> , <i>Acidithiobacillus</i> , <i>Leptospirillum</i>	Nural Yaman et al., 2020
Bahia Gold Belt mine, Brazil	Tailings	16S rRNA metagenomics	<i>Acidithiobacillus</i> spp., <i>Acidithiobacillus ferrooxidans</i> , <i>Acidiphilium</i> spp., <i>Leptospirillum</i> type II, and <i>Sulfobacillus</i> spp.	Bernardez et al., 2021

denitrificans, *A. ferrooxidans*, and *Acidithiobacillus thiooxidans*), methylotrophs (methane/methanol-oxidizers), and anaerobic aromatic compound-degraders (*Syntrophorhabdus* sp.) are enriched at the end of the remediation process (Nicomrat et al., 2006; Falagán et al., 2017; Vasquez et al., 2018; Roth et al., 2019). A down flow structured bed bioreactor (DFSBR) treatment of synthetic AMD treatment using sugar vinasse as an electron donor for SRB, resulted in efficient metal sulfide precipitation attributed to high microbial diversity and syntrophism of sulfate and metal reducers *Geobacter* and *Desulfovibrio* and fermenters such as *Parabacteroides* and *Sulfurovum* (Nogueira et al., 2021).

Comparatively, there is limited number of studies on the impact of active treatment technologies on the microbial community structure of AMD-polluted habitats and water. Currently, bulk of work done focuses mainly on the impact of the active treatment technologies on physiochemical components such pH, and HM components of the treated AMD (Othman et al., 2017), as well as their influence in promoting the growth of crops (Choudhury et al., 2017; Nkongolo et al., 2017; Madiseng, 2018; Narendrula-Kotha et al., 2019). However, available literature indicate that active treatments technologies also exert variable influence on microbial diversity of AMD wastewater and contaminated soils. For example, Pang et al. (2019) observed increased species richness and the enrichment of members of Acidobacteria and Chloroflexi (Bacteria domain) and symbiotrophs fungal communities (Eukarya domain) upon liming treatment of sugarcane farm impacted by AMD. In this study, consecutive liming was associated improvement on microbial community richness and evenness, their functions, soil nutrient status, and crop yield in a sugarcane cropping system. Similarly, Narendrula-Kotha and Nkongolo (2017) also detected dominance of bacterial phyla such as Actinobacteria, Acidobacteria, Chloroflexi, Firmicutes, and Proteobacteria and fungal phyla Basidiomycota in limed than unlimed mining-impacted soils. The authors observed higher microbial diversity and biomass in the

limed than the unlimed sites, with Bradyrhizobiaceae family including the nitrogen fixing *Bradyrhizobium* genus was more abundant (representing 50% relative abundance) in limed sites compared to unlimed areas. However, Ascomycota was the most predominant fungal phylum in unlimed soils (46%) while Basidiomycota phylum represented 86% of all fungi in the limed areas. Quicklime treatment (at rate 0.75 g.kg⁻¹) (pH < 5) impact positively the bacterial and fungal diversity of strongly acidic soils of tobacco plants, enrichment of bacterial genera *Rhodanobacter*, *Gaiellales*, *Streptomyces*, and *Terrabacter*. *Mortierella*, *Penicillium*, *Trichoderma*, *Aspergillus*, *Talaromyces*, and *Fusarium* were the abundant fungal genera after 50th day treatment (Liang et al., 2021). Several studies have also reported increase in the bacterial and fungal community diversity in acid/metal-contaminated soils after treatment with fly ash (Garcia-Sánchez et al., 2015; Leclercq-Dransart et al., 2019).

MICROBIAL DIVERSITY CHANGES IN AMD-CONTAMINATED AGRICULTURAL SOIL

Many studies have demonstrated that irrigation AMD water could result in the shift of soil basic characteristics that may influence microbial diversities that play pivotal ecological roles related to bulk and rhizospheric soil health (Wang et al., 2018, 2019a; Narendrula-Kotha et al., 2019; Wu et al., 2019; Li et al., 2020; Xin et al., 2021). The changes in microbial diversity are influenced by the AMD-induced changes, with the bacterial and archaeal community diversity majorly dependent on soil pH and HM content, respectively (Wang et al., 2018; Li et al., 2020). Heavy metals toxicity may manifest through alteration of physiological and biochemical properties of microorganisms through various mechanisms such as nucleic acid structure damage leading to functional disturbance, disruption of cell membranes, enzymatic activity inhibition, and

TABLE 2 | Summary of the microbial diversity in selected passive and active treated mining AMD sites and agricultural soils.

AMD sites	Treatment methods	Microbial diversity	Reference
Abandoned coal mine AMD, Munkyeong City, South Korea	Passive [Successive alkalinity producing systems (SAPS) bioreactor]	Deltaproteobacteria, Clostridia, Nitrospirae, Thermodesulfobiaceae, Bacilli (<i>Bacillus</i> , <i>Lysinibacillus</i> , and <i>Ureibacillus</i>), and <i>Thermodesulfobacteria</i> . Euryarchaeota and Crenarchaeota in the archaea domain	Jung et al., 2014
Wheat Jane tin mine, Cornwall, UK	Passive (compost bioreactor)	<i>Thiomonas</i> sp. and other SRB/iron oxidizing bacteria	Johnson and Hallberg, 2005
Inyanda Coal Mine water dam, Emalahleni	Passive (domestic wastewater assisted bioreactor)	<i>Chlorobium</i> spp., <i>Ornithobacterium</i> spp., <i>Desulfovira</i> spp., <i>Sphingobacteria</i> spp., <i>Lentisphaerales</i> and <i>Victivallales</i> , <i>Caulobacteraceae</i> spp., <i>Rhizobiales</i> spp., <i>Rhodopseudomonas</i> , <i>Salinarimonas</i> , <i>Rhizobium</i> , Rhodospirillales (<i>Fodincurvata</i> and <i>Magnetospirillum</i>), and Epsilonproteobacteria (<i>Campylobacteriales</i> spp., <i>Spirochaetes</i> spp., <i>Firmicutes</i> spp., and <i>Clostridia</i> spp. including <i>Ruminococcaceae</i> , <i>Sporobacterium</i> and <i>Lutispora</i>)	Van den Berg et al., 2016
Carnoulès As-rich AMD, France	Passive (bioreactor)	<i>Gallionella</i> , <i>Ferrovum</i> , <i>Leptospirillum</i> , <i>Acidithiobacillus</i> , <i>Ferritrophicum</i> , <i>Thiomonas</i> related bacteria	Laroche et al., 2018
Greater Sudbury nickel mining, Northern Ontario, Canada	Active (liming with dolomite limestone)	<i>Acidobacterium</i> , <i>Afiplia</i> , <i>Aquicella</i> , <i>Bradyrhizobium</i> , <i>Geobacillus</i> , <i>Granulicella</i> , <i>Nitrosococcus</i> , <i>Rhodoplanes</i> , <i>Skermanella</i> , <i>Solirubrobacter</i> , <i>Thermosporothrix</i> , and <i>Thioalkalispira</i>	Narendrula-Kotha and Nkongolo, 2017
As contaminated groundwater, Florida USA	Active (SRB, Inorganic fertilizer, and organic substrates amendments)	<i>Desulfovibrio</i> spp., <i>Desulfotomaculum</i> spp., and other soil-rich SRB	Lee et al., 2019
El Oro de Hidalgo and Zacualpan Mine tailings, México.	Passive (bioremediation)	<i>Delftia tsuruhatensis</i>	Bautista-Hernández et al., 2012
Middle Branch Coal mine drainage treatment, Pennsylvania, USA	Passive (Vertical flow ponds and Aerobic wetland)	Sulfate reducers (<i>Desulfobulbaceae</i> , <i>Desulfobacteraceae</i> , and <i>Desulfomonile</i>), Sulfur-oxidizers (<i>Thiovirga</i> , <i>Chlorobiaceae</i> , and <i>Chromatiaceae</i>)	Ly et al., 2019
Wingfield Pines Passive remediation treatment system, Pennsylvania, USA	Passive (Vertical flow ponds and Aerobic wetland)	Proteobacteria (<i>Anaeromyxobacter</i> , <i>Desulfobacterium</i> , <i>Desulfobulbus</i> , and <i>Pelobacter</i>), Bacteroidetes (<i>Anaerophaga</i> , <i>Bacteroides</i> , <i>Cytophaga</i> , <i>Solitalea</i> , <i>Pedosphaera</i> , <i>Rhodocyclus</i> , <i>Alkaliflexus</i> , <i>Chitinophaga</i> , <i>Rhodoferax</i> , <i>Ignavibacterium</i> , and <i>Solitalea</i>)	Roth et al., 2019
Abandoned coal mine sites	Passive (biobleaching using Iron reducing and SRB consortia)	<i>Acidibacillus ferrooxidans</i> , <i>Acidiphilium</i> sp., <i>Geobacter psychrophilus</i> , <i>Sulfuricella denitrificans</i> , and <i>Syntrophorhabdus</i> sp.	Falagán et al., 2017
Acid coal mine drainage (AMD)	Passive (constructed wetland)	<i>Acidithiobacillus ferrooxidans</i> and <i>Acidithiobacillus thiooxidans</i> , <i>Acidiphilium</i> spp., and <i>Leptospirillum ferrooxidans</i>	Nicomrat et al., 2006
Zipaquirá Mining District of Colombia	Passive (Biochemical passive reactors)	Cellulose-degrading genera (<i>Devosia</i> , <i>Paludibacter</i> , <i>Bacteroidetes</i> , <i>Sphingobacterium</i> , and <i>Sphingomonas</i>), SRB (<i>Desulfovibrio</i> , <i>Desulfomicrobium</i> , and <i>Desulfobulbus</i>)	Vasquez et al., 2016, 2018
Acid mine drainage water	Passive (Sulfur reducing vertical downflow reactor amended with rice bran)	<i>Ferrimicrobium acidiphilum</i> , <i>Metallibacterium</i> , <i>Clostridium</i> , <i>Microbacter</i> , <i>Candidatus Moranbacteria</i> , <i>Candidatus Adlerbacteria</i> <i>Alishewanella agri</i> , <i>Mitsuaria chitosanitabida</i> , <i>Geobacter anodireducens</i> , <i>Desulfomonile tiedjei</i>	Aoyagi et al., 2018
As-contaminated paddy soils	Active (Sorption with amino biochar modified by nano zero-valent iron (ABC/NZVI))	<i>Geobacter</i> , <i>Kaistobacter</i> , <i>Flavisolibacter</i> , <i>Anaerolinea</i> and <i>Nitrospira</i> , <i>Leptolyngbya</i> , <i>Thermogymnomonas</i> , <i>Methanobacterium</i> , <i>Methanoseta</i> and <i>Nitrososphaera</i> Chytridiomycota, Basidiomycota Ascomycota, Endogone, Nuclearia, Camarops	Liu et al., 2017
AMD impacted soils, Malanjikhand Copper Project, India	Active (soil amendment with organic carbon sources)	Members of Clostridiaceae, Peptococcaceae, Veillonellaceae, Christensenellaceae, Lachnospiraceae, Bacillaceae	Gupta et al., 2018
		Fermentative (<i>Clostridium sensu stricto 1</i> and <i>Fonticella</i>), iron-reducing (<i>Acidocella</i> , <i>Anaeromyxobacter</i> , and <i>Clostridium sensu stricto 1</i>), and sulfate-reducing (<i>Desulfovibrio</i> , <i>Desulfotomaculum</i> , <i>Desulfosporosinus</i> , and <i>Desulfobacteraceae</i>) bacteria.	Gupta and Sar, 2019
AMD impacted soils, Malanjikhand Copper Project, India	Active [Combined bioaugmentation (enriched consortium) and biostimulation (cellulose)]	<i>Clostridium sensu stricto 1</i> , <i>Clostridium sensu stricto 10</i> , <i>Clostridium sensu stricto 12</i> , <i>Bacillus</i> , <i>Lysinibacillus</i> , <i>Paenibacillus</i> , <i>Sporomusa</i> , <i>Ruminococcaceae incertae sedis</i> , <i>Ruminococcus</i> , and uncultured members of Clostridiales and Bacillales (Family XIII and Family XII)	Gupta and Sar, 2020

oxidative phosphorylation, increased ROS inducing oxidative damage, and impaired ion regulation (Jacob et al., 2018; Medfu Tarekegn et al., 2020). Overall, richness and alpha diversity of AMD associated microbial communities vary widely across the type of ecosystem, with communities inhabiting the AMD water being less diverse than those from impacted soils, sediments, or bioreactors from AMD treatment (Villegas-Plazas et al., 2019). Interestingly, community-level functional acclimatization occurs in response to the AMD perturbation despite the extreme condition of the acidity and high concentrations of toxic metal and sulfate.

From sustainable agricultural production and biotechnological standpoint, the enrichment of soil acidophilic, HM, and sulfate-adapted microbial taxa contributed by both AMD water and autochthonous soil microbiota that might play beneficial interrelated functions key to optimal plant growth and productivity and bioremediation of AMD-polluted agricultural soils. For example, AMD irrigation of paddy rice considerably enriched the bacterial phylum Acidobacteria and the archaeal phylum Crenarchaeota correlating to AMD-related environmental factors of pH and HM (Cu, Pb, and Zn) (Wang et al., 2018). Notably, the dominance of Acidobacterial genera *Candidatus Solibacter* and *Candidatus Koribacter* in the highly contaminated sites were key to stabilization of the energy metabolic processes related to C/N related pathways under AMD contamination. Similarly, the increased of metabolic activities that generate alkalinity and the abundance and the diversity of SRB and iron-reducing bacteria in the long-term AMD-irrigated paddy soil has also been reported (Wang et al., 2016, 2021a; Ding et al., 2017). In summary, the key beneficial and interrelated microbial functions under AMD pollution can largely be grouped into: (i) metal bioremediation; (ii) plant growth promotion; and (iii) sulfates/iron reduction and biogeochemical N and C recycling. **Figure 1** provides the schematic representation of the diverse microbial diversity and functions key to plant growth and productivity under AMD-contaminated agricultural soils.

HM Bioremediation and Plant Growth Promoting Activity

Soil microbiota, particularly rhizomicrobime, play a critical role in metal bioremediation contaminated soils due to their ability to degrade, detoxify, and even accumulate HM, with metal-microbe interactions important in reducing HM stress in plants. In AMD-polluted habitats and agricultural soils, selection, and enrichment of microbes having high metabolic capacity supported by molecular machinery to adapt and perform in the presence of high concentration of HM is common feature. The adaptability of these microorganisms indicates their potential bioremediation application for rehabilitation of AMD-irrigated paddy soil and mined sites. The inherent metal-microbe and plant-microbe interactions are important to protect the plant from HM stress as well as help in natural attenuation of HM in soil (Mishra et al., 2017; Henao and Ghneim-Herrera, 2021). Generally, these microorganisms utilize various mechanisms ranging from biosorption (including precipitation, chemical adsorption, and ion exchange, surface precipitation, complexation to organic ligands, and redox reactions), biomineralization (bioleaching,

dissolution, or complexation), to bio-oxidation (Jin et al., 2018; Hou et al., 2020).

Both bulk soil and plant-associated microbes play critical role in bioremediation and microbe-assisted phytoremediation of HM under AMD conditions. Notably, higher abundance of members of bacterial phyla Actinobacteria, Proteobacteria, Firmicutes, and Bacteroidetes and archaeal phyla Euryarchaeota and Crenarchaeota in the rhizosphere of plants growing in AMD-polluted and other extreme environments has attracted great attention in the last three decades. Specifically, the potential application of metal-tolerant plant growth promoting rhizobacteria (PGPRs) has become attractive as an efficient bio-inoculants for metal remediation for sustainable agriculture (Backer et al., 2018). The PGPRs generally play key roles in nutrient acquisition and assimilation, toxic HM bioremediation, improved soil texture, secreting, and modulating extracellular molecules such as hormones, secondary metabolites, antibiotics, and various signal compounds, these attributes collectively contributing to enhancement of plant adaptability to metal stress and productivity (Mishra et al., 2017). Li and Ramakrishna (2011) reported improved growth and copper uptake by maize (*Zea mays*) and sunflower (*Helianthus annuus*) under HM pollution in presence of copper resistant *Pseudomonas* strains exhibiting higher Zn and Pb bioaccumulation and plant growth promoting indole-3-acetic acid (IAA), iron chelating siderophore, and solubilization of mineral phosphate and metals ability. The use of copper-tolerant rhizobacteria *Brevundimonas diminuta* MYS6 and *Pseudomonas vermicola* to efficiently remove Cu improving plant growth, biomass and chlorophyll under Cu stress in sunflower (Rathi and Yogalakshmi, 2021) and lentils (Islam et al., 2016), respectively, has also been reported. Wu et al. (2019) also isolated indigenous HM-resistant plant growth-promoting bacteria (PGPRs) genera *Burkholderia*, *Paraburkholderia*, *Cupriavidus*, *Pseudomonas*, and *Ralstonia* AMD-impacted farmlands in Le'an River basin, China. Two bacterial strains *Burkholderia* sp. strain S6-1 and *Pseudomonas* sp. strain S2-3 possessed both greater PGP activities and metal-resistant characteristics significantly increased the height, dry weight and N uptake of sorghum (*Sorghum bicolor* L.). The importance of PGPR-mediated metal phytoremediation by various plant species under wetland and agricultural ecosystems impacted by AMD have also been documented (Checcucci et al., 2017; Mishra et al., 2017; Song et al., 2020). These examples illustrate AMD-impacted soils PGPRs as potential tools for sustainable agriculture.

Sulfate-Reducing and Iron-Reducing Activities

Acid mine drainage-impacted habitats and agricultural soils is also rich in Fe- and S-metabolizing bacteria that may play key role in bioremediation. Generally, SRB oxidize simple organic molecules using the sulfate ion as an electron acceptor producing hydrogen sulfide (H₂S) and the bicarbonate ions (HCO₃⁻) that are effective in reducing high AMD sulfate concentration and neutralizing its acidity. The sulfates are removed as H₂S while the HM ions can be precipitated as insoluble metal sulfides by the biogenic H₂S produced due to sulfate reduction by SRB. Sulfur-reducing bacteria can be classified into several

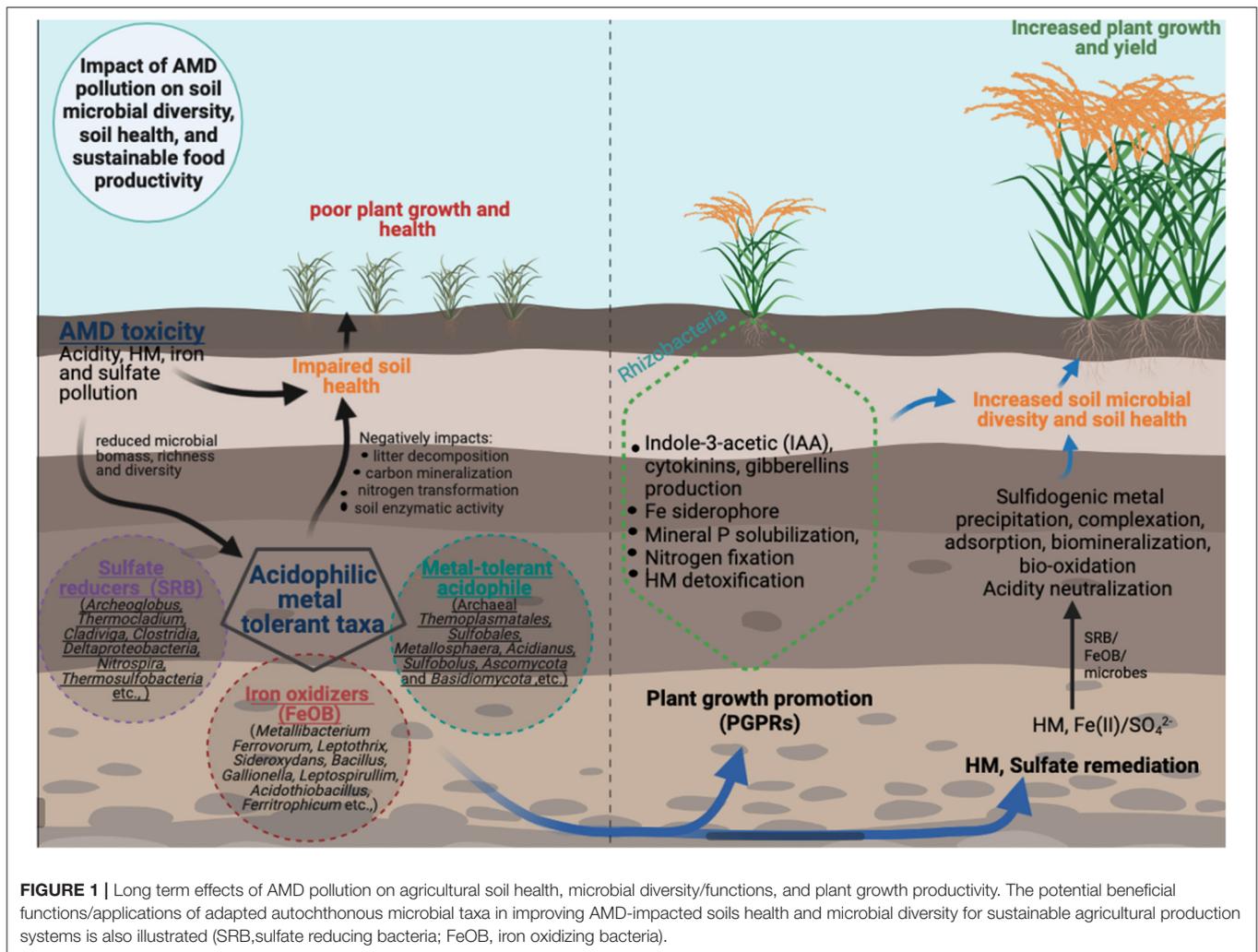


FIGURE 1 | Long term effects of AMD pollution on agricultural soil health, microbial diversity/functions, and plant growth productivity. The potential beneficial functions/applications of adapted autochthonous microbial taxa in improving AMD-impacted soils health and microbial diversity for sustainable agricultural production systems is also illustrated (SRB, sulfate reducing bacteria; FeOB, iron oxidizing bacteria).

bacterial phylotypes belonging to class Deltaproteobacteria, Clostridia, Nitrospira, and Thermosulfobacteria, as well as archaeal genera *Archeoglobus*, *Thermocladium*, and *Caldivirga* (Xu and Chen, 2020). Currently, active and passive technologies utilizing sulfidogenic bioreactors involving SRB has become attractive for treatment and recovery of HM in acidic sulfate-containing wastewater such as AMD. The performance including the microbial communities of sulfidogenic reactors treating AMD comprising fermentative-, acetogenic-, and SRB as well as methanogenic archaea has been documented (Sánchez-Andrea et al., 2014; Aoyagi et al., 2018; Ayangbenro et al., 2018; Xu and Chen, 2020; Nogueira et al., 2021). In addition, innate activity of diverse FeOB ranging from members of genera *Metallibacterium*, *Ferrovum*, *Leptothrix*, *Sideroxydans*, *Bacillus*, *Gallionella*, *Leptospirillum*, *Acidithiobacillus*, and *Ferritrophicum* are important for robust oxidative precipitation of Fe from AMD, suggesting their biotechnological relevance in the treatment of AMD impacted environment (Brantner et al., 2014).

In agricultural soils, long-term AMD irrigation of paddy soil has been associated with increased abundance of SRB and bacterial lineages such as *Desulfobacca*, *Desulfovibrio*, *Syntrophobacter*, *Desulforhopalus*, *Desulfarculus*, and

Desulfobulbus mainly correlating to soil pH, the organic matter and the sulfate than the HMs (Wang et al., 2016). Furthermore, the effects of root associated FeOB in increasing phosphate nutrition and influencing root to shoot partitioning of iron in tolerant plant *Typha angustifolia* under AMD conditions have been reported (Ghosh et al., 2014). Similarly, the application of As-resistant FeOB strains (*Bacillus* sp. T2, *Pseudomonas* sp. Yangling I4, and *Bacillus* sp. TF1-3) in decreasing As in brown rice growing in mine polluted soils through promotion of root Fe plaque formation that sequesters As and reduces As(III) influx has been reported (Xiao et al., 2020). These few examples illustrate the potential biotechnological application SRB and FeOB in improving agricultural productivity and bioremediation of agricultural soils.

Nutrient (N and C) Recycling

Heavy metal concentration in the soil significantly influences its chemical properties such pH, carbon (C), and nitrogen (N) content. Under the oligotrophic and metal-rich AMD environments, organic C, and bioavailable N content can be growth limiting, with AMD contamination documented to impact the both carbon and nitrogen cycle in several ways

(Méndez-García et al., 2015). Metabolic processes related to carbon-fixation, nitrogen fixation, and denitrification by *in situ* microbiome are important. Acid mine drainage contamination influence on the distribution of both autotrophic carbon-fixing phylotypes (such as *Leptospirillum* and *Metallibacterium*) and heterotrophs/facultative autotrophs (such as *Bradyrhizobium*, *Rhizobium*, and *Burkholderia*) dependent of TOC level (Wang et al., 2016; Sun et al., 2020). Whereas, *Metallibacterium* are chemolithoautotrophs participating in carbon fixation and sulfur oxidation, *Leptospirillum* are iron-oxidizers capable of dissimilatory sulfate reduction. Nitrogen-fixing bacteria (*Bradyrhizobium*, *Rhizobium*, and *Burkholderia*) and *Leptospirillum* performs the dual function of heterotrophic carbon-fixation and providing bioavailable N to the harsh environments and help sustain the function of the ecosystem. However, higher AMD contamination significantly decreases the number of soil nitrogen bacterial species and species richness, with a consequence of impairing both the nitrogen fixation and dissimilatory nitrate reduction (DNRA) activity, altered uptake, and utilization of nutrients (Wang et al., 2019a). This may explain the importance of organic and inorganic amendments to boost both N and C content to efficiently treat AMD in passive bioreactor-based technologies.

CONCLUSION

The objective of the present review was to provide a comprehensive assessment on the impact of AMD pollution on microbial diversity and functioning, highlighting the main implications and challenges of long-term AMD-irrigated agriculture on soil health, and sustainable agricultural productivity. Overall, HM toxicity and highly acidic conditions is associated with reduced microbial biomass, richness, and diversity, negatively impacting on soil microbial functions and processes such as litter decomposition, carbon mineralization, nitrogen transformations, and soil enzymatic activity, that may detrimental to soil health and plant productivity in agricultural soils. The dual drawbacks on food safety (potential biomagnification of toxic HM along food chain) and detrimental effect on agricultural productivity coupled with environmental degradation, imply that untreated AMD water is unsuitable for irrigated agriculture. Currently, there are numerous technologies for passive or active treatment

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of AMD wastewater and contaminated agricultural soils, differentiated by their cost effectiveness, and efficiency in HM removal. Interestingly, AMD impacted habitats are unique ecological niches for novel acidophilic, HM, and sulfate-adapted microbial phylotypes that might be beneficial to optimal plant growth and productivity and bioremediation of AMD-polluted agricultural soils. This review has highlighted the impact active and passive treatment technologies on AMD microbial diversity. The discussion is further extended to the interrelated microbial diversity and beneficial functions such as metal bioremediation, acidity neutralization, symbiotic rhizomicrobiome assembly and plant growth promotion, sulfates/iron reduction and biogeochemical N and C recycling under AMD-impacted environment, elucidating and discussing the significance of SRB, FeOB, and PGPRs passive and active systems dedicated to bioremediation and microbe-assisted phytoremediation. Despite bioremediation being attractive alternative for AMD management, current understanding on the link between microbial community dynamics, process stability, and functions in engineered active and passive systems for bioremediation is still limited. Furthermore, bioremediation is a constantly-evolving multidisciplinary endeavor, thus, future studies integrating meta-omics and process engineering on AMD impacted microbiomes will be important in the design and optimization of robust approaches to improve bioremediation processes.

AUTHOR CONTRIBUTIONS

RM wrote the manuscript. HO and DM critically edited the manuscript. All authors contributed to the article and approved the submitted version.

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