

酸性矿山废水微生物组时空演变特征及微生物-矿物互作机制

冯乙晴^{1,3}, 郝立凯^{1,2,3*}, 郭圆¹, 徐绯⁴, 徐恒⁴

1. 中国科学院地球化学研究所/环境地球化学国家重点实验室, 贵州 贵阳 550081;

2. 中国科学院第四纪科学与全球变化卓越创新中心, 陕西 西安 710061; 3. 中国科学院大学, 北京 100049; 4. 四川大学, 四川 成都 610065

摘要: 酸性矿山废水 (Acid Mine Drainage, AMD) 是世界范围内最严重的环境问题之一。微生物是 AMD 形成过程的主要驱动者, 主导了该系统中 Fe-S 地球化学循环, 并与矿物之间存在复杂的相互作用关系。对其群落结构、功能和代谢特征的深入分析有助于揭示极端酸性环境中优势物种和稀有物种的生态意义, 有利于制定科学合理的 AMD 污染防控和修复措施。采用微生物组学 (基因组、转录组、蛋白组、代谢组和表型组) 方法进行系统研究有助于明确极端环境胁迫下微生物适应性反应的分子机制。AMD 微生物组在尾矿酸化过程、生物膜发育过程、生物处理过程和水热驱动的季节演替等不同时间序列及局部和精细空间尺度上具有明显的系统聚类趋势, 体现了其适应极端酸性和有毒金属环境的生态策略。AMD 系统 Fe-S 生物地球化学梯度对微生物群落结构和功能具有显著的影响, 铁硫代谢相关微生物对环境梯度变化的响应又驱动了 Fe-S 生物地球化学循环, 主导了 AMD 矿物的演变过程、相变平衡及金属元素的形态转化。酸性矿山废水微生物成矿作用是生物和非生物反应相互作用的结果, 表面反应控制是矿物微生物氧化反应机理的关键, 接触机制是其主导机制。此外, AMD 矿物的微生物还原遵循电化学过程, 含铁矿物是 AMD 系统微生物胞外呼吸最重要的电子受体之一, 铁呼吸过程驱动了 AMD 系统的元素生物地球化学循环, 进而驱动其微生物群落和功能、代谢等的演化。

关键词: 酸性矿山废水 (AMD); 微生物组; 微生物成矿; 微生物-矿物作用 (MMI); Fe-S; 生物地球化学循环

DOI: 10.16258/j.cnki.1674-5906.2022.05.019

中图分类号: X172

文献标志码: A

文章编号: 1674-5906 (2022) 05-1032-15

引用格式: 冯乙晴, 郝立凯, 郭圆, 徐绯, 徐恒, 2022. 酸性矿山废水微生物组时空演变特征及微生物-矿物互作机制[J]. 生态环境学报, 31(5): 1032-1046.

FENG Yiqing, HAO Likai, GUO Yuan, XU Fei, XU Heng, 2022. Spatio-temporal evolution characteristics of microbiome in acid mine drainage and microbial-mineral interaction mechanism [J]. Ecology and Environmental Sciences, 31(5): 1032-1046.

酸性矿山废水 (Acid Mine Drainage, AMD) 是以硫铁矿为主的矿石和尾矿暴露于空气、水等介质中, 在由微生物主导作用下反应产生的低 pH、高 SO_4^{2-} 且富含各种重 (类) 金属的废水 (Akcil et al., 2006; Moncur et al., 2009)。AMD 会对受纳环境系统产生十分严重的危害, 如加重岩溶含水层的污染 (Ren et al., 2021), 改变有毒金属的赋存形态并影响区域土壤微生物群落 (Pan et al., 2021), 是世界范围内最严重的环境问题之一 (Simate et al., 2014)。

微生物是 AMD 形成过程的主要驱动者, 对 AMD 元素环境地球化学循环、生物成矿和污染修复具有重要作用 (Johnson et al., 2003; Nordstrom et al., 2015)。尽管 AMD 酸度极高, 但使用传统的培养方法和高通量组学方法, 已鉴定出了多种多样

的微生物, 包括细菌、古菌和真核生物 (主要是真核微生物和藻类) (Olsson et al., 2015; Chen et al., 2016; Abinandan et al., 2019; Abinandan et al., 2020)。近年来, 微生物组学技术 (基因组学、转录组学、蛋白组学、代谢组学、表型组学) 的快速发展为原核微生物、真核微生物的群落多样性特征和时空演变特征研究打开了广阔视角 (Edwards et al., 2000)。该技术能够识别微生物群落的基因、功能和代谢特征 (Schloss et al., 2005; Sahoo et al., 2021), 为 AMD 微生物群落、功能和代谢多样性的时空演变特征研究提供了技术支持, 也为 AMD 生物处理系统的工程应用提供了理论支撑 (Hallberg, 2010; Villegas-Plazas et al., 2019)。

本文系统综述了微生物组学技术在 AMD 系统研究中的应用及其在不同时间序列 (尾矿酸化过

基金项目: 国家重点研发计划项目 (2018YFC1802601); 国家自然科学基金项目 (41877400); 中国科学院 B 类战略性先导科技专项资助 (XDB40020300); 中国科学院启动经费 (2017-020); 环境地球化学国家重点实验室开放课题 (SKLEG2018911)

作者简介: 冯乙晴 (1991 年生), 女, 博士研究生, 研究方向为地球微生物学。E-mail: fengyiqing@mail.gyig.ac.cn

*通信作者: 郝立凯 (1980 年生), 男, 研究员, 博士, 研究方向为地球微生物学。E-mail: haolikai@mail.gyig.ac.cn

收稿日期: 2022-03-17

程、生物膜发育过程和生物处理过程及季节演替)和空间尺度(地理隔离、局部空间中的纵横分布、精细尺度)上的演变特征,分析了微生物群落在AMD系统铁硫生物地球化学循环和水质自净中的重要作用,进一步梳理了AMD系统中微生物-矿物相互作用的可能机制,最后提出了整合微生物组学技术和矿物学分析技术在AMD微生物生态演替、进化和应用研究中的展望,以期从生态学、地球化学和矿物学等多学科角度为AMD污染修复提供科学依据。

1 组学技术在AMD微生物学研究中的应用

1998年,Handelsman et al. (1998)首次将“宏基因组”定义为特定环境中全部微生物及其遗传信息的集合。自2006年以来,随着高通量测序和质谱等技术的飞跃发展,以“DNA—RNA—蛋白质—代谢物”为中心法则的多组学技术(图1)彻底改变了微生物学领域。Stulberg et al. (2016)将微生物组定义为在特定环境下的多物种微生物群落,强调运用宏基因组技术对微生物从群落到功能、代谢等层面进行全面分析。此后,随着微生物生态研究的深入,转录组学、蛋白组学、代谢组学和表型组学等技术逐步发展并得到广泛应用。

宏基因组学有助于确定AMD系统中关键的微生物过程及其群落组成在不同的生态位之间的相互作用,并可指导AMD生物处理中的微生物群落组装以高效去除或提取水体中的金属元素(Allen et

al., 2005; Desoeuvre et al., 2016; Liu et al., 2019c; Liu et al., 2019a; Liu et al., 2019b; Grettenberger et al., 2021; Pan et al., 2021)。2004年, Tyson et al. (2004)运用宏基因组学技术从AMD生物膜中获得了完整的*Leptospirillum* II和*Ferroplasma* type II基因组序列,以及*Leptospirillum* III、*Ferroplasma* type I和G-plasma的部分基因组序列。此后,研究人员进一步发现变形菌门(Proteobacteria)、硝化螺菌属(*Nitrospira*)、放线菌门(Actinobacteria)、厚壁菌门(Firmicutes)、酸杆菌门(Acidobacteria)、产水菌门(Aquificae)和候选糖杆菌(*Candidate saccharibacteria*)代表了AMD微生物群落的主要谱系,其中铁硫氧化细菌——*Acidithiobacillus* (γ -Proteobacteria)、*Leptospirillum* (Nitrospirae)和*Ferroplasma* (β -Proteobacteria)为优势属(Hua et al., 2015; Méndez-García et al., 2015; Chen et al., 2016)。

转录组学研究识别了可以解释极端微生物功能特征的基因序列,其中部分序列可能是通过水平基因转移获得的,如已被确定的*Galdieria suluraria* (Schönknecht et al., 2013)和嗜酸*Chlamydomonas eustigma* (Hirooka et al., 2017)的基因组序列。此外,该组学研究还揭示了嗜酸微藻在酸性和富金属环境中生存的独特基因,强调采用多组学方法(图1)进行系统研究的必要性,以明确重金属毒性和微生物适应性反应之间的分子机制(Olsson et al., 2015; Long et al., 2016; Puente-Sánchez et al., 2016; Olsson et al., 2017; Tripathi et al., 2021),以及

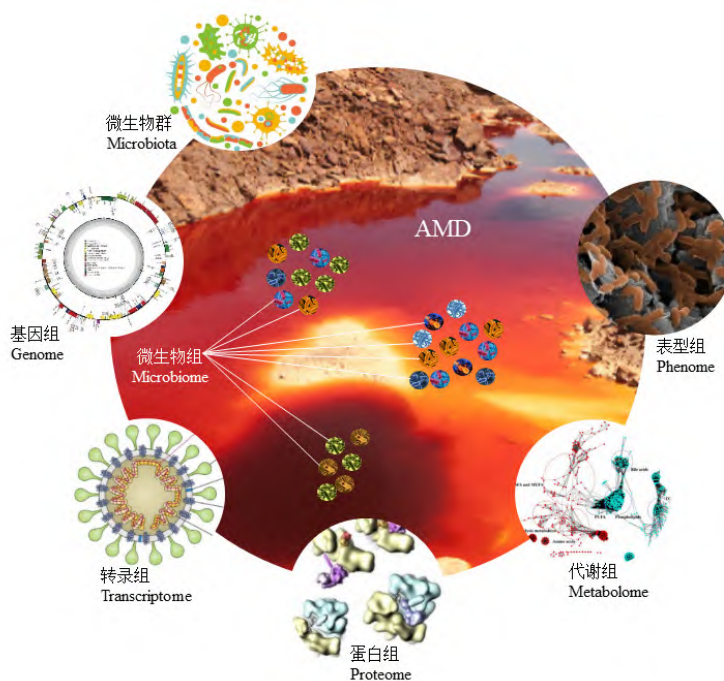


图1 多组学技术在AMD微生物生态学研究中的应用

Figure 1 Application of multi-omics techniques in microbial ecology of AMD

AMD 系统中常见和稀有原核生物的生态作用 (Hua et al., 2015)。

蛋白质组学研究证明了 AMD 系统中金属抗性和耐酸性蛋白的重要性, 表明与特异性功能相关的基因片段和与某种功能相关的蛋白质组分之间存在差异, 这可能是微生物在极端酸性、富金属环境中适应特定生态位的关键机制 (Tyson et al., 2004; Ram et al., 2005; Lo et al., 2007; Zhang et al., 2019), 而代谢途径和基因表达谱重建分析揭示了其潜在的生理机制 (Anantharaman et al., 2016; Long et al., 2016)。例如, Whitaker et al. (2006) 发现了 AMD 生物膜群落中的单核苷酸多态性, 揭示了极端条件下微生物群落的种群动态和进化; Xie et al. (2011) 通过分析微生物对 AMD 金属胁迫的代谢特性, 发现菌株对高浓度 Cu 的耐受性响应是下调氨基酸代谢途径, 以此作为其在 AMD 中的一种生存机制; 还有研究发现, 微生物可通过调节膜脂质成分来应对极端酸性环境胁迫 (Dean et al., 2019)。

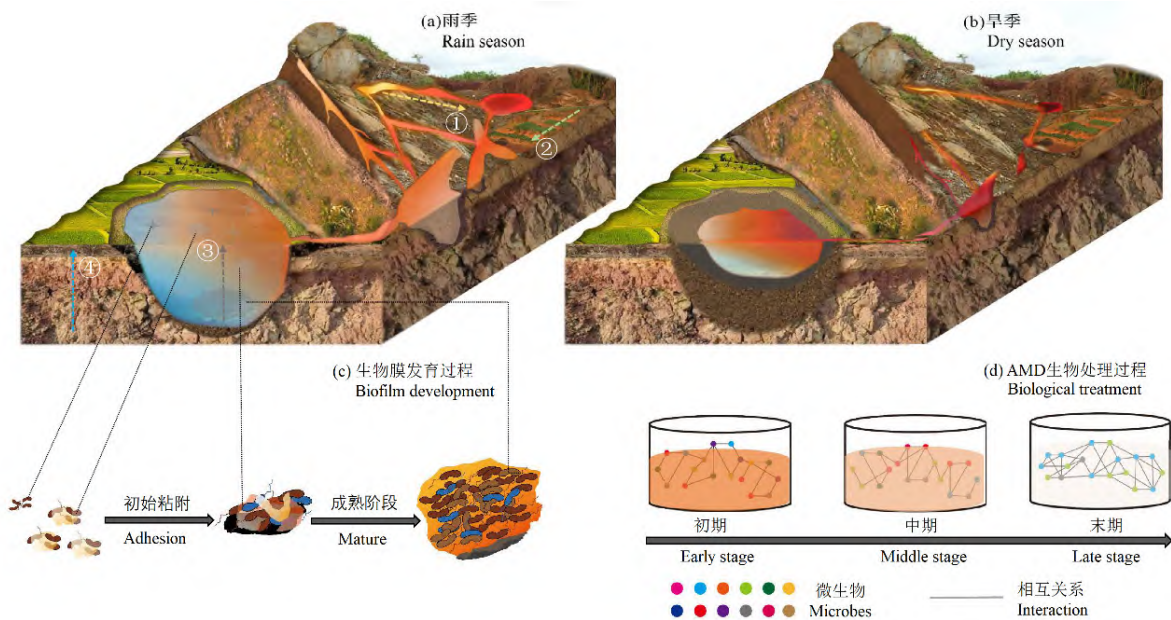
运用表型组学可进一步直观揭示 AMD 环境中微生物-矿物作用 (Microbial-mineral Interaction, MMI) 特征, 研究发现 MMI 是驱动 AMD 表型性状 (如离子强度、pH、pO₂、ORP 等) 演化的主要作用力, 促使其积累异质性较大的次级产物或中间产物, 以及形成时间和空间序列上的离子和 pH 梯

度 (Xia et al., 2020), 最终导致 AMD 系统微生物群落、功能、代谢等的演化。

组学技术在 AMD 系统微生物生态学研究中的广泛应用为 AMD 生物处理中微生物菌群组装提供了理论指导, 同时有助于生物浸矿技术的开发和应用。

2 AMD 微生物组时空演变特征

微生物群落的形成过程取决于空间、时间及系统发育尺度, 不同的生态过程可能在不同规模的生态系统上占主导地位, 研究 AMD 微生物组的时空演变特征有助于明确哪些生态过程对微生物群落的构建具有重要作用 (Ladau et al., 2019)。基于生态位的微生物群落形成过程由环境的多样性模式和 pH、氧化梯度等环境化学梯度变化主导 (Lozupone et al., 2007), 而基于尾矿酸化过程 (图 2a①)、生物膜发育过程 (图 2c)、生物处理过程 (图 2d) 和水热驱动的季节演替 (图 2a、b) 的不同时间序列及基于局部 (图 2a②、③、④) 和精细空间尺度的 AMD 系统所提供的生态位独特多样, 适应极端酸性和有毒金属环境的微生物能够在这些独特的生态位上进行活跃的代谢。AMD 生物处理是一个多尺度的复杂问题, 借助微生物组学技术可以充分理解其复杂的微生物群落结构是如何发挥



①尾矿酸化过程; ②水平方向: 梯田 (上层—下层); ③垂直方向: 湖泊 (底层—表层); ④垂直方向: 土壤 (底层—表层)。沿箭头方向环境 pH 逐渐降低, 微生物群落结构趋于简单化

①Tailings acidification; ②Horizontal scale: terraced fields (upper to lower); ③Vertical scale: pool (bottom to surface); ④Vertical scale: soil (bottom to surface). Microbial community structure tends to be simplified with the gradual decrease of environmental pH along the arrow direction

图 2 AMD 微生物群时空演变特征

Figure 2 Spatio-temporal evolution characteristics of microbiota in AMD

作用的, 及其组分在各自的生态位上的作用规律, 从而为 AMD 生物处理提供生态学理论指导。

2.1 AMD 微生物组在不同时间序列上的演变特征

2.1.1 不同尾矿酸化过程

矿山尾矿酸化是 AMD 的主要成因。研究人员大多采用空间替代时间(图 2a①)的方法对与尾矿酸化相关的微生物多样性和群落功能的动态变化进行研究(Huang et al., 2011; Chen et al., 2013; Liu et al., 2014; 曹子敏等, 2019), 结果表明, 大多数优势菌系的 α 多样性和相对丰度与 pH 值具有显著相关性, pH 在调节嗜酸微生物群落结构和功能方面具有重要性(Belnap et al., 2011a), 尾矿酸化的不同阶段具有不同的微生物群落组成特征(Tan et al., 2008; Belnap et al., 2010; Belnap et al., 2011b; Chen et al., 2013; Dean et al., 2019; Abinandan et al., 2020)。例如, 未发生酸化的尾矿中的微生物种群与中酸性或极酸性尾矿中的微生物种群具有显著差异, 古菌、*A. ferrooxidans* 和 *Leptospirillum* spp. 的丰度在黄铁矿发生氧化前很低(Huang et al., 2011); 而在极酸性尾矿中, *Ferrovum* 成为优势种群, 其在铅锌矿尾矿的生物地球化学过程中具有重要作用(Tan et al., 2008; Huang et al., 2016)。也有研究表明, AMD 微生物多样性在体系 pH 低于 3.0 时才出现显著下降(Chen et al., 2014)。值得注意的是, AMD 系统微生物群落 Simpson 多样性指数的结果符合中期物种丰富度假说(Howard et al., 2003), 即尾矿酸化中期微生物物种最丰富。最后, 在 AMD 自然衰减过程中, 由于酸胁迫程度降低, 产酸铁硫氧化菌和(类)金属相关菌群以及特定菌群的丰度呈上升趋势(Liu et al., 2019c)。

2.1.2 不同生物膜发育过程

AMD 系统中微生物群落结构、代谢过程和功能表达均以生物膜为发生场所(Denef et al., 2010)。生物膜发育一般经历初始粘附阶段(低发育)、成熟阶段(高发育)和分离阶段, 而不同基因型微生物群体在生物膜发育的不同阶段占主导地位(图 2c)(Wilmes et al., 2009a; Liu et al., 2020), 表明这种群落分化可能引发不同的生态策略(Denef et al., 2010)。在生物膜中观察到的微尺度上的异质性反映了 AMD 生态系统中微生物群落的高度多样性(Simmons et al., 2008; Yelton et al., 2013; Røder et al., 2019; Pandey et al., 2021), 证明了 AMD 细菌和古菌在相对较短的时间尺度(几年)上通过突变、迁移和基因重组(包括质粒或噬菌体的水平基因转移)发生进化(Yelton et al., 2013)。在生物膜低发育阶段, 来自嗜铁氧化的 *Leptospirillum* II 细菌的蛋白质占据蛋白质组的绝大多数; 而在成熟

阶段, 生物膜定植体蛋白质丰度较高, 古菌占据优势地位(Mueller et al., 2010), 此时生物膜上的微生物具有更多样的异养代谢过程(Wilmes et al., 2009b; Justice et al., 2012)。快速的适应性进化促使 *Leptospirillum* II 种群成为成熟生物膜中的主要初级生产者和最活跃的铁氧化菌, 从而推动了 AMD 的形成(Denef et al., 2012)。

2.1.3 不同生物处理过程

微生物是 AMD 生物处理器的主导者, 而生物处理效率的提高有赖于对其群落组成、功能和基因的深入探析。在 AMD 生物处理过程中, 系统 pH 逐渐上升, 微生物群落的结构和丰度都发生了变化(图 2d)(彭珂萍等, 2020), 其中, 古菌总数量在不同生物处理阶段之间波动, 真菌群落丰度则随着处理时间的推移出现波动或下降, 而细菌丰度呈先上升后下降趋势(Drury, 1999; Deng et al., 2016; Coral et al., 2018)。在连续搅拌槽式反应器中, 由于厌氧环境不适合某些微生物生存, 微生物丰度在生物处理过程中呈逐渐下降趋势(Akinpelu et al., 2021)。此时, 严格厌氧和兼性厌氧的厚壁菌门微生物之间表现出协同作用, 从而成为 AMD 生物处理器中的优势菌群(Kamika et al., 2014; Méndez-García et al., 2015; Teng et al., 2017), 尤其是芽孢杆菌(*Bacillus* spp.), 对 AMD 的极酸性具有较高的适应能力, 是对受污染环境进行生物修复的理想材料(Coral et al., 2018; Akinpelu et al., 2021)。随着 AMD 生物处理进程的推进, 携带关键功能基因的微生物种群丰度和多样性不断增加, 尤其是硫酸盐还原菌(Lin et al., 2021)。

2.1.4 季节演替

水热驱动的干湿季变化导致 AMD 环境条件(温度、养分、水量补给等)出现季节性变化(图 2a、b)(Fonyuy et al., 2008), 其微生物群落多样性、优势种群一般也随之发生相应的季节性变化(Baker et al., 2009; Tan et al., 2009; Hao et al., 2017; Xin et al., 2021)。雨季 AMD 生物膜易被雨水冲洗, 依附生物膜生长的特定菌群的多样性可能会下降(Denef et al., 2012)。例如, 加利福尼亚州铁矿 AMD 生物膜中细菌种群比例以 1 月份的最高(95%), 真核生物几乎不存在; 而古菌群落比例以 7 月和 9 月的最高(50%), 冬季几乎不存在。研究揭示了细菌和古菌种群变化与电导率和降雨量存在相关关系(Edwards et al., 1999)。对安徽省南山受 AMD 污染湖泊的研究也证实了原核生物群落和真核生物群落均表现出强烈的季节性变化, 其中真核生物群落季节变化比原核生物群落变化更剧烈; 光自养藻类(初级生产者)与原生动物

或鞭毛虫（顶级消费者）为适应四季更替形成了独特的食物网，温度是主导这些微生物群落季节性变化的环境因子；棕鞭藻和衣藻（导致冬季高水华）因生长温度不同，分别出现在秋夏季和冬春季（Hao et al., 2017; Xin et al., 2021; 裴理鑫等, 2016; 曹子敏等, 2019）。Lake Paitu 的原核生物组成存在明显的季节变化，但在大多数季节，*Ferrovum* 是主要的铁氧化细菌；衣藻是该湖泊主要的真核生物，在 12 月底高度繁殖，为异养细菌提供了丰富的营养物质（Xin et al., 2021）。而在樊口尾砂氧化带和氧化锋中，以嗜酸 *Ferroplasma acidiphilum* 为主的古菌是该矿区土著原核微生物的优势物种，季节变化虽未导致土著微生物群落组成发生显著变化，但春季微生物多样性指数显著高于冬季，且优势物种丰度也发生了一定变化（Huang et al., 2011）。

2.2 AMD 微生物组在不同空间尺度上的演变特征

2.2.1 地理隔离

AMD 系统微生物生态学的相关研究表明，pH 是主导 AMD 微生物群落组成、功能和代谢的决定性因素（Sul et al., 2011; Kuang et al., 2013; Huang et al., 2016）。尽管地理距离较远且基质类型不同，AMD 系统微生物主要群体均为嗜酸菌（Sul et al., 2011; Huang et al., 2016）。从尾矿（Gupta et al., 2017）、矿坑（Gonzalez-Toril et al., 2013）、地表水（Villegas-Plazas et al., 2019）、沉积物（Jin et al., 2022）、土壤和孔隙水（Pan et al., 2021）等不同的 AMD 环境中分离出的微生物，其 16S rRNA 序列具有高度相似性（Edwards et al., 2000; Golyshina et al., 2000; Kuang et al., 2013; 谢学辉等, 2009），主要类群均为变形菌门、酸杆菌门、厚壁菌门、硝化螺旋菌门（Nitrospirae）、放线菌门和广古菌门（Euryarchaeota）等，参与这些类群的能量生产、营养代谢和生物反应的基因是该微生物群落结构的主导基因。而来自世界各地的 AMD 系统的微生物群落的 16S rRNA 基因测序数据表明，AMD 水体及生物膜中的微生物群落多样性通常低于受其影响的土壤/沉积物及生物反应器中的（Villegas-Plazas et al., 2019）。地理隔离导致的不同 AMD 空间类型对微生物群落异质性的贡献有限（Kuang et al., 2013）。然而，AMD 环境中的微生物谱系并不是随机分布的，而是在更小的空间尺度上呈现出更强的系统聚类趋势。

2.2.2 局部空间

2.2.2.1 水平分布

在 AMD 特定地点的连续性空间中（图 2a②），其环境地球化学条件常沿水平方向存在多个梯度

分布，如河流上游—下游、梯田下层—上层（刘帆等, 2019），导致其微生物群落结构和功能基因，如异化亚硫酸盐还原酶基因（Moreau et al., 2010）、砷相关基因（Desoeuvre et al., 2016），沿环境化学梯度呈多样性分布。研究人员采集了 AMD 单向径流上游和下游两个位点（相距约 140 m）的生物膜进行研究，发现 *Leptospirillum* III 基因型在上游生物膜中占据主导地位，在下游采集的 3 个生物膜中仅有 1 个出现同类现象，而即使上下游位点都存在 *Leptospirillum* III，其基因组也是不同的（Denef et al., 2012）。在铀浓缩厂的入口和出口处，氧化还原梯度变化塑造了原生含水层厌氧、微氧生境中的微生物群落结构，AMD 的注入使这些微环境中的微生物群落结构发生了剧烈的变化，细菌丰度和多样性都出现大幅下降（Coral et al., 2018）。在受 AMD 污染梯田中，上层田土壤微生物种群以酸杆菌占优，而下层田以广古菌占优，金属杆菌（*Metallibacterium*）、钩端螺杆菌（*Leptospirillum*）和微古念珠菌（*Candidatus microrarchaeum*）显著富集于下层田中，富集在较低层区域的细菌类群具有不同的代谢策略，其固碳和硫酸化过程相对活跃（Xu et al., 2020; Sun et al., 2020b）。在 AMD 汇入河流中，从上游站点的样本中鉴定出的操作分类单元（Operational Taxonomic Unit, OTU）数量更多，微生物多样性也更高（Pan et al., 2021）。

2.2.2.2 垂直分布

在受 AMD 污染的水体（图 2a③）和土壤（图 2a④）/沉积物中，通常存在多个环境化学条件的垂直分布梯度，这种垂直环境梯度驱动了微生物群落多样性和结构的分化，而 pH 值是影响该垂向空间微生物分布格局的关键驱动因素（Gao et al., 2020; She et al., 2021a; Zhou et al., 2022）。相关研究表明，与自然水体的分层相比，AMD 湖泊中 pH、重金属和硫酸盐浓度等的化学分层通常较显著。底层水体由于环境选择压力较小，微生物群落多样性和丰度较高（Torres et al., 2015; Salmon et al., 2017; She et al., 2021a）。原核微生物群落结构在 AMD 湖泊水体垂直梯度上存在显著变化，微生物多样性随深度增加而增大，其中变形菌门在表层水中占主导地位，厚壁菌门和广古菌门则富集于底层，这是由于上层水体承受的酸胁迫较强，导致微生物的环境选择压力突出，故微生物多样性显著降低，物种共现频率升高。这种由酸胁迫主导的环境效应驱动了湖泊 AMD 微生物群的聚集和共存，奠定了 AMD 湖泊微生物群落功能的垂向分布格局（España et al., 2009; Cerón et al., 2014; Falagán et al., 2014）。此外，光强度、溶解氧和有机质含量的垂直变化亦

对 AMD 水体微生物的群落的分布具有重要影响 (Grettenberger et al., 2020; She et al., 2021b)。同样地, 在 AMD 污染土壤中, 酸性水在土壤垂直剖面上引起的地球化学梯度改变了有毒金属形态, 并富集了适应不同环境化学条件的土壤微生物群落 (Li et al., 2019; Pan et al., 2021)。

2.2.3 精细尺度

在精细尺度上研究微生物群落组成和物种丰度的变化有助于准确判定驱动群落结构变化的决定因素 (Doney et al., 2012; Stocker, 2012)。目前, 在 AMD 系统中进行精细尺度上的微生物群落研究鲜有报道, 以 Liang et al. (2017) 研究为代表, 其将采样量定义为不同的独立空间尺度, 研究了不同精细空间尺度 (1 mL—10 L) 下 AMD 微生物群落组成的变化。结果表明, 在门水平上, 大尺度样品中广古菌门的相对丰度明显高于小尺度样品中的, 而厚壁菌门的相对丰度则呈现相反的趋势; 在属水平上, γ -Proteobacteria 和 *Nitrospira* 的相对丰度在不同空间尺度上存在显著差异, 而 α -Proteobacteria 的丰度在不同空间尺度上保持相对稳定。微生物群落组成具有明显的空间体积依赖性, 空间尺度差异越大, 样品间微生物群落组成差异越显著。研究推测, 群落组成在精细尺度上的异质性可能是共存物种之间相互作用的结果 (Stocker, 2012), 生物和生态相互作用驱动细菌群落重组的速率比水体本身的物理运动速率更快 (Yannarell et al., 2004; Yannarell et al., 2005; Lear et al., 2009)。

3 微生物驱动的 AMD 系统 Fe-S 生物地球化学循环

在 AMD 生态系统中, 铁和硫的微生物氧化是产生 Fe^{3+} 和 SO_4^{2-} 的重要地球化学过程, 且在特定环境条件下, 铁还原菌 (IRB) 和硫酸盐还原菌 (SRB) 可以还原 Fe^{3+} 和 SO_4^{2-} , 完成该生态系统的铁硫循环 (Baker et al., 2003; Schippers et al., 2010; Sahoo et al., 2021)。在 $\text{pH}<3$ 的 AMD 中, 铁硫元素的氧化以微生物作用为主, 如氧化亚铁钩端螺旋杆菌 (*Leptospirillum ferrooxidans*) (Vera et al., 2013)、氧化亚铁硫杆菌 (*Acidithiobacillus ferrooxidans*) (Feng et al., 2022) 等均能加速金属硫化物的氧化, 该微生物氧化速率比化学氧化速率高 30—300 倍 (Nordstrom et al., 2018)。AMD 酸度沿水流方向逐渐衰减, 水体中的 Fe^{3+} 和 SO_4^{2-} 在该衰减过程中极易发生再沉淀, 形成多种铁硫次生矿物。此过程消耗了水体中部分 O_2 和 H^+ , 致使 AMD 水体出现局部相对厌氧和中性环境, 为 *Citrobacter* sp.、*Geobacter*、*Acidiphilium*、*Desulfovibrio*、

Thiomonas 和 *Halethiobacillus* 等 IRB 和 SRB 的生长、代谢创造了生存条件 (Garcia-Rios et al., 2021; 汪涵, 2018; 姜梦戈, 2020)。这些次生矿物的稳定性差, 而 Fe-S 功能微生物群的存在使得 AMD 中的次生矿物极易发生矿相转变, 形成结晶度更高的赤铁矿、针铁矿等 (Bao et al., 2018)。此外, 在 AMD 生物修复过程中, 铁氧化菌可充分将 Fe^{2+} 及其他重金属元素氧化, 进而通过吸附、沉淀去除 AMD 系统中的金属元素; 在外源有机物支持下, AMD 水体 SRB 可高效还原 SO_4^{2-} , 促进金属硫化物沉淀从而净化 AMD (方迪等, 2010); 同时, 该过程产生的碱度 (HCO_3^-) 可提高处理水体 pH (Senko et al., 2009; Deng et al., 2016; Singh et al., 2022; 方迪等, 2010)。

近些年来, 研究人员对硫化物的地球化学和微生物学进行了大量研究, 以了解 AMD 生态系统中微生物群落和功能多样性的形成机制 (Moreau et al., 2010; Giloteaux et al., 2013; Méndez-García et al., 2015; Quatrini et al., 2018; Sun et al., 2020a; Qian et al., 2021)。研究表明, 影响 AMD 污染梯田微生物多样性和相互作用的主要环境因子是 pH、Fe(III) 和硫酸盐 (Xu et al., 2020)。在受 AMD 长期影响的水体中, 铁和硫代谢微生物占主导地位, 是介导硫酸盐矿物转化的功能微生物 (Bao et al., 2018), 同时不同的嗜酸性微生物群在极端酸性环境中占据不同的生态位, 进而通过对铁和硫的代谢作用反作用于酸性环境 (Xin et al., 2021)。例如, β -Proteobacteria 中的 *Ferroplasma* 在 AMD 环境中具有重要的生物地球化学循环作用, 主要是促进铁的快速氧化 (Hallberg et al., 2006; Havig et al., 2017), 常与异养嗜酸菌或其他铁氧化菌共存 (Kipry et al., 2013); *Leptospirillum* 也可能参与金属和硫代谢, 一般认为其为携带异化硫酸盐还原基因的铁氧化菌 (Goltsman et al., 2009)。特定 AMD 系统的不同位点中总 S 和 SO_4^{2-} 含量的显著变化可能导致硫代谢微生物群落和功能的差异。随着 SO_4^{2-} 浓度的降低, 与 S 循环有关的功能基因 *dsrAB* 和 *aprAB* 的丰度也相应降低, 表明较高的 SO_4^{2-} 浓度可能促使硫酸盐发生生物还原反应 (Sun et al., 2020a)。总 Fe 和 Fe(III) 均与 S 氧化、 SO_4^{2-} 还原显著相关, 表明铁代谢相关微生物对 S 的地球化学循环具有影响 (Valente et al., 2008; Chen et al., 2014; Liu et al., 2014; Sun et al., 2020a; Pan et al., 2021)。

综上所述, AMD 系统 Fe-S 生物地球化学梯度对微生物群落结构和功能具有显著的影响, 而铁和硫的相关微生物种群对环境梯度变化的响应又驱动 Fe-S 生物地球化学循环。

4 微生物对 AMD 生物成矿的控制机制

4.1 矿物在 AMD 系统中的演变特征及环境效应

AMD 环境中矿物的种类、赋存状态、理化性质决定了其污染潜力和环境危害性 (Gomes et al., 2006; Valente et al., 2009), 其性能由其所处环境的地球化学条件决定 (Valente et al., 2013; Meng et al., 2014), 如离子浓度、酸度、水含氧量等。微生物介导了 AMD 硫化矿物溶解 (McGuire et al., 2001), 同时, 原生矿物再沉淀形成次生矿物的过程也与微生物作用密切相关 (Clarke et al., 1997; Sanchez-Espana et al., 2011; Caraballo et al., 2019)。铁元素广泛存在于金属硫化物中, 因此铁氧化物矿物是最普遍的次生矿物, 主要包括赤铁矿、施氏矿物、黄钾铁矾和针铁矿等。这些次生矿物具有巨大的比表面积、丰富的表面官能团、较强的吸附能力和良好的沉淀作用, 可在不同 pH 条件下吸附、络合、共沉淀 AMD 系统中的金属元素, 实现水体自净 (Burgos et al., 2012; Ayora et al., 2016; Baleeiro et al., 2018; Zhang et al., 2021; 周立祥, 2008)。

近年来, 对 AMD 系统铁相次生矿物的类型、特征、形成条件和环境响应等方面进行了大量研究, 发现 IRB 和 SRB 都能介导施氏锰矿石和黄钾铁矾的转化 (Senko et al., 2009; Coggon et al., 2012; Carbone et al., 2013), 微生物活性是驱动 AMD 河流沉积物中施氏矿物、黄钾铁矾转化为针铁矿的主要作用力 (Bao et al., 2018), 针铁矿的沉淀和相变过程在控制 AMD 有毒微量金属的环境化学行为中发挥着重要作用 (Jiang et al., 2013; Kim et al., 2014; Baleeiro et al., 2018; Hajji et al., 2019; Kim et al., 2021)。然而, 在多变的地球化学条件下, 某些相变是可逆的, 如施氏矿物可能转化为针铁矿或黄钾铁矾, 黄钾铁矾可能被针铁矿或施氏矿物取代 (Samborska et al., 2013)。若环境中缺乏足够的钾, 则可能形成黄铵铁矾或草黄铁矾等; 若环境中含有较多的 PO_4^{3-} , 可能形成红磷铁矿等磷酸盐矿物 (Lu et al., 2019)。pH<3 时, 富含 Na^+ 、 K^+ 、 NH_4^+ 等一价阳离子的 AMD, 在微生物诱导下容易形成黄铁矾类矿物; 当 AMD 中一价阳离子浓度较低时, 则易形成施氏矿物 (Zhu et al., 2012; Vithana et al., 2015; 周立祥, 2008)。微生物促使 AMD 铁硫次生矿物发生矿相转变的第一步是 Fe(III) 的还原 (Bao et al., 2018), 在 pH 较高和相对厌氧环境中, IRB 和 SRB 直接将次生矿物中的 Fe(III) 还原为 Fe(II) (Jones et al., 2006; Ouyang et al., 2014)。第二步是稳定相矿物的形成 (Ouyang et al., 2014), 微生物还原产生的 Fe(II) 极易被吸附在不稳定相矿物表面, 在厌氧条件下与矿物中的 Fe(III) 发生电子

转移, 从而催化针铁矿的形成 (Burton et al., 2007)。

微生物作用类型及环境化学微环境决定了生物成矿的终点物质的类型、形态和性质 (Rodriguez-Navarro et al., 2007; Baumgartner et al., 2013; Hasiotis et al., 2019), 同时, MMI 驱动了 AMD 矿物的演变过程、相变平衡及金属元素赋存形态的动态变化, 对 AMD 污染水体净化具有重要作用 (Liu et al., 2018; Lu et al., 2021; 刘奇缘等, 2017)。

4.2 AMD 微生物-矿物相互作用机制

AMD 微生物成矿作用是生物和非生物反应相互作用的结果 (Melton et al., 2014)。AMD 系统元素地球化学行为受次生矿物的反应 (如氢氧化铁的溶解) 的强烈控制 (Elghali et al., 2021), 而微生物可以通过直接或间接氧化还原反应参与 AMD 铁生物地球化学循环 (Melton et al., 2014)。大部分可溶性 Fe(II) 和 Fe(III) 与溶解有机物络合充当电子穿梭体极大地促进了微生物铁循环, 加速了微生物介导的整个氧化还原过程 (Kügler et al., 2019)。

目前的共识是铁氧化微生物在无氧和微氧环境中通过铁氧化过程获取能量, 分泌带状胞外有机物 (生物大分子) 作为“模板”, 调控矿物的生长 (Banfield et al., 2000; Chan et al., 2011; 徐轶群等, 2013)。这些有机物主要是由一些含有高比例酸性氨基酸 (特别是天冬氨酸) 和磷酸化酶组分的蛋白质、多糖和糖蛋白组成的大分子群, 能有序调节参与形成生物矿物所必需的组分。微生物细胞通过细胞膜主动泵吸胞内阳离子或通过胞内囊泡富集阳离子, 然后将阳离子运输至“模板”的某个区域, 构成“就地”成矿点, 在特定酶的催化下连续不断地进行矿化作用, 导致 AMD 局部环境中的 pH-Eh 发生变化 (Elghali et al., 2021; Lee et al., 2022; 贾蓉芬等, 2009)。铁还原菌在厌氧环境中与 Fe(III) 矿物接触时, 通过菌毛等特殊结构直接将自身代谢产生的带有特殊官能团 ($-\text{SH}$ 、 $-\text{OH}$ 、 $-\text{NH}_2$ 、 $-\text{COO}$ 等) 的生物大分子传递至矿物表面, 或将由胞内外的有机基质产生的电子穿梭传递至矿物表面, 从而还原 Fe(III) 矿物, Fe(II) 又在矿物表面与 Fe(III) 发生电子转移, 催化稳定相铁矿物的合成 (Burton et al., 2007; Luef et al., 2013)。

在微生物成矿过程中, 一方面, 生物大分子携带的特殊功能团的键能决定了矿化产物的类型, 另一方面, 生物大分子的结构决定了矿物成核的位置和形态 (贾蓉芬等, 2009), 特定晶型的出现遵循能量最小化原则, 即有机物调控下生长的矿物晶体消耗生物体最少的能量 (Pacella et al., 2018)。微生物-矿物结构是一个高度动态的

系统 (Lower et al., 2001; Shi et al., 2016), 在此复杂系统中, 微生物细胞-有机质-矿物三者之间相互作用、相互影响, 导致产生复杂的环境-生物地球化学过程异质性 (Benzerara et al., 2011; Zhu et al., 2015b)。

由上可知, 含铁矿物质的形成受微生物群落结构、功能和代谢作用及环境化学条件共同控制 (Johannessen et al., 2017), 且生物矿化中的生物物质矿物形态受分子模板、矿物-微生物界面性质等因素的影响 (Gilbert et al., 2005)。微生物膜与矿物界面是一个化学梯度大、反应活性分子集中、氧化还原作用活跃的微观界面, 是矿物发生表面侵蚀和氧化分解的活跃界面 (Mielke et al., 2003; Zhu et al., 2014)。通过挖掘矿物-微生物界面表面微观结构、组成、形态和功能的演变, 可以得到相关的微观表型性状, 该性状可由矿物和微生物胞外聚合物 (Extracellular Polymeric Substances, EPS) 的表面性质定义 (Zhang et al., 2014; Hao et al., 2016)。由 EPS 介导的细胞和矿物之间的接触促进了矿物的溶解, 为矿物的化学行为提供了反应空间 (Sand et al., 2006)。其中, 表面反应控制是 AMD 微生物-矿物相互作用的关键机制 (Su et al., 2020; Xia et al., 2020), 而接触机制则是矿物发生微生物氧化的主导机制 (陆现彩等, 2019)。首先, 细胞粘附矿物表面, 形成 AMD 生物膜雏形 (Zhu et al., 2015a; Li et al., 2016); 其次, 嗜酸性微生物 (如 *Ferroplasma* spp.) 在酸性环境中分泌的大量膜脂 (Macalady et al., 2004) 极大地促进了生物膜的形成, 微生物得以快速繁衍; 最后, 随着时间的推移, 细菌胞体在与其接触的矿物表面覆盖了一层致密的生物膜, 通过多层吸附实现其与矿物之间的表面相互作用, 直至将矿物侵蚀 (Su et al., 2020)。

此外, AMD 矿物的微生物还原遵循电化学过程, 胞外电子传递 (Extracellular Electron Transfer, EET) 是该作用过程的一个关键步骤 (Lovley, 2008; Rozendal et al., 2008; Ni et al., 2018)。这是由于 EET 过程是微生物胞外呼吸作用的重要组成部分, 影响着 AMD 环境中的物质转变和能量交换; 而胞外呼吸又是微生物的主要能量代谢方式, 是微生物与胞外受体间进行电子传递的主要方式 (陈丹丹等, 2017; 张多瑞等, 2018)。具体表现为内层生物膜上的微生物通过鞭毛 (如 *Geobacter sulfurreducens* 的 IV 型鞭毛是一种纳米导线) 搭建导电网络, 形成多级电子跃迁机制, 而外层细胞膜上丰富的 c-型细胞色素直接与矿物表面接触, 进行直接电子传递 (Malvankar et al., 2014)。

值得注意的是, 含铁矿物是 AMD 系统微生物胞外呼吸最重要的电子受体之一 (张玉龙等, 2021), 微生物铁呼吸过程伴随大量 H^+ 的消耗, 改变了 AMD 系统碳、氮、硫元素循环, 同时耦合多种重金属的迁移转化, 从而改变微生物的生长与竞争关系, 导致 AMD 系统微生物群落、功能和代谢等的演化。

5 结论与展望

预测 AMD 微生物群落组成和功能性状随环境变化的动态过程是 AMD 系统生态学研究的一个重要目标, 目前仍是一个重大挑战。微生物组学研究获得的微生物群落结构、功能、代谢等信息为在系统水平上理解 AMD 微生物生态学的时空演变提供了丰富的科学证据。AMD 微生物群落组成和功能性状在不同时空尺度和地球化学梯度上的演替特征研究将有助于阐明微生物群落及其生态功能对极端酸性环境变化的响应, 有助于揭示优势物种和稀有物种在 AMD 生物处理中的生态作用。AMD 极端环境中的微生物多样性模式与 Fe-S 生物地球化学循环过程紧密联系, 微生物群落功能控制 AMD 金属离子的生物地球化学过程, 同时微生物群落与地球化学条件的相互作用驱动了其自身的生态适应性进化。未来仍可通过整合微生物组学技术探索 AMD 微生物组对极端环境胁迫的响应机制及其对 AMD 生物成矿的控制机制, 为 AMD 生物处理系统的优化和维护提供进一步指导。

虽然目前研究人员已掌握了 AMD 微生物成矿的基本过程, 但是其微生物-矿物相互作用的具体机制尚不明确, 尤其在不同的 AMD 环境化学梯度下, 微生物-矿物互作关系如何演化, 主导其演化的基因如何编码 Fe 转运蛋白、细胞色素、细菌鞭毛等的机制研究匮乏。现代环境分析显微镜技术被广泛应用于生物物质矿物的高分辨率结构和组成分析, 可直观呈现微生物-矿物聚合体的微观晶体化学特征 (Mann, 1987; McLaren, 1991)。光谱学分析可以表征微生物介导的生物物质矿物晶型转变 (Geesey et al., 2002)、界面电子转移 (Williams et al., 2004) 以及光谱诱导矿物极化特征 (Zhang et al., 2012) 等。此外, 大型同步辐射科学设备和超级计算中心的发展 (Xia et al., 2020), 为 AMD 微生物-矿物聚合体的表型组学研究提供了技术支撑。未来可通过整合微生物组学方法和矿物学分析技术 (XPS、FTIR、FIB-SEM、TEM、XRD 等), 系统地探索 AMD 不同环境地球化学条件下的微生物组-矿物组的表型关系, 从而揭示生命和矿物在极端酸性环境中协同演化的微观机制。

参考文献:

- ABINANDAN S, PERERA I A, SUBASHCHANDRABOSE S R, et al., 2020. Acid-adapted microalgae exhibit phenotypic changes for their survival in acid mine drainage samples [J]. *FEMS Microbiology Ecology*, 96(11): 1-12.
- ABINANDAN S S R, SUBASHCHANDRABOSE N, COLE R, et al., 2019. Sustainable production of biomass and biodiesel by acclimation of non-acidophilic microalgae to acidic conditions [J]. *Bioresource Technology*, 271: 316-324.
- AKCIL A, SONER K, 2006. Acid mine drainage (AMD): Causes, treatment and case studies [J]. *Journal of Cleaner Production*, 14(12): 1139-1145.
- AKINPELU E A, NTWAMPE S K O, FOSSO-KANKEU E, et al., 2021. Performance of microbial community dominated by *Bacillus* spp. in acid mine drainage remediation systems: A focus on the high removal efficiency of SO_4^{2-} , Al^{3+} , Cd^{2+} , Cu^{2+} , Mn^{2+} , Pb^{2+} and Sr^{2+} [J]. *Heliyon*, 7(6): e07241.
- ALLEN, ERIC E, JILLIAN F, BANFIELD, 2005. Community genomics in microbial ecology and evolution [J]. *Nature Reviews Microbiology*, 3(6):489-498.
- ANANTHARAMAN K, CHRISTOPHER B, LAURA H, et al., 2016. Thousands of microbial genomes shed light on interconnected biogeochemical processes in an aquifer system [J]. *Nature Communications*, 7(1): 13219.
- ANGÉLIQUE D, CASIOT C, HÉRY M, 2016. Diversity and distribution of arsenic-related genes along a pollution gradient in a river affected by acid mine drainage [J]. *Microbial Ecology*, 71(3): 672-685.
- AYORA C, MACÍAS F, TORRES E, et al., 2016. Recovery of rare earth elements and yttrium from passive remediation systems of acid mine drainage [J]. *Environmental Science & Technology*, 50(15): 8255-8262.
- BAKER B J, BANFIELD J F, 2003. Microbial communities in acid mine drainage [J]. *FEMS Microbiology Ecology*, 44(2): 139-152.
- BAKER B, TYSON G, GOOSHERST L, et al., 2009. Insights into the diversity of eukaryotes in acid mine drainage biofilm communities [J]. *Applied and Environmental Microbiology*, 75(7): 2192-2199.
- BALEEIRO A, FIOLE S, OTERO-FARIÑA A, et al., 2018. Surface chemistry of iron oxides formed by neutralization of acidic mine waters: Removal of trace metals [J]. *Applied Geochemistry*, 89: 129-137.
- BANFIELD J F, WELCH S, ZHANG H Z, et al., 2000. Aggregation-based crystal growth and microstructure development in natural iron oxyhydroxide biomineralization products [J]. *Science (New York)*, 289: 751-754.
- BAO Y P, GUO C L, LU G N, et al., 2018. Role of microbial activity in Fe(III) hydroxysulfate mineral transformations in an acid mine drainage-impacted site from the Dabaoshan Mine [J]. *Science of The Total Environment*, 616-617: 647-657.
- BARTSCH K, KNITTLER K, BOROWSKI C, et al., 2017. Absence of RNase H₂ triggers generation of immunogenic micronuclei removed by autophagy [J]. *Human molecular genetics*, 26(20): 3960-3972.
- BAUMGARTNER J, MORIN G, MENGUY N, et al., 2013. Magnetotactic bacteria form magnetite from a phosphate-rich ferric hydroxide via nanometric ferric (oxyhydr) oxide intermediates [J]. *Proceedings of the National Academy of Sciences*, 110(37): 14883.
- BELNAP C, PAN C, DENEFF V, et al., 2011. Quantitative proteomic analyses of the response of acidophilic microbial communities to different pH conditions [J]. *The ISME Journal*, 5(7): 1152-1161.
- BELNAP C, PAN C, VERBERKMOES N, et al., 2010. Cultivation and quantitative proteomic analyses of acidophilic microbial communities [J]. *The ISME Journal*, 4(4): 520-530.
- BENZERARA K, MIOT J, MORIN G, et al., 2011. Significance, mechanisms and environmental implications of microbial biomineralization [J]. *Comptes Rendus Geoscience*, 343(2): 160-167.
- BURGOS W D, BORCH T, TROYER L D, et al., 2012. Schwertmannite and Fe oxides formed by biological low-pH Fe(II) oxidation versus abiotic neutralization: Impact on trace metal sequestration [J]. *Geochimica et Cosmochimica Acta*, 76: 29-44.
- BURTON E D, BUSH R T, SULLIVAN L A, et al., 2007. Reductive transformation of iron and sulfur in schwertmannite-rich accumulations associated with acidified coastal lowlands [J]. *Geochimica et Cosmochimica Acta*, 71(18): 4456-4473.
- CARABALLO M A, WANTY R B, VERPLANCK P L, et al., 2019. Aluminum mobility in mildly acidic mine drainage: Interactions between hydrobasaluminite, silica and trace metals from the nano to the meso-scale [J]. *Chemical Geology*, 519: 1-10.
- CARBONE C, DINELLI E, MARESCOTTI P, et al., 2013. The role of AMD secondary minerals in controlling environmental pollution: Indications from bulk leaching tests [J]. *Journal of Geochemical Exploration*, 132: 188-200.
- CERÓN, J, MARIA T, JOSÉ B, et al., 2014. Hydrochemical characterization of an acid mine drainage-affected reservoir: The Sancho Reservoir, Huelva, southwest Spain [J]. *Hydrological Sciences Journal*, 59(6): 1213-1224.
- CHAN C, SIRINE F, DAVID E, et al., 2011. Lithotrophic iron-oxidizing bacteria produce organic stalks to control mineral growth: Implications for biosignature formation [J]. *The ISME Journal*, 5(4): 717-727.
- CHEN L X, HUANG L N, MÉNDEZ-GARCÍA C, et al., 2016. Microbial communities, processes and functions in acid mine drainage ecosystems [J]. *Current Opinion in Biotechnology*, 38: 150-158.
- CHEN LIN X, LI J T, CHEN Y T, et al., 2013. Shifts in microbial community composition and function in the acidification of a lead/zinc mine tailings [J]. *Environmental Microbiology*, 15(9): 2431-2444.
- CHEN Y T, LI J T, CHEN L X, et al., 2014. Biogeochemical processes governing natural pyrite oxidation and release of acid metalliferous drainage [J]. *Environmental Science & Technology*, 48(10): 5537-5545.
- CLARKE W A, KONHAUSER K O, JULIA C, et al., 1997. Ferric hydroxide and ferric hydroxysulfate precipitation by bacteria in an acid mine drainage lagoon [J]. *FEMS Microbiology Reviews*, 20(3): 351-361.
- COGGON M, BECERRA C A, NÜSSLEIN K, et al., 2012. Bioavailability of jarosite for stimulating acid mine drainage attenuation [J]. *Geochimica et Cosmochimica Acta*, 78: 65-76.
- CORAL T, MICHAËL D, HÉLÈNE D B, et al., 2018. Microbial communities associated with uranium in-situ recovery mining process are related to acid mine drainage assemblages [J]. *Science of The Total Environment*, 628-629: 26-35.
- DEAN A P, ANTONI H, OWEN A, et al., 2019. Metabolic adaptation of a *Chlamydomonas acidophila* strain isolated from acid mine drainage ponds with low eukaryotic diversity [J]. *Science of the Total Environment*, 647: 75-87.
- DENEFF V, BANFIELD J, 2012. In situ evolutionary rate measurements show ecological success of recently emerged bacterial hybrids [J]. *Science (New York)*, 336: 462-466.

- DENEFF V, MUELLER R, BANFIELD J, 2010. AMD biofilms: Using model communities to study microbial evolution and ecological complexity in nature [J]. *The ISME Journal*, 4(5): 599-610.
- DENG D Y, WEIDHAAS J L, LIN L S, 2016. Kinetics and microbial ecology of batch sulfidogenic bioreactors for co-treatment of municipal wastewater and acid mine drainage [J]. *Journal of Hazardous Materials*, 305: 200-208.
- DONEY S C, RUCKELSHAUS, DUFFY M J E, et al., 2012. Climate change impacts on marine ecosystems [J]. *Annual Review of Marine Science*, 4: 11-37.
- DRENNAN D M, DINA M, ROBERT A, et al., 2017. Spatial impacts of inorganic ligand availability and localized microbial community structure on mitigation of zinc laden mine water in sulfate-reducing bioreactors [J]. *Water Research*, 115: 50-59.
- DRURY W J, 1999. Treatment of acid mine drainage with anaerobic solid-substrate reactors [J]. *Water Environment Research*, 71(6): 1244-1250.
- EDWARDS K J, BOND P L, GIHRING T M, et al., 2000. An archaeal iron-oxidizing extreme acidophile important in acid mine drainage [J]. *Science*, 287(5459): 1796-1799.
- EDWARDS K J, GIHRING T M, BANFIELD J F, 1999. Seasonal variations in microbial populations and environmental conditions in an extreme acid mine drainage environment [J]. *Applied and Environmental Microbiology*, 65(8): 3627-3632.
- ELGHALI A, MOSTAFA B, HASSAN B, et al., 2021. Role of secondary minerals in the acid generating potential of weathered mine tailings: crystal-chemistry characterization and closed mine site management involvement [J]. *Science of the Total Environment*, 784: 147105.
- ESPAÑA, J, PAMO E, DIEZ M, et al., 2009. Physicochemical gradients and meromictic stratification in Cueva de la Mora and other acidic pit lakes of the Iberian Pyrite Belt [J]. *Mine Water and The Environment*, 28: 15-29.
- FONYUY E W, ATEKWANA E A, 2008. Effects of acid mine drainage on dissolved inorganic carbon and stable carbon isotopes in receiving streams [J]. *Applied Geochemistry*, 23(4): 743-764.
- GARCIA-RIOS M, DE WINDT L, LUQUOT L, et al., 2021. Modeling of microbial kinetics and mass transfer in bioreactors simulating the natural attenuation of arsenic and iron in acid mine drainage [J]. *Journal of Hazardous Materials*, 405: 124133.
- GEESEY G G, NEAL A L, SUCI P A, et al., 2002. A review of spectroscopic methods for characterizing microbial transformations of minerals [J]. *Journal of Microbiological Methods*, 51(2): 125-139.
- GILBERT P U P A, ABRECHT M, FRAZER B H, 2005. The organic-mineral interface in biominerals [J]. *Reviews in Mineralogy & Geochemistry*, 59: 157-185.
- GILOTEAUX L, DURAN R, CASIOT C, et al., 2013. Three-year survey of sulfate-reducing bacteria community structure in Carnoulès acid mine drainage (France), highly contaminated by arsenic [J]. *FEMS Microbiology Ecology*, 83(3): 724-737.
- GOLTSMAN D S A, DENEFF V J, SINGER S W, et al., 2009. Community genomic and proteomic analyses of chemoautotrophic iron-oxidizing "*Leptospirillum rubrum*" (Group II) and "*Leptospirillum ferrodiazotrophum*" (Group III) bacteria in acid mine drainage biofilms [J]. *Applied and Environmental Microbiology*, 75(13): 4599-4615.
- GOLYSHINA O, PIVOVAROVA T A, KARAVAIKO G, et al., 2000. *Ferroplasma acidiphilum* gen. nov., sp. nov., an acidophilic, autotrophic, ferrous-iron-oxidizing, cell-wall-lacking, mesophilic member of the *Ferroplasmaceae* fam. nov., comprising a distinct lineage of the Archaea [J]. *International Journal of Systematic and Evolutionary Microbiology*, 50(3): 997-1006.
- GOMES M E P, FAVAS P J C, 2006. Mineralogical controls on mine drainage of the abandoned Ervedosa tin mine in north-eastern Portugal [J]. *Applied Geochemistry*, 21(8): 1322-1334.
- GONZALEZ-TORIL E, SANTOFIMIA E, LOPEZ-PAMO E, et al., 2013. Microbial ecology in extreme acidic pit lakes from the Iberian Pyrite Belt (SW Spain) [M]/Integration of Scientific and Industrial Knowledge on Biohydrometallurgy. *Advanced Materials Research*, 825: 23-27.
- GUPTA A, DUTTA A, SARKAR J, et al., 2017. Metagenomic exploration of microbial community in mine tailings of Malanjkhand copper project, India [J]. *Genomics Data*, 12(1): 11-13.
- HAJJI S, MONTES-HERNANDEZ G, SARRET G, et al., 2019. Arsenite and chromate sequestration onto ferrihydrite, siderite and goethite nanostructured minerals: Isotherms from flow-through reactor experiments and XAS measurements [J]. *Journal of Hazardous Materials*, 362(2): 358-367.
- HALLBERG K B, COUPLAND KRIS, KIMURA S, et al., 2006. Macroscopic streamer growths in acidic, metal-rich mine waters in North Wales consist of novel and remarkably simple bacterial communities [J]. *Applied and Environmental Microbiology*, 72(3): 2022-2030.
- HALLBERG K B, 2010. New perspectives in acid mine drainage microbiology [J]. *Hydrometallurgy*, 104(3-4): 448-453.
- HANDELSMAN J, RONDON M R, BRADY S F, et al., 1998. Molecular biological access to the chemistry of unknown soil microbes: A new frontier for natural products [J]. *Chemistry & Biology*, 5(10): R245-R249.
- HAO C, WEI P, PEI L, et al., 2017. Significant seasonal variations of microbial community in an acid mine drainage lake in Anhui Province, China [J]. *Environmental Pollution*, 223(5): 507-516.
- HAO L, GUO Y, BYRNE J M, et al., 2016. Binding of heavy metal ions in aggregates of microbial cells, EPS and biogenic iron minerals measured in-situ using metal- and glycoconjugates-specific fluorophores [J]. *Geochimica et Cosmochimica Acta*, 180: 66-96.
- HASIOTIS S T, BRAKE S S, 2019. Macroscopic and microscopic morphological features of stromatolites related to activity of eukaryote-dominated biofilms in an acid mine drainage environment: Biosignatures and understanding preservation of stromatolites as trace fossils [J]. *Geomicrobiology Journal*, 36(7): 651-671.
- HAVIG J R, HAMILTON T L, BACHAN A, et al., 2017. Sulfur and carbon isotopic evidence for metabolic pathway evolution and a four-stepped earth system progression across the Archean and Paleoproterozoic [J]. *Earth-Science Reviews*, 174: 1-21.
- HIROOKA S, HIROSE Y, KANESAKI Y, et al., 2017. Acidophilic green algal genome provides insights into adaptation to an acidic environment [J]. *Proceedings of the National Academy of Sciences of the United States of America*, 114(39): E8304-E8313.
- HOWARD L F, LEE T D, 2003. Temporal patterns of vascular plant diversity in southeastern New Hampshire forests [J]. *Forest Ecology and Management*, 185(1-2): 5-20.
- HUA Z S, HAN Y J, CHEN L X, et al., 2015. Ecological roles of dominant and rare prokaryotes in acid mine drainage revealed by metagenomics and metatranscriptomics [J]. *The ISME Journal*, 9(6): 1280-1294.

- HUANG L N, KUANG J L, SHU W S, 2016. Microbial ecology and evolution in the acid mine drainage model system [J]. *Trends in microbiology*, 24(7): 581-593.
- HUANG L N, ZHOU W H, HALLBERG KEVIN B, et al., 2011. Spatial and temporal analysis of the microbial community in the tailings of a Pb-Zn mine generating acidic drainage [J]. *Applied and Environmental Microbiology*, 77(15): 5540-5544.
- JIANG W, LV J, LUO L, et al., 2013. Arsenate and cadmium co-adsorption and co-precipitation on goethite [J]. *Journal of Hazardous Materials*, 262: 55-63.
- JIN L, GERSON J R, ROCCA J D, et al., 2022. Alkaline mine drainage drives stream sediment microbial community structure and function [J]. *Science of The Total Environment*, 805: 150189.
- JOHANNESSEN K C, VANDER ROOST J, DAHLE H, et al., 2017. Environmental controls on biomineralization and Fe-mound formation in a low-temperature hydrothermal system at the Jan Mayen Vent Fields [J]. *Geochimica et Cosmochimica Acta*, 202: 101-123.
- JOHNSON D B, HALLBERG K B, 2003. The microbiology of acidic mine waters [J]. *Research in Microbiology*, 154: 466-473.
- JONES E, NADEAU T-L, VOYTEK M, et al., 2006. Role of microbial iron reduction in the dissolution of iron hydroxysulfate minerals [J]. *Journal of Geophysical Research*, 111(G1): G000089.
- JUSTICEN B, PANB C, MUELLERA R, et al., 2012. Heterotrophic archaea contribute to carbon cycling in low-pH, suboxic biofilm communities [J]. *Applied and Environmental Microbiology*, 78: 8321-8330.
- KAMIKA I, MOMBA M, 2014. Microbial diversity of emalahleni mine water in south Africa and tolerance ability of the predominant organism to vanadium and nickel [J]. *PLoS One*, 9(1): e86189.
- KIM D K, ZHANG W, HIRIART-BAER V, et al., 2014. Towards the development of integrated modelling systems in aquatic biogeochemistry: A Bayesian approach [J]. *Journal of Great Lakes Research*, 40(S): 73-87.
- KIM H J, KIM Y, 2021. Schwertmannite transformation to goethite and the related mobility of trace metals in acid mine drainage [J]. *Chemosphere*, 269: 128720.
- KIPRY J, JWAI R J, GELHAAR N, et al., 2013. Enrichment of "Ferrovum" spp. and *Gallionella relatives* using artificial mine water [C]. *Advanced Materials Research*, 825: 54-57.
- KUANG J L, HUANG L N, CHEN L X, et al., 2013. Contemporary environmental variation determines microbial diversity patterns in acid mine drainage [J]. *The ISME Journal*, 7(5): 1038-1050.
- KüGLER S, COOPER R E, WEGNER C E, et al., 2019. Iron-organic matter complexes accelerate microbial iron cycling in an iron-rich fen [J]. *Science of The Total Environment*, 646: 972-988.
- LADAU J, ELOE-FADROSH E A, 2019. Spatial, temporal, and phylogenetic scales of microbial ecology [J]. *Trends in microbiology*, 27(8): 662-669.
- LEAR G, NIYOGI D, HARDING J, et al., 2009. Biofilm bacterial community structure in streams affected by acid mine drainage [J]. *Applied and Environmental Microbiology*, 75(11): 3455-3460.
- LEE J S, LITTLE B J, 2022. Chapter 4-Biomineralization: Applied to biodeterioration and bioremediation [C]//AMJAD Z, DEMADIS K D. *Water-Formed Deposits*. Elsevier: 69-77.
- LI H, ZHA J, SUN Q, 2019. Effects of acid mine drainage on the abundance of functional genes involved in nitrogen cycle in soil profiles [J]. *Biotechnology Bulletin*, 35(9): 249-256.
- LI Q, WANG Q, ZHU J, et al., 2016. Effect of extracellular polymeric substances on surface properties and attachment behavior of *Acidithiobacillus ferrooxidans* [J]. *Minerals*, 6(4): 100.
- LIANG J L, LI X J, SHU H Y, et al., 2017. Fine-scale spatial patterns in microbial community composition in an acid mine drainage [J]. *FEMS Microbiology Ecology*, 93(10): 124.
- LIN Y, GREMBI J A, GOOTS S S, et al., 2021. Advantageous microbial community development and improved performance of pilot-scale field systems treating high-risk acid mine drainage with crab shell [J]. *Journal of Hazardous Materials*, 420: 126665.
- LIU J L, YAO J, DURAN R, et al., 2019a. Bacterial shifts during in-situ mineralization bio-treatment to non-ferrous metal (loid) tailings[J]. *Environmental Pollution*, 255: 113165.
- LIU J L, YAO J, LU C, et al., 2019b. Microbial activity and biodiversity responding to contamination of metal (loid) in heterogeneous nonferrous mining and smelting areas [J]. *Chemosphere*, 226: 659-667.
- LIU J L, YAO J, WANG F, et al., 2019c. Bacterial diversity in typical abandoned multi-contaminated nonferrous metal (loid) tailings during natural attenuation [J]. *Environmental Pollution*, 247: 98-107.
- LIU J, HUA Z, CHEN L-X, et al., 2014. Correlating microbial diversity patterns with geochemistry in an extreme and heterogeneous environment of mine tailings [J]. *Applied and Environmental Microbiology*, 80(12): 3677-3686.
- LIU L Z, NIE Z Y, YANG Y, et al., 2018. In situ characterization of change in superficial organic components of thermoacidophilic archaeon *Acidianus manzaensis* YN-25 [J]. *Research in Microbiology*, 169(10): 590-597.
- LIU Q, WANG J, HE R, et al., 2020. Bacterial assembly during the initial adhesion phase in wastewater treatment biofilms [J]. *Water Research*, 184: 116147.
- LO I, DENEFF V, VERBERKMOES N, et al., 2007. Strain-resolved community proteomics reveals recombining genomes of acidophilic bacteria [J]. *Nature*, 446(7135): 537-541.
- LONG P E, WILLIAMS K H, HUBBARD S S, et al., 2016. Microbial metagenomics reveals climate-relevant subsurface biogeochemical processes [J]. *Trends in microbiology*, 24(8): 600-610.
- LOVLEY D, 2008. Extracellular electron transfer: Wires, capacitors, iron lungs, and more [J]. *Geobiology*, 6(3): 225-231.
- LOWER S, TADANIER C, HOCELLA M, 2001. Dynamics of the mineral-microbe interface: Use of biological force microscopy in biogeochemistry and geomicrobiology [J]. *Geomicrobiology Journal*, 18(1): 63-76.
- LOZUPONE C, KNIGHT R, 2007. Global pattern in bacterial diversity [J]. *Proceedings of the National Academy of Sciences of the United States of America*, 104(27): 11436-11440.
- LU C, YANG B, CUI X, et al., 2021. Characteristics and environmental response of white secondary mineral precipitate in the acid mine drainage from Jinduicheng Mine, Shaanxi, China [J]. *Bulletin of Environmental Contamination and Toxicology*, 107(6): 1012-1021.
- LUEF B, FAKRA S, CSENCISITS R, et al., 2013. Iron-reducing bacteria accumulate ferric oxyhydroxide nanoparticle aggregates that may support planktonic growth [J]. *The ISME Journal*, 7(2): 338-350.
- MACALADY J L, VESTLING M M, BAUMLER D, et al., 2004. Tetraether-linked membrane monolayers in *Ferroplasma* spp: A key to survival in acid [J]. *Extremophiles*, 8(5): 411-419.

- MALVANKAR N S, YALCIN S E, TUOMINEN M T, et al., 2014. Visualization of charge propagation along individual pili proteins using ambient electrostatic force microscopy [J]. *Nature nanotechnology*, 9(12): 1012-1017.
- MANN S, 1987. The study of biominerals by high resolution transmission electron microscopy [J]. *Scanning Electron Microscopy*, 1986(2): 393-413.
- MCGUIRE M M, EDWARDS K J, BANFIELD J F, et al., 2001. Kinetics, surface chemistry, and structural evolution of microbially mediated sulfide mineral dissolution [J]. *Geochimica et Cosmochimica Acta*, 65(8): 1243-1258.
- MCLAREN A C, 1991. Transmission electron microscopy of minerals and rocks [M]//*Cambridge Topics in Mineral Physics and Chemistry*. Cambridge: Cambridge University Press.
- MELTON E D, SWANNER E, BEHRENS S, et al., 2014. The interplay of microbially mediated and abiotic reactions in the biogeochemical Fe cycle [J]. *Nature Reviews Microbiology*, 12: 797-808.
- MÉNDEZ-GARCÍA C, PELAEZ A, MESA V, et al., 2015. Microbial diversity and metabolic networks in acid mine drainage habitats [J]. *Frontiers in microbiology*, 6: 00475.
- MENG S, WANG H, LIU H, et al., 2014. Evaluation of the ability of ferrihydrite to bind heavy metal ions: Based on formation environment, adsorption reversibility and ageing [J]. *Applied Geochemistry*, 45: 114-119.
- MIELKE R, PACE D, PORTER T, et al., 2003. A critical stage in the formation of acid mine drainage: Colonization of pyrite by *Acidithiobacillus ferrooxidans* under pH-neutral conditions [J]. *Geobiology*, 1(1): 81-90.
- MONCUR M C, JAMBOR J L, PTACEK C J, et al., 2009. Mine drainage from the weathering of sulfide minerals and magnetite [J]. *Applied Geochemistry*, 24(12): 2362-2373.
- MOREAU J W, ZIERENBERG R A, BANFIELD J F, 2010. Diversity of dissimilatory sulfite reductase genes (*dsrAB*) in a salt marsh impacted by long-term acid mine drainage [J]. *Applied and Environmental Microbiology*, 76(14): 4819-4828.
- MUELLER R S, DENEV V J, KALNEJAIS L H, et al., 2010. Ecological distribution and population physiology defined by proteomics in a natural microbial community [J]. *Molecular Systems Biology*, 6: 374.
- NI G, SIMONE D, PAMLA D, et al., 2018. A novel inorganic sulfur compound metabolizing *Ferroplasma*-like population is suggested to mediate extracellular electron transfer [J]. *Frontiers in microbiology*, 9: 2945.
- NORDSTROM D K, BLOWES D W, PTACEK C J, 2015. Hydrogeochemistry and microbiology of mine drainage: An update [J]. *Applied Geochemistry*, 57: 3-16.
- NORDSTROM D K, SOUTHAM G, 2018. Chapter 11. Geomicrobiology of sulfide mineral oxidation Geomicrobiology: Interactions between microbes and minerals [M]//*Geomicrobiology*. Berlin: De Gruyter: 361-390.
- OLSSON S, PENACHO V, PUENTE-SÁNCHEZ F, et al., 2017. Horizontal gene transfer of phytochelatin synthases from bacteria to extremophilic green algae [J]. *Microbial Ecology*, 73: 50-60.
- OLSSON S, PUENTE-SÁNCHEZ F, GÓMEZ M J, et al., 2015. Transcriptional response to copper excess and identification of genes involved in heavy metal tolerance in the extremophilic microalga *Chlamydomonas acidophila* [J]. *Extremophiles*, 19(3): 657-672.
- OUYANG B J, LIU HUAN, LI JUAN, et al., 2014. Reduction of jarosite by *Shewanella oneidensis* MR-1 and secondary mineralization [J]. *Geochimica et Cosmochimica Acta*, 124: 54-71.
- PAN Y, YE H, LI X, et al., 2021. Spatial distribution characteristics of the microbial community and multi-phase distribution of toxic metals in the geochemical gradients caused by acid mine drainage, South China [J]. *Science of The Total Environment*, 774: 145660.
- PACELLA M S, GRAY J J, 2018. A benchmarking study of peptide-biomineral interactions [J]. *Crystal Growth & Design*, 18(2): 607-616.
- PANDEY S, FOSSO-KANKEU E, REDELINGHUYS J, et al., 2021. Implication of biofilms in the sustainability of acid mine drainage and metal dispersion near coal tailings [J]. *Science of The Total Environment*, 788: 147851.
- PUENTE-SÁNCHEZ F, OLSSON S, AGUILERA A, 2016. Comparative transcriptomic analysis of the response of *Dunaliella acidophila* (Chlorophyta) to short-term cadmium and chronic natural metal-rich water exposures [J]. *Microbial Ecology*, 72(3): 595-607.
- QIAN G, FAN R, HUANG J, et al., 2021. Oxidative dissolution of sulfide minerals in single and mixed sulfide systems under simulated acid and metalliferous drainage conditions [J]. *Environmental Science & Technology*, 55(4): 2369-2380.
- QUATRINI R, JOHNSON D B, 2018. Microbiomes in extremely acidic environments: Functionalities and interactions that allow survival and growth of prokaryotes at low pH [J]. *Current Opinion in Microbiology*, 43: 139-147.
- RAM R J, VERBERKMOES N C, THELEN M P, et al., 2005. Community proteomics of a natural microbial biofilm [J]. *Science*, 308(5730): 1915-1920.
- REN K, ZENG J, LIANG J, et al., 2021. Impacts of acid mine drainage on karst aquifers: Evidence from hydrogeochemistry, stable sulfur and oxygen isotopes [J]. *Science of The Total Environment*, 761: 143223.
- RØDER H L, LIU W, SØRENSEN S J, et al., 2019. Interspecies interactions reduce selection for a biofilm-optimized variant in a four-species biofilm model [J]. *Environmental Microbiology Reports*, 11(6): 835-839.
- RODRIGUEZ-NAVARRO C, JIMENEZ-LOPEZ C, RODRIGUEZ-NAVARRO A, et al., 2007. Bacterially mediated mineralization of vaterite [J]. *Geochimica et Cosmochimica Acta*, 71(5): 1197-1213.
- ROZENDAL R, HAMELERS H V M, RABAEY K, et al., 2008. Towards practical implementation of bioelectrochemical wastewater treatment [J]. *Trends in biotechnology*, 26(8): 450-459.
- SAHOO H, KISKU K, NAIK U C, 2021. Chapter 21-Application of omics tools for microbial community structure and function analysis [B]//*Wastewater Treatment*. Elsevier.
- SALMON S U, HIPSEY M R, WAKE G W, et al., 2017. Quantifying lake water quality evolution: Coupled geochemistry, hydrodynamics, and aquatic ecology in an acidic pit lake [J]. *Environmental Science & Technology*, 51(17): 9864-9875.
- SAMBORSKA K, SITEK S, BOTTRELL S, et al., 2013. Modified multi-phase stability diagrams: An AMD case study at a site in Northumberland, UK [J]. *Mine Water and the Environment*, 32: 185-194.
- SANCHEZ-ESPANA J, YUSTA I, DIEZ-ERCILLA M, 2011. Schwertmannite and hydrobasaluminite: Are-evaluation of their solubility and control on the iron and aluminium concentration in acidic pit lakes [J]. *Applied Geochemistry*, 26(9-10): 1752-1774.

- SAND W, GEHRKE T, 2006. Extracellular polymeric substances mediate bioleaching/biocorrosion via interfacial processes involving iron(III) ions and acidophilic bacteria [J]. *Research in Microbiology*, 157(1): 49-56.
- SCHIPPERS A, BREUKER A, BLAZEJAK A, et al., 2010. The biogeochemistry and microbiology of sulfidic mine waste and bioleaching dumps and heaps, and novel Fe(II)-oxidizing bacteria [J]. *Hydrometallurgy*, 104: 342-350.
- SCHLOSS P D, HANDELSMAN J, 2005. Metagenomics for studying unculturable microorganisms: Cutting the Gordian knot [J]. *Genome Biology*, 6(8): 229.
- SCHÖNKNECHT G, CHEN W H, TERNES C M, et al., 2013. Gene transfer from bacteria and archaea facilitated evolution of an extremophilic eukaryote [J]. *Science*, 339(6124): 1207-1210.
- SENKO J, ZHANGF G, MCDONOUGH J, et al., 2009. Metal reduction at low pH by a *Desulfosporosinus* species: Implications for the biological treatment of acidic mine drainage [J]. *Geomicrobiology Journal*, 26(2): 71-82.
- SHE Z, WANG J, HE C, et al., 2021. The stratified distribution of dissolved organic matter in an AMD lake revealed by multi-sample evaluation procedure [J]. *Science of The Total Environment*, 55(12): 8401-8409.
- SHI L, DONG H, REGUERA G, et al., 2016. Extracellular electron transfer mechanisms between microorganisms and minerals [J]. *Nature Reviews Microbiology*, 14(10): 651-662.
- SIMATE G S, NDLOVU S, 2014. Acid mine drainage: Challenges and opportunities [J]. *Journal of Environmental Chemical Engineering*, 2(3): 1785-1803.
- SIMMONS S, DIBARTOLO G, DENEFF V, et al., 2008. Population genomic analysis of strain variation in *Leptospirillum* group II bacteria involved in acid mine drainage formation [J]. *PLoS biology* 6(7): 1427-1442.
- SINGH S, CHAKRABORTY S, 2022. Biochemical treatment of coal mine drainage in constructed wetlands: Influence of electron donor, biotic-abiotic pathways and microbial diversity [J]. *Chemical Engineering Journal*, 440: 135986.
- STOCKER R, 2012. Marine microbes see a sea of gradients [J]. *Science*, 338(6107): 628-633.
- STULBERG E, FRAVEL D, PROCTOR L M, et al., 2016. An assessment of US microbiome research [J]. *Nature Microbiology*, 1: 15015.
- SU G, DENG X, HU L, et al., 2020. Comparative analysis of early-stage adsorption and biofilm formation of thermoacidophilic archaeon *Acidianus manzaensis* YN-25 on chalcopyrite and pyrite surfaces [J]. *Biochemical engineering journal*, 163: 107744.
- SUL W J, COLE J R, JESUS E da C, et al., 2011. Bacterial community comparisons by taxonomy-supervised analysis independent of sequence alignment and clustering [J]. *Proceedings of the National Academy of Sciences of the United States of America*, 108(35): 14637-14642.
- SUN R, ZHANG L, WANG X, et al., 2020a. Elemental sulfur-driven sulfidogenic process under highly acidic conditions for sulfate-rich acid mine drainage treatment: Performance and microbial community analysis [J]. *Water Research*, 185: 116230.
- SUN W, SUN X, LI B, et al., 2020b. Bacterial response to sharp geochemical gradients caused by acid mine drainage intrusion in a terrace: Relevance of C, N, and S cycling and metal resistance [J]. *Environment International*, 138: 105601.
- TAN G L, SHU W, LI F, et al., 2008. Culturable and molecular phylogenetic diversity of microorganisms in an open-dumped, extremely acidic Pb/Zn mine tailings [J]. *Extremophiles: life under extreme conditions*, 12: 657-664.
- TAN G L, SHU W, ZHOU W H, et al., 2009. Seasonal and spatial variations in microbial community structure and diversity in the acid stream draining across an ongoing surface mining site [J]. *FEMS Microbiology Ecology*, 70(2): 121-129.
- TAN S, LIU J, FANG Y, et al., 2019. Insights into ecological role of a new deltaproteobacterial order *Candidatus Acidulode sulfobacterales* by metagenomics and metatranscriptomics [J]. *The ISME Journal*, 13(8): 2044-2057.
- TENG W, KUANG J, LUO Z, et al., 2017. Microbial diversity and community assembly across environmental gradients in acid mine drainage [J]. *Minerals*, 7(6): 106.
- TORRES E, COUTURE R M, SHAFEI B, et al., 2015. Reactive transport modeling of early diagenesis in a reservoir lake affected by acid mine drainage: Trace metals, lake overturn, benthic fluxes and remediation [J]. *Chemical Geology*, 419: 75-91.
- TRIPATHI S, POLURI K M, 2021. Heavy metal detoxification mechanisms by microalgae: Insights from transcriptomics analysis [J]. *Environmental Pollution*, 285: 117443.
- TYSON G W, CHAPMAN J, HUGENHOLTZ P, et al., 2004. Community structure and metabolism through reconstruction of microbial genomes from the environment [J]. *Nature*, 428: 37-43.
- VALENTE T, GOMES C, 2008. Fuzzy modelling of acid mine drainage environments using geochemical, ecological and mineralogical indicators [J]. *Environmental Geology*, 57: 653-663.
- VALENTE T, GRANDE J A, DE LA TORRE M L, et al., 2013. Mineralogy and environmental relevance of AMD-precipitates from the Tharsis mines, Iberian Pyrite Belt (SW, Spain) [J]. *Applied Geochemistry*, 39: 11-25.
- VALENTE T M, LEAL GOMES C, 2009. Occurrence, properties and pollution potential of environmental minerals in acid mine drainage [J]. *Science of The Total Environment*, 407(3): 1135-1152.
- VILLEGAS-PLAZAS M, SANABRIA J, JUNCA H, 2019. A composite taxonomical and functional framework of microbiomes under acid mine drainage bioremediation systems [J]. *Journal of Environmental Management*, 251: 109581.
- VITHANA C L, SULLIVAN L A, BURTON E D, et al., 2015. Stability of schwertmannite and jarosite in an acidic landscape: Prolonged field incubation [J]. *Geoderma*, 239-240: 47-57.
- WHITAKER R, BANFIELD J, 2006. Population genomics in natural microbial communities [J]. *Trends in ecology & evolution*, 21(9): 508-516.
- WILLIAMS A G B, SCHERER M M, 2004. Spectroscopic evidence for Fe(II)-Fe(III) electron transfer at the iron oxide-water interface [J]. *Environmental Science & Technology*, 38(18): 4782-4790.
- WILMES P, BOND P L, 2009a. Microbial community proteomics: elucidating the catalysts and metabolic mechanisms that drive the Earth's biogeochemical cycles [J]. *Current opinion in microbiology*, 12(3): 310-317.
- WILMES P, REMIS J P, HWANG M, et al., 2009b. Natural acidophilic biofilm communities reflect distinct organismal and functional organization [J]. *The ISME Journal*, 3: 266-270.
- XIA J, LIU H, NIE Z, et al., 2020. Taking insights into phenomics of microbe-mineral interaction in bioleaching and acid mine drainage: Concepts and methodology [J]. *Science of The Total Environment*, 729: 139005.

- XIE J, HE Z, LIU X, et al., 2011. GeoChip-based analysis of the functional gene diversity and metabolic potential of microbial communities in acid mine drainage [J]. *Applied and Environmental Microbiology*, 77(3): 991-999.
- XIN R, BANDA J F, HAO C, et al., 2021. Contrasting seasonal variations of geochemistry and microbial community in two adjacent acid mine drainage lakes in Anhui Province, China [J]. *Environmental Pollution*, 268: 115826.
- XU R, LI B, XIAO E, et al., 2020. Uncovering microbial responses to sharp geochemical gradients in a terrace contaminated by acid mine drainage [J]. *Environmental Pollution*, 261: 114226.
- YANNARELL A, TRIPLETT E, 2004. Within- and between-lake variability in the composition of bacterioplankton communities: Investigations using multiple spatial scales [J]. *Applied and Environmental Microbiology*, 70(1): 214-223.
- YANNARELL A C, TRIPLETT E W, 2005. Geographic and environmental sources of variation in lake bacterial community composition [J]. *Applied and Environmental Microbiology*, 71(1): 227-239.
- YELTON A P, COMOLLI L R, JUSTICE N B, et al., 2013. Comparative genomics in acid mine drainage biofilm communities reveals metabolic and structural differentiation of co-occurring archaea [J]. *BMC Genomics*, 14: 485.
- ZHANG C, SLATER L, REDDEN G, et al., 2012. Spectral induced polarization signatures of hydroxide adsorption and mineral precipitation in porous media [J]. *Environmental Science & Technology*, 46(8): 4357-4364.
- ZHANG P, CHEN Y P, GUO J S, et al., 2014. Adsorption behavior of tightly bound extracellular polymeric substances on model organic surfaces under different pH and cations with surface plasmon resonance [J]. *Water Research*, 57: 31-39.
- ZHANG X, TANG S, WANG M, et al., 2019. Acid mine drainage affects the diversity and metal resistance gene profile of sediment bacterial community along a river [J]. *Chemosphere*, 217: 790-799.
- ZHANG Z, WANG L, ZHOU B, et al., 2021. Adsorption performance and mechanism of synthetic schwertmannite to remove low-concentration fluorine in water [J]. *Bulletin of Environmental Contamination and Toxicology*, 107(5): 1191-1201.
- ZHU J, WANG Q, ZHOU S, et al., 2015a. Insights into the relation between adhesion force and chalcopyrite-bioleaching by *Acidithiobacillus ferrooxidans* [J]. *Colloids Surf B Biointerfaces*, 126: 351-357.
- ZHU M, LEGG B, ZHANG H, et al., 2012. Early stage formation of iron oxyhydroxides during neutralization of simulated acid mine drainage solutions [J]. *Environmental Science & Technology*, 46(15): 8140-8147.
- ZHU T, LU X, LIU H, et al., 2014. Quantitative X-ray photoelectron spectroscopy-based depth profiling of bioleached arsenopyrite surface by *Acidithiobacillus ferrooxidans* [J]. *Geochimica et Cosmochimica Acta*, 127: 120-139.
- ZHU X, WANG R, LU X, et al., 2015b. Secondary minerals of weathered orpiment-realgar-bearing tailings in Shimen carbonate-type realgar mine, Changde, Central China [J]. *Mineralogy and Petrology*, 109: 1-15.
- 曹子敏, BANDA J F, 裴理鑫, 等, 2019. 安徽某铁矿不同矿山废水库中微生物群落结构特征[J]. *微生物学报*, 59(6): 1076-1088.
- CAO Z M, BANDA J F, PEI L X, 2019. Microbial community structure characteristics in different mine drainage lakes of an iron mine in Anhui Province [J]. *Acta Microbiologica Sinica*, 59(6): 1076-1088.
- 陈丹丹, 罗小波, 李芳柏, 2017. 穿梭体影响微生物群落胞外电子传递过程的研究[J]. *生态环境学报*, 26(8): 1419-1425.
- CHEN D D, LUO X B, LI F B, 2017. Effects of shuttles on extracellular electron transfer of microbial community [J]. *Ecology and Environmental Sciences*, 26(8): 1419-1425.
- 方迪, 王方, 单红仙, 等, 2010. 硫酸盐还原菌对酸性废水中重金属的生物沉淀作用研究[J]. *生态环境学报*, 19(3): 562-565.
- FANG D, WANG F, SHAN H X, et al., 2010. Bio-precipitation of heavy metals from a synthetic acidic wastewater by sulfate-reducing bacteria in a bench scale continuous-flow stirred tank reactor [J]. *Ecology and Environmental Sciences*, 19(3): 562-565.
- 贾蓉芬, 高梅影, 彭先芝, 等, 2009. 微生物成矿[M]. 北京: 科学出版社.
- JIA R F, GAO M Y, PENG X Z, 2009. Microbial mineralization [M]. Beijing: Science Press.
- 姜梦戈, 2020. 柠檬酸杆菌 *Citrobacter* sp.对铁氧化物和铁硫化物还原转化机制研究 [M]. 广州: 华南理工大学.
- JIANG M Y, 2020. Reduction and transformation mechanism of Fe-oxides and Fe(III)-oxyhydroxysulfate minerals by *Citrobacter* sp. [D]. Guangzhou: South China University of Technology.
- 刘帆, 张晓辉, 唐宋, 等, 2019. 酸性矿山废水对沉积物真核微生物群落的影响[J]. *中国环境科学*, 39(12): 5285-5292.
- LIU F, ZHANG X H, TANG S, et al., 2019. Effects of acid mine drainage on eukaryotic community in river sediments [J]. *China Environmental Science*, 39(12): 5285-5292.
- 刘奇缘, 陈炳辉, 周永章, 等, 2017. 粤北大宝山槽坑酸性矿山废水中不同沉积层次生矿物研究[J]. *地球与环境*, 45(3): 259-266.
- LIU Q Y, CHEN B H, ZHOU Y Z, et al., 2017. A study on secondary minerals in different sediments of Caodukeng acid mine drainage, Dabaoshan Mine, North Guangdong Province, China [J]. *Earth and Environment*, 5(3): 259-266.
- 陆现彩, 李娟, 刘欢, 等, 2019. 金属硫化物微生物氧化的机制和效应 [J]. *岩石学报*, 35(1): 153-163.
- LU X C, LI J, LIU H, et al., 2019. Microbial oxidation of metal sulfides and its consequences [J]. *Acta Petrologica Sinica*, 35(1): 153-163.
- 裴理鑫, 鲁青原, 郝春博, 等, 2016. 安徽某铁矿酸性矿山废水夏季和秋季微生物群落结构特征[J]. *环境科学学报*, 36(7): 2397-2407.
- PEI L X, LU Q Y, HAO C B, et al., 2016. Shifts of the microbial community structure of an acid mine drainage from summer to autumn in Anhui Province [J]. *Acta Scientiae Circumstantiae*, 36(7): 2397-2407.
- 彭珂萍, 曾伟民, 2020. 紫金山铜矿酸性矿山废水微生物群落多样性[J]. *微生物学通报*, 47(9): 2887-2896.
- PENG Y P, ZENG W M, 2020. Diversity of microbial community in acid mine drainage from Zijinshan copper mine [J]. *Microbiology China*, 47(9): 2887-2896.
- 汪涵, 2018. 酸性矿山废水长期灌溉稻田土壤中微生物群落结构时空变化特征及其响应机制[D]. 广州: 华南理工大学.
- WANG H, 2018. Characteristics of microbial community spatial and temporal change in paddy soil under long-term acid mine drainage irrigation and its response mechanism [D]. Guangzhou: South China University of Technology.
- 谢学辉, 肖升木, 柳建设, 2009. 矿山废水中微生物生态多样性研究[J]. *微生物学通报*, 36(4): 528-537.

- XIE X H, XIAO S M, LIU J S, 2009. Diversity of microbial communities in waste mining water [J]. *Microbiology China*, 36(4): 528-537.
- 徐轶群, 顾园园, 姚婷, 等, 2013. 铁细菌胞外多聚物对铁矿物的调控形成及其环境意义[J]. *岩石矿物学杂志*, 32(6): 782-788.
- XU Y Q, GU Y Y, YAO T, et al., 2013. Regulating formation of iron minerals by iron bacteria/EPS and its environmental significance [J]. *Acta Petrologica et Mineralogica*, 32(6): 782-788.
- 张多瑞, 聂珍媛, 刘李柱, 等, 2018. 微生物胞外电子传递过程及其应用研究进展[J]. *生命科学*, 30(6): 680-689.
- ZHANG D R, NIE Z Y, LIU L Z, et al., 2018. Mechanisms of microbial extracellular electron transfer and its application [J]. *Chinese Bulletin of Life Sciences*, 30(6): 680-689.
- 张玉龙, 陈雪丽, 吴云当, 2021. 电子穿梭体及其介导的环境与地球化学过程研究进展[J]. *生态环境学报*, 30(1): 213-222.
- ZHANG Y L, CHEN X L, WU Y D, 2021. Electron shuttle-mediated microbial extracellular electron transfer: Mechanisms and geochemical implications [J]. *Ecology and Environmental Sciences*, 30(1): 213-222.
- 周立祥, 2008. 酸性矿山废水中生物成因次生高铁矿物的形成及环境工程意义[J]. *地学前缘*, 15(6): 74-82.
- ZHOU L X, 2008. Biogenic iron oxyhydroxysulfate and iron oxyhydroxide occurring in acid mine drainage and their environmental engineering implications [J]. *Earth Science Frontiers*, 15(6): 74-82.

Spatio-temporal Evolution Characteristics of Microbiome in Acid Mine Drainage and Microbial-mineral Interaction Mechanism

FENG Yiqing^{1,3}, HAO Likai^{1,2,3*}, GUO Yuan¹, XU Fei⁴, XU Heng⁴

1. State Key Laboratory of Environmental Geochemistry/Institute of Geochemistry, Chinese Academy of Sciences, Guiyang 550081, P. R. China;

2. CAS Center for Excellence in Quaternary Science and Global Change, Xi'an 710061, P. R. China;

3. University of Chinese Academy of Sciences, Beijing 100049, P. R. China; 4. Sichuan University, Chengdu 610065, P. R. China

Abstract: Acid mine drainage (AMD) is one of the most serious environmental problems in the world. Microorganism are responsible for the formation of AMD via Fe-S geochemical cycle, in which has complex interaction with minerals. In-depth analysis of the microbial community structure, function and metabolic characteristics will be helpful to reveal the ecological significance of dominant and rare species in extreme acidic environments, contributing to the remediation of AMD contamination. Systematic studies using multi-omics methods, including genome, transcriptome, proteome, metabolism and phenome, are helpful to clarify the molecular mechanism of microbe-environment interactions. Microbiome in AMD were clustered in different time series such as tailings acidification process, biofilm development process, biological treatment process and seasonal succession driven by water and heat, and regional and fine spatial scales, reflecting their ecological strategies adapting to extreme acidic and toxic metal environments. The Fe-S biogeochemical gradient in AMD system has a significant impact on the structure and function of microbial communities. The response of Fe- and S-metabolizing microbial populations to environmental gradient changes drives the Fe-S biogeochemical cycle and leads to the evolution process, phase transformation equilibrium of AMD minerals, and the transformation of metal elements. The microbial mineralization in AMD is the result of the interaction between biotic and abiotic reactions. The control of surface reaction plays a key role for mineral microbial oxidation, which is driven by the contact mechanism. In addition, the microbial reduction of minerals in AMD follows the electrochemical process. The iron-bearing mineral is one of the most important electron acceptors of extracellular respiration of microorganisms in AMD system, so that the iron respiration drives the biogeochemical cycle of elements, and further drives the evolution of microbial community, function and metabolism in AMD system.

Keywords: acid mine drainage (AMD); microbiome; microbial mineralization; microbial-mineral interaction (MMI); Fe-S; biogeochemical cycle