Microbial Ecology and Biogeochemistry in Oceans and Lakes 海洋与湖泊微生物生态及生物地球化学作用

红树林湿地硫酸盐还原菌的多样性及其参与驱动的元素耦合机制

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摘　要：红树林生态系统是热带和亚热带地区重要的滨海湿地，具有营养物质形态多样化和高效动态变化的特征，是驱动碳、氮、硫等元素循环的热区。硫酸盐还原菌 (sulfate-reducing prokaryotes，SRPs)是地球最古老的微生物生命形式之一，在推动早期地球地质演化以及现代生物地球化学循环中发挥关键作用，但其在红树林湿地还缺乏全面深入研究。本文基于 Genome Taxonomy Database 中原核生物基因组的挖掘，系统总结了硫酸盐还原菌的类群，梳理了近年来国内外红树林中硫酸盐还原菌的分布情况及影响其分布的因素，分析了硫酸盐还原菌在红树林生态系统的碳、氮、硫及铁等元素地球化学循环中的作用，并对硫酸盐还原菌未来的研究方向进行了展望，以期为深入研究硫酸盐还原菌参与驱动的元素生物地球化学循环及其耦合机制提供参考。

关键词：红树林沉积物；硫酸盐还原菌；生态分布；硫代谢；元素耦合

Sulfate-reducing prokaryotes in mangrove wetlands: diversity and role in driving element coupling

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Abstract: Mangrove ecosystems are important coastal wetlands with highly efficient nutrient dynamics in the tropics and subtropics, and the hot zones driving the cycling of elements such as carbon, nitrogen, and sulfur. Sulfate-reducing prokaryotes (SRPs), one of the oldest microbial life forms on Earth, play a key role in driving early geological evolution and modern biogeochemical cycles of the Earth, while their role in mangrove wetlands remains to be studied. Only by fully understanding the processes and characteristics of the element biogeochemical cycles that SRPs participate in mangrove ecosystems can we capture the key aspects and clarify the coupling mechanisms. The development of bioinformatics has led to the discovery of more and more uncultured SRPs. In this paper, we systematically summarized the classification of sulfate-reducing bacteria and expand the taxa of SRPs based on the Genome Taxonomy Database prokaryotic genomes. We then introduced the distribution of SRPs in mangroves at home and abroad in recent years and the factors affecting the distribution to reveal the horizontal distribution diversity of SRPs in mangrove ecosystems. Further, we expounded the role of SRPs in the intertwined cycles of carbon, nitrogen, sulfur, and iron in mangrove wetlands, with emphasis on the molecular processes of SRPs in the sulfur cycle, especially dissimilatory sulfate reduction. Finally, we made an outlook on the future research directions of SRPs, aiming to provide references for further research on the element biogeochemical cycling and coupling driven by SRPs.

Keywords: mangrove sediment; sulfate-reducing prokaryotes; ecological distribution; sulfur metabolism; element coupling

红树林湿地是位于海岸潮间带的动态生态系统，是连接海洋与陆地之间物质循环与能量交换的重要枢纽[1]。潮间带环境的周期性变化赋予了红树林湿地介于陆地与海洋生态系统之间的特性，如强还原性、盐渍化、较强酸性、富营养化等，使得红树林湿地成为生物圈中营养物质形态高效动态变化的特殊生态系统[2−3]。红树林湿地蕴含着丰富的营养物质以及驱动碳、氮、硫等地球元素化学循环关键过程的微生物资源，是研究微生物地球化学作用的天然实验室。潮汐带海陆交替演替后的沉积物是支撑红树林湿地生物地球化学循环的重要物质基础，经典的近海沉积物早期成岩理论认为，有机物成岩作用会依次受到氧气、硝酸盐、锰(IV)氧化物、铁(III)氧化物、硫酸盐和二氧化碳等电子受体的氧化[4]。红树林生态系统中红树植物的根茎和气生根能从海水和海滩淤泥中获得丰富的硫，而其根系和凋零物的滞留也会产生硫以及大量复杂有机营养成分[5]。微生物利用红树林表层沉积物中氧气、硝酸盐和锰(IV)等电子受体氧化复杂有机营养成分，而硫会继续沉积加剧红树林富硫环境[4,6]。红树林沉积物中的硫主要为硫酸盐和黄铁矿，硫酸盐还原菌(sulfate-reducing prokaryotes，SRPs)与红树林湿地中有机

质周转以及铁硫等元素耦合过程密切相关[7−9]。厌氧产甲烷菌主要活跃在有机碳源与硫酸盐枯竭的深层沉积物中，将二氧化碳氧化成甲烷[9]。

　　SRPs 是一类可以利用硫酸盐作为电子受体进行异化硫酸盐还原获得能量并释放出大量硫化物的厌氧菌，是红树林中最丰富的微生物类群之一[10]。缺氧或厌氧层中的硫酸盐还原作用是红树林湿地沉积物中重要的生物化学过程[10−11]，不仅参与驱动有机质矿化以及沉积物地球化学元素循环与耦合[12−14]，还对重金属污染控制、污染物降解以及生态修复等多种过程发挥重要的调控作用(图 1)[15−17]。近年来，基于宏基因组学等多组学技术，在红树林湿地环境中发现除了硫酸盐还原细菌外，阿斯加德古菌超门 (*Gerdarchaeota*、*Heimdallarchaeota* 和 *Thorarchaeota*)、TACK 超门(*Bathyarchaeota*)、
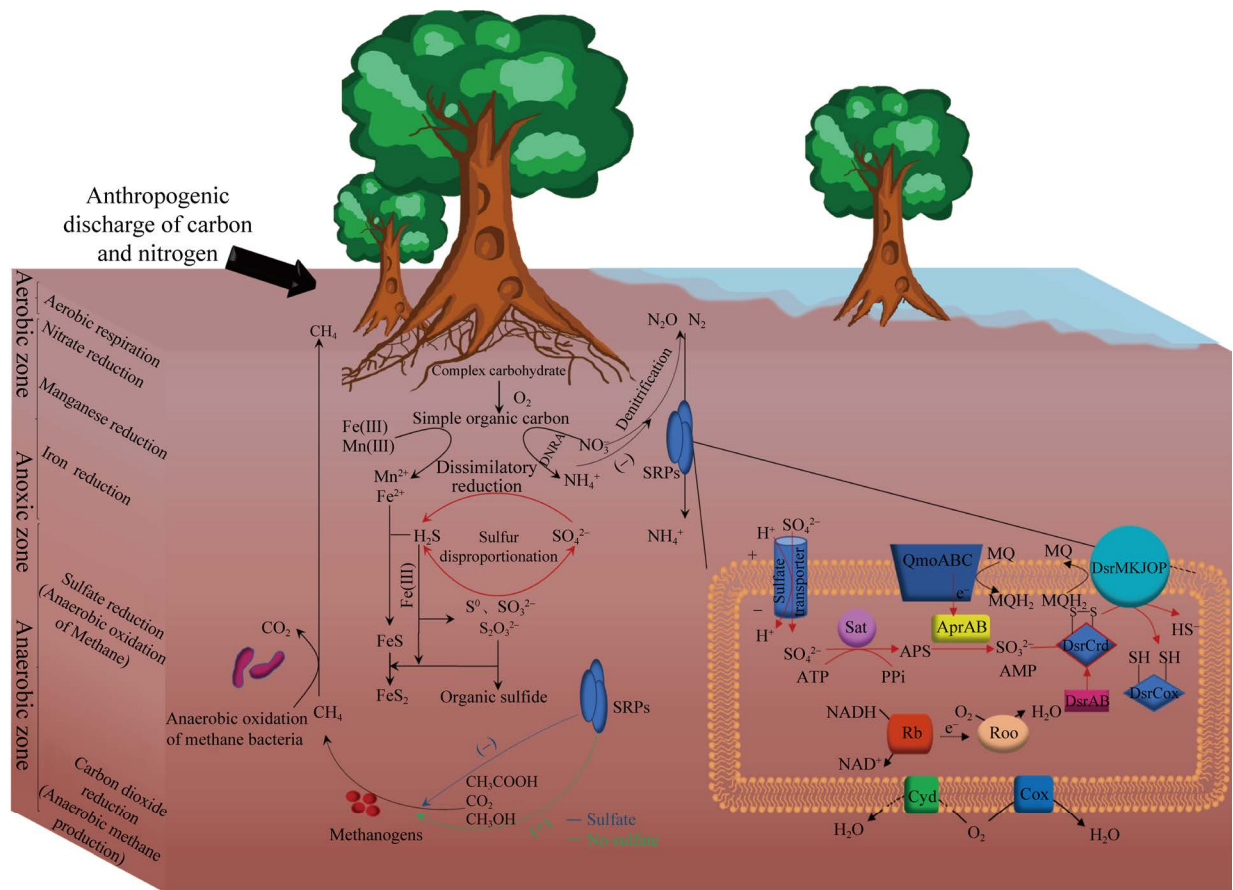

图 1　红树林沉积物中 SRPs 参与驱动的碳、氮、硫及金属元素等的耦合概况

Figure 1　Coupling of carbon, nitrogen, sulfur, and metal elements in mangrove sediments driven by sulfate-reducing prokaryotes. Sulfate-reducing prokaryotes participate in the sulfur metabolism process (red arrow). Sulfate-reducing prokaryotes compete with methanogens for organic substrates in the presence of sulfate (blue arrow) and provide organic substrates for methanogens through fermentation when the sulfate is used up (green arrow). Sat, AprAB, QmoABC, DsrAB, DsrC, and DsrMKJOP are enzymes related to the sulfate dissimilation-reduction process in sulfate-reducing prokaryotes, wherein DsrCrd is reduced DsrC and DsrCox is oxidized DsrC. Roo-Rb and Cyd-Cox are sulfate-reducing bacteria enzymes involved in oxygen metabolism in cytoplasm and membrane, respectively. Anthropogenic emissions of carbon and nitrogen pollutants in mangrove forests (bold black arrow).

Thermoprofundales 以及 *Hydrothermarchaeota* 等古菌成员均具有还原硫酸盐的潜力，说明它们是红树林湿地元素地球化学循环的重要参与者，这也极大地扩充了人们对于细菌、古菌等微生物物种和功能多样性的理解[18−23]。为了进一步梳理 SRPs 在红树林湿地的生态功能及其地球化学作用，本文综述了 SRPs 的分类，红树林湿地中 SRPs 的分布和影响分布的主要因素以及 SRPs 参与驱动的碳氮硫及金属元素的耦合过程，以期为揭示以 SRPs 为关键物种的微生物活性功能模块在红树林生态系统的生态功能提供理论参考。

1 硫酸盐还原菌

　　硫酸盐还原菌是一类能将硫酸盐或亚硫酸盐转化成硫化氢的微生物，一般被认为是一种严格厌氧菌[24]。硫酸盐还原菌广泛分布于湿地[25]、地下[26]、海洋[27]生态系统、油田[28]、生活污水[29]和工业废水处理过程[30]的缺氧环境中，甚至在极端环境如北极沉积物[31]、深海热液喷口[32]、火山喷气孔[33]和盐碱湖[34]等也发现了硫酸盐还原菌。系统发育分析和稳定同位素研究表明，微生物异化硫酸盐还原过程是地球历史上存在 35 亿年演化历史的古老过程[35−36]。研究发现在埃迪卡拉纪(6.35−5.41 亿年前)早期深层海水的硫酸盐含量被严重低估，说明硫酸盐还原菌对深海的早期氧化起到关键作用[37]。在厌氧条件下，硫酸盐还原菌可能具有化能有机异养、化能有机自养和化能无机自养等多种营养类型[24]。尽管氧气的存在会影响硫酸盐还原过程，但仍有研究在有氧环境中发现了 SRPs 成员脱硫弧菌(*Desulfovibrio*)[38]，这可能是脱硫弧菌在长期的演化过程中对氧气形成了适应机制。SRPs 可以代谢氢、甲醇、乙醇、乙酸盐、乳酸盐、丙酸盐、丁酸盐、碳氢化合物以及有机废物等多种物质，这为 SRPs 在厌氧环境中提供优势竞争力[39]。研究人员发现，SRPs 一方面会导致生物腐蚀，促使海上石油和天然气的变质[40−41]，另一方面又是处理重金属与矿山酸性废水、去除回收含重金属和硫化合物以及降解有机化合物和抗生素的重要工具[15−17,42−44]。

1.1 硫酸盐还原菌分类

　　Castro 等[45]于 2000 年基于 16S rRNA 基因序列分析将硫酸盐还原菌分为革兰氏阴性嗜中温 SRB (Gram-negative mesophilic sulfate-reducing bacteria)、革兰氏阳性孢子形成 SRB (Gram-positive spore forming sulfate-reducing bacteria)、嗜热细菌 SRB (thermophilic bacterial sulfate-reducing bacteria)以及嗜热古菌 SRA (thermophilic archaeal sulfate-reducing archaea) 4 类。革兰氏阴性嗜中温 SRB 主要为 δ-变形菌纲成员，如来自脱硫杆菌目(*Desulfobacterales*)的脱硫叶菌属 (*Desulfobulbus*)、脱硫盒菌属(*Desulfocapsa*)、脱硫棒菌属(*Desulfofustis*)、脱硫杆菌属 (*Desulfobacter*)、脱硫菌属 (*Desulfobacterium*)、脱硫球菌属(*Desulfococcus*)、脱硫线菌属(*Desulfonema*)、脱硫八叠球菌属 (*Desulfosarcina*) 和脱硫橄榄样菌属 (*Desulfobacula*) 等，脱硫弧菌目 (*Desulfovibrionales*) 的脱硫微菌属 (*Desulfomicrobium*)、脱硫单胞菌属 (*Desulfomonas*)和脱硫弧菌属以及互营杆菌目 (*Syntrophobacterales*) 的脱硫念珠菌属 (*Desulfomonile*)等。革兰氏阳性孢子形成 SRB 主要为厚壁菌门(*Firmicutes*)中梭菌目(*Clostridiales*)的脱硫肠状菌属(*Desulfotomaculum*)和脱硫芽孢弯曲菌属(*Desulfosporosinus*)。嗜热细菌 SRB 主要是热脱硫杆菌目(*Thermodesulfobacteriales*)的热脱硫杆菌属 (*Thermodesulfobacterium*)以及硝化螺旋菌目 (*Nitrospirales*) 的热脱硫弧菌属 (*Thermodesulfovibrio*)。嗜热古菌 SRA 主要为古生球菌目 (*Archaeoglobales*) 的古生球菌属 (*Archaeoglobus*) (图 2A)。
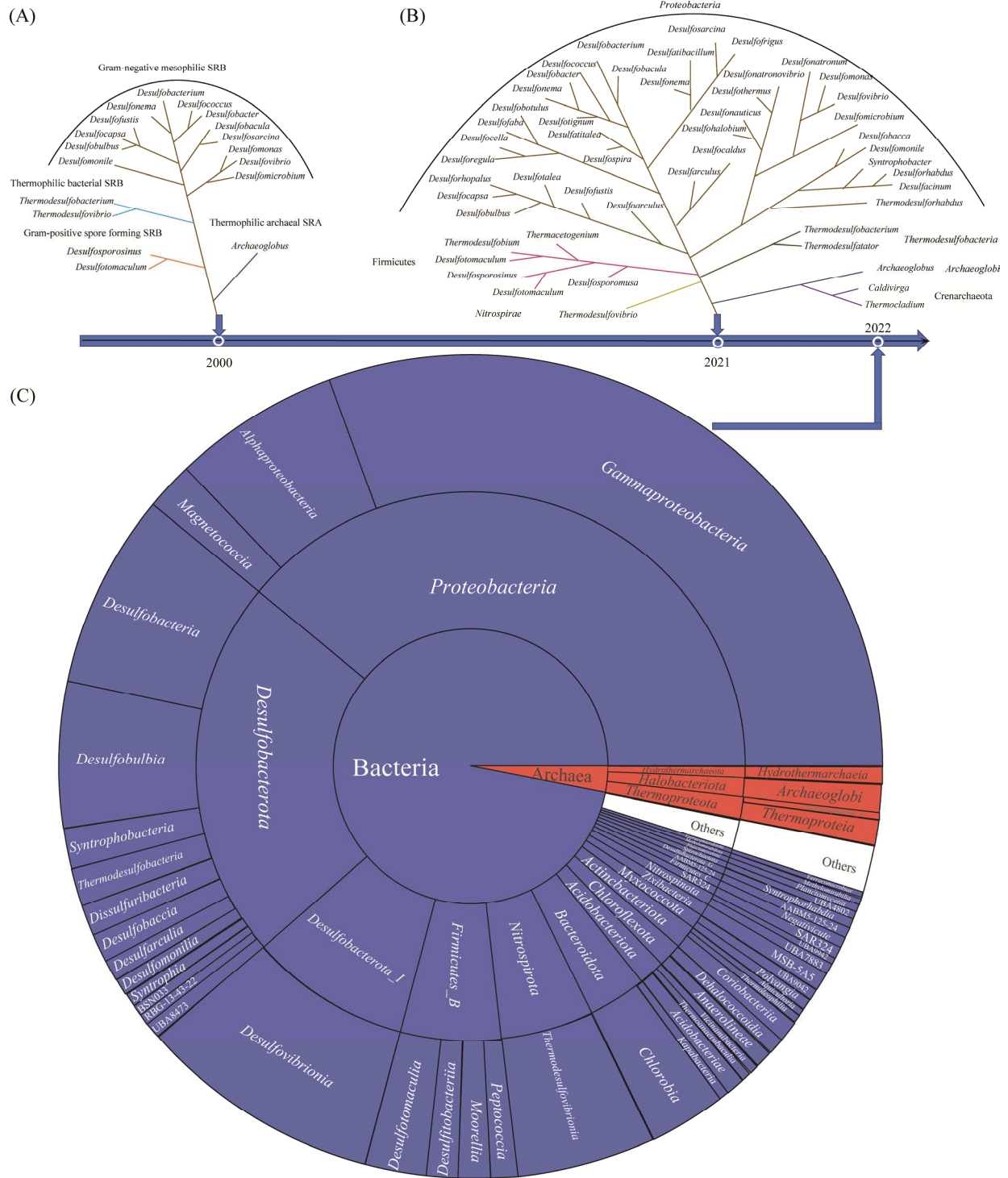
图 2　不断扩大的 SRPs 物种多样性谱系

Figure 2　The expanding lineages of SRPs diversity. In 2000, SRPs were divided into four groups (A). From 2000 to 2021, the development of pure culture technology and sequencing technology revealed more SRPs (B). Based on the Genome Taxonomy Database (GTDB, version r207) prokaryotic reference genomes encoding the *dsrB* gene at the class level taxonomic information, showing that the potential taxa of SRPs continue to expand (C). SRB: sulfate-reducing bacteria; SRA: sulfate-reducing archaea.

随后，随着纯培养技术和测序技术的发展，SRPs 家族不断地壮大。目前报道较多的 SRPs 主要分布在 δ-变形菌纲、硝化螺菌纲(*Nitrospirae*)、厚壁菌门的梭菌纲(*Clostridia*)和厚壁菌纲 (*Negativicutes*) 以及热脱硫菌纲(*Thermodesulfobacteria*) 5 个细菌纲，泉古菌门热变形菌纲(*Thermoprotei*)和广古菌门的古丸菌纲(*Archaeoglobi*) 2 个古菌纲中[46−48]。δ-变形菌纲是目前 SRPs 丰富度最高的纲，其中包括互营杆菌目、脱硫弧菌目、脱硫杆菌目和脱硫盒菌目 (*Desulfarculales*) 4 个目，互营菌科(*Syntrophaceae*) 、 互 营 杆 菌 科 (*Syntrophobacteraceae*)、*Thermodesulforhabdaceae*、脱硫弧菌科(*Desulfovibrionaceae*)、脱硫苏打菌科(*Desulfonatronumaceae*) 、 脱 硫 微 菌 科 (*Desulfomicrobiaceae*) 、 脱 硫 盐 菌 科 (*Desulfohalobiaceae*) 、 脱 硫 棒 菌 科 (*Desulfobulbaceae*) 、 脱 硫 杆 菌 科 (*Desulfobacteraceae*)、*Desulfoarculaceae* 和脱硫盒菌科(*Desulfarculaceae*)等 11 个科总计 38 个属。硝化螺菌纲中 SRPs 目前仅包括硝化螺旋菌科(*Nitrospiracea*)的热脱硫弧菌属。梭菌纲中 SRPs 主要在 *Thermoanaerobiales* 、热厌氧杆菌目(*Thermoanaerobacterales*)和梭菌目 3 个目中，总计 6 个属。厚壁菌纲中 SRPs 主要为月形单孢菌目(*Selenomonadales*)的 *Desulfosporomusa* 中。热脱硫杆菌纲中 SRPs 主要在热脱硫杆菌属中。热变形菌纲中 SRPs 主要在热变形菌科(*Thermoproteaceae*)的 2 个属中。古丸菌纲中 SRPs 主要在古生球菌属中(图 2B)。*dsrAB* 基因编码的异化硫酸盐还原酶能催化亚硫酸盐转化为硫化物是 SRPs 异化还原硫酸盐的最后一步，并且异化硫酸盐还原酶以及编码它的 *dsrAB* 基因在所有 SRPs 中都是保守的，因此 *dsrAB* 基因常作为 SRPs 的分子标记[49]。基于 Genome

Taxonomy Database (GTDB，r207 版本)原核生物参考基因组中编码的 *dsrB* 基因将原属于 δ-变形菌纲的互营杆菌目、脱硫弧菌目和脱硫杆菌目单独划分为 1 个新门 *Desulfobacterota*。此外，在变形菌门的其他纲、*Firmicutes*、*Nitrospirota*、*Bacteroidota*、*Acidobacteriota*、*Chloroflexota*、*Actincbacteriota*、*Myxococcota* 和 *Zixibacteria* 等 细 菌 纲 门 以 及 *Thermoproteota* 、*Halobacteriota* 和 *Hydrothermarchaeota* 等古菌门也含有 *dsrB* 基因的类群(图 2C)。由于 GTDB 与 National Center for Biotechnology Information (NCBI)对于 SRPs 的分类注释有较大差别，且 GTDB 的分类在学术界尚未达成共识，为了避免读者混乱，本文主要基于 NCBI 的分类进行阐述。

1.2 红树林湿地中硫酸盐还原菌的分布及环境影响因素

Pérez-Jiménez 等[50]对全球 4 大洲 16 个地区的沉积物样品的异化亚硫酸还原酶基因 *dsrAB* 进行末端限制性片段长度多样性分析(terminal restriction fragment length polymorphism，TRFLP)，TRFLP 聚类结果表明在几百或者几千公里大范围跨度下，SRPs 群落能够跨越地理阻隔与较远的地点聚类，其中印度-太平洋地区作为 SRPs 物种多样性最丰富的辐射源，很可能是 SRPs 物种的重要起源地。脱硫杆菌目、互营杆菌目和脱硫弧菌目是印度-太平洋地区红树林湿地中最常见的 SRPs 类群(表 1)[51−67]。虽然位于亚洲东部的中国红树林总面积不足全球红树林总面积的 0.2%[68]，但 SRPs 在中国红树林中分布广泛，具有较高的物种多样性。目前在广东、广西、海南、福建、香港和台湾等地区的红树林中都有报道[51−60,69]。脱硫杆菌目 SRPs 是驱动广东[51,55]、广西[52]、香港[53]以及海南[54]等地区红树林湿地碳硫循环的重要菌群，其中脱硫叶菌属、

表 1　不同地区红树林中 SRPs 成员分布情况

Table 1　Distribution of SRPs members in mangroves in different areas

Sample area	SRPs members	Ecological functions	References
Golden Bay mangrove in Guangdong, China	*Desulfobacterales*	Carbon and sulfur cycle	[51]
Beilun estuary mangrove in Guangxi, China	*Desulfocapsa*, *Desulfobulbus*, *Desulfococcus*	Carbon and sulfur cycle	[52]
Mai Po mangrove in Hong Kong, China	*Desulfobulbus*, *Desulfobacterium*, *Desulforhopalus*, *Desulfofustis*	Carbon and sulfur cycle	[53]
Dongzhaigang mangrove in Hainan, China	*Syntrophobacteraceae*, *Desulfobulbus*, *Desulfococcus*, *Desulfobacterium*	Carbon and sulfur cycle	[54]
Hanjiang river estuary mangrove in Guangdong, China	*Desulfatibacillum*	Carbon and sulfur cycle	[55]
Futian mangrove in Guangdong, China	*Syntrophobacteraceae*	Metal and sulfur cycle	[56]
Sanya River mangrove in Hainan, China	*Desulfobacteraceae*, *Desulfovibrionaceae*	Nitrogen fixation	[57]
Chiu-lung River mangrove in Fujian, China	*Desulfovibrio salexigenes*	Cellulose degradation	[58]
Guandu Nature Park in Taiwan, China	*Desulfovibrio*	Biodegradation of tetrabromobisphenol-A	[59]
Qinglan Port mangrove in Hainan, China	*Desulfobaculum xiamenensis*	Carbon and sulfur cycle	[60]
Mangrove in Goa, India	*Desulfovibrio desulphuricans aestuarii*, *Desulfovibrio salexigens*, *Desulfovibrio sapovorans*, *Desulfotomaculum orientis*, *Desulfotomaculum acetoxidans*, *Desulfosarcina variabilis*, *Desulfococcus multivorans*	Carbon and sulfur cycle	[63]
Mangrove in Sundarbans, India	*Desulfovibrio*	Carbon and sulfur cycle	[64]
Bhitarkanika mangrove in Odisha, India	*Desulfotomaculum*, *Desulfovibrio*, *Desulfomonas*	Carbon and sulfur cycle	[65]
Mangrove in Merbok river estuary, Malaysia	*Desulfobacterales*	Carbon and sulfur cycle	[66]
Matang Mangrove in Perak State, Malaysia	*Desulfococcus oleovorans*, *Desulfobacterium autotrophicum*	Sulfur cycle	[67]
Mangrove in Mida Creek and Gazi Bay, Kenya	*Desulfobacteraceae*, *Syntrophobacteraceae*	Carbon and sulfur cycle	[70]
Mtoni mangrove in Tanzania	*Desulfosarcina*	Carbon and sulfur cycle	[9,71]
Mangrove in São Paulo State, Brazil	*Desulfococcus*, *Desulfatibacillum*, *Desulfovibrionales*	Associated with petroleum metabolism	[72–73]
Mangrove in Pará State, Brazil	*Desulfovibrio*	Carbon and sulfur cycle	[74]
Serinhaém estuary mangrove in Bahia State, Brazil	*Desulfobacteraceae*	Sulfur and iron cycle	[75]

脱硫球菌属与脱硫菌属是较为常见的优势属。互营杆菌科与互营杆菌科是广东和海南红树林中常见的 SRPs[54,56]。脱硫弧菌目的 SRPs 成员分布广泛生态功能多样，Yang 等[59]在台湾红树林中发现脱硫弧菌可以厌氧降解四溴双酚 A，脱硫弧菌 *Desulfovibrio salexigenes* 是福建红树林可培养纤维素富集菌群中的绝对优势菌[58]。Zhao

等[60]在海南红树林里通过分离培养得到脱硫弧菌科 SRPs 新种 *Desulfobaculum xiamenensis*。此外，Zhang 等[57]还报道脱硫杆菌科和脱硫弧菌科 SRPs 是海南三亚河红树林根际固氮的优势菌群。在亚洲南部印度红树林中厌氧氧化乳酸和乙酸 SRPs 是红树林生态系统中的重要组成部分[61–62]，目前已经分离得到了脱硫弧菌、脱

硫肠状菌、脱硫八叠球菌、脱硫单胞菌属以及脱硫球菌等 SRPs 成员[63−65]。在东南亚的马来西亚梅尔博克河红树林保护区脱硫杆菌目的 SRPs 是与有机碳代谢以及产甲烷过程相关的优势微生物类群[66]，脱硫球菌 *Desulfococcus oleovorans* 和脱硫菌 *Desulfobacterium autotrophicum* 是驱动马当红树林硫循环丰度最高的 SRPs 类群[67]。

其他地区的红树林中 SRPs 与印度太平洋地区具有一致性，也以脱硫杆菌目、互营杆菌目和脱硫弧菌目成员为主(表 1)[9,70−75]。脱硫杆菌科和互营杆菌科的 SRPs 是非洲东部肯尼亚美达溪 Mida Creek 和 Gazi Bay 红树林根际微生物的优势类群[70]。Lyimo 等[9,71]在坦桑尼亚 Mtoni 红树林发现了硫酸盐还原菌和产甲烷菌代谢共存的证据，并且分离培养得到一株以硫酸盐为电子受体，能厌氧氧化二甲基硫化物和甲硫醇的脱硫八叠球菌属 SRPs 新种。在美洲南部，脱硫杆菌目成员广泛分布在巴西东南部的圣保罗州红树林中，而脱硫弧菌目主要分布在有石油泄露和人为干扰严重的红树林中[72]，脱硫杆菌目的脱硫球菌属和 *Desulfatibacillum* 成员也是参与石油代谢以及人为污染的主要微生物类群[73]；脱硫弧菌属是亚马孙河附近的红树林主要的 SRPs 类群[74]。脱硫杆菌科的 SRPs 成员是锡里尼亚恩红树林潮间带硫铁元素循环优势微生物[75]。

从垂直方向来看，SRPs 在红树林湿地中主要聚集在缺氧和厌氧层，会受非生物因素与生物因素的影响。非生物因素包括有机质含量[9,76−78]、O_2 含量[9,76]、盐度[78−80]、氧化还原电位[81−83]、温度[8,84−86]、pH[87−90]和金属元素含量[56,91−93]等环境因素。生物因素包括红木植物种类[14,84,94−95]与小动物的活动[96]等。红树林沉积物的好氧层仅为几毫米，表层的有机质含量高，这为 SRPs

在表层活动提供了重要的物质基础。受到有机质含量的制约，SRPs 通常会随深度增加而降低[9,76]，但是在更深层的硫酸盐还原带会出现丰度上升的现象。Taketani 等[76]的研究表明，互营杆菌目成员在红树林表层和次表层间无显著差异，而脱硫杆菌目的成员随深度显著变化。有机碳是影响印度孙德尔班红树林中微生物种群总量的最显著因素[77]。Tam[78]对红树林土壤进行了淋滤实验，结果表明有机质和盐度对红树林土壤微生物活动的影响比重金属更显著。硫酸盐还原在缺氧盐沼沉积层总呼吸中最高可达 90%，SRPs 的异化还原过程只有在活性有机质被消耗殆尽或硫酸盐含量匮乏(小于 4 mmol/L)时才停止[79,97]。群落结构的差异会影响微生物对有机质的反应[76,80]，揭示群落结构差异与有机质之间的响应机制很可能是对 SRPs 定性和定量分析的新方法。此外，SRPs 活跃程度与氧化还原电位密切相关，它们需要较低的氧化还原电位进行生命活动[81]。Harter 等[82]通过实验观察到 SRPs 在氧化还原电位为−75 mV 时开始与硫酸盐发生反应，氧化还原电位越低 SRPs 越易产生硫化物。Wu 等[83]通过对各种硫化物形态转化的吉布斯自由能计算，发现 SRPs 适宜的氧化还原电位为−60 mV 到−520 mV，这与 Harter 等[82]的研究结果一致。Yu 等[84]的研究表明，温度是影响红树林沉积物中微生物群落变化的关键因素；同一样地在不同年际之间的碳矿化速率变化相对稳定，但在同一年间受温度的影响较大，夏季的土壤碳矿化速率高于秋冬季节[8,85−86]。Liu 等[87]的研究表明，pH 是驱动无瓣海桑(*Sonneratia apetala*) 和拉关木 (*Laguncularia racemosa*)红树林微生物群落的主要环境因子。研究还表明，大多数 SRPs 适宜中性 pH 环境，而厚壁菌门脱硫芽孢弯曲菌属和热脱硫菌属(*Thermodesulfobium*)的物种更适宜酸性环境[89−90]。

在 Zn、Pb 和 Hg 等重金属污染的表层沉积物中，脱硫弧菌科成员中比互营杆菌科和脱硫杆菌科成员具有更高的 *dsrA* 转录活性[91]，这说明脱硫弧菌相较于互营杆菌和脱硫杆菌成员可能存在较多的机制来适应 Zn、Pb 和 Hg 等重金属变化。此外，沉积物中的 Fe^{3+} 含量升高会负向调控 SRPs 的硫酸盐还原率，甚至会抵消有机质的正向调控[92−93]，Wu 等[56]的研究表明，Cd 浓度的降低和 Ni 浓度的升高会负向驱动深圳福田、西乡和沙井红树林湿地 SRPs 的丰度，其中互营杆菌科对金属污染最为敏感。由此可知，不同的 SRPs 类群对于同一或者不同的重金属存在较大的相应差异，解析其分子机制是未来利用 SRPs 生态修复重金属污染的重要前提条件。

红树林湿地的其他生物通过对其周围微环境的改变也会对 SRPs 的生长产生影响。例如，植物的出现提高了盐沼沉积物中碳矿化速率[14]，无瓣海桑 (*Sonneratia apetala*) 和拉关木 (*Laguncularia racemosa*)的种植改变了红树林沉积物的营养状况以及生境特性，进而影响 SRPs 丰度的变化[84,95]。另外，底栖动物的活动，比如底泥中螃蟹的挖掘和建造洞穴等会改变土壤生境的微地形，也会影响 SRPs 的代谢过程[98]。

2　硫酸盐还原菌参与驱动的硫代谢

2.1　硫酸盐异化还原过程

硫酸盐异化还原过程首先通过 SRPs 的硫酸盐转运蛋白将环境中的 $SO_4^{2−}$ 运输到细胞内，然后细胞内的 $SO_4^{2−}$ 由 ATP 硫酸化酶(由 *Sat* 基因编码)激活形成腺嘌呤酰硫酸盐(adenosine-5′-phosphosulfate，APS)[99]。ATP 硫酸化酶是一类广泛存在于能进行异化硫酸盐还原生物体中的酶[100]，它在硫酸盐氧化菌中更倾向于 ATP 和 $SO_4^{2−}$ 的合成[101]。醌相互作用的膜结合氧化还原酶复合物(quinone-interacting membrane-bound oxidoreductase complex，QmoABC) (由 *qmoABC* 基因编码)和 APS 还原酶(由 *aprAB* 基因编码)相互作用催化 APS 还原生成亚硫酸盐 $(SO_3^{2−})$ 和单磷酸腺苷 (adenosine 5′-monophosphate，AMP)[102−103]。QmoABC 能够作为 APS 还原酶的电子供体，该复合物亚基由 2 个细胞质可溶性蛋白(QmoA 和 QmoB)和面向细胞质的可溶性结构域膜结合蛋白(QmoC)组成[104]。异化硫酸盐还原酶(由 *dsrAB* 基因编码)是亚硫酸盐还原过程中的关键酶，由 α 亚基(由 *dsrA* 基因编码)和 β 亚基(由 *dsrB* 基因编码)组成[105]，同源基因 *dsrA* 和 *dsrB* 可能源于早期的基因复制[106]。几乎所有 SRPs 基因组的 *dsrAB* 都包含编码硫转移蛋白 *dsrC*，因此起初认为 DsrC 是 DsrAB 的亚基。然而随着研究的深入发现 DsrC 并不是 DsrAB 的亚基，它的 C 端含有 2 个严格保守的半胱氨酸，可以与 DsrAB 相互作用形成二硫键产生 DsrCox 参与硫酸盐异化还原过程[107−108]。$S_2O_3^{2−}$ 和 $S_3O_6^{2−}$是亚硫酸盐过程中必不可少的中间产物，在亚硫酸盐异化还原酶(dissimilatory sulfite reductase)、三硫酸盐还原酶(trithionate reductase)和硫代硫酸盐还原酶(thiosulfate reductase)的参与下会形成三硫化物[109−110]。亚硫酸盐、三硫化物会与 DsrAB 和 DsrCox 的活性位点结合通过 DsrMKJOP 膜复合物进一步还原为硫化物[104]，同时还原后的 DsrC (DsrCrd) 从亚硫酸盐还原过程中释放出来(图 1)[111]。

2.2　SRPs 的硫歧化反应

据估算，硫歧化过程与硫酸盐还原均具有至少 35 亿年的演化历史[35,112]，可能是起源于同一时期的生化过程。歧化反应被认为是一种无机发酵过程，微生物将单质硫、硫代硫酸盐和亚硫酸盐同时作为电子供体和受体，最终生成硫化物和硫酸盐[113]。已有许多研究发现 SRPs

可以进行硫歧化反应，例如在脱硫棒菌科的脱硫叶菌属、脱硫棒菌属和脱硫盒菌属中发现了能够歧化单质硫生长的微生物。能歧化硫代硫酸盐和亚硫酸盐并生长的微生物大多隶属于脱硫弧菌属[114−115]。尽管歧化作用具有独特性，但是对 SRPs 的硫歧化过程研究却是一个长期存在的难题。有研究对能够歧化硫代硫酸盐和单质硫的硫歧化菌 (sulfur disproportionating bacteria，SDB)进行了纯培养、全基因组测序和酶提取，结果表明 SDB 与已发现的 SRPs 不仅在系统发育上接近，而且具有硫酸盐异化还原的全套基因[114,116]。系统发育分析表明，SDB 中发生过复杂的基因垂直转移过程，硫歧化与硫酸盐还原这 2 个古老的代谢途径之间可能存在潜在的进化过渡[36,116]。SDB 和 SRPs 在生物化学和进化历史上有很多相似之处，目前仍没有发现特异性基因或基因簇可以作为功能标记来区分没有歧化能力的 SRPs、缺乏硫酸盐异化还原能力的 SDB 以及具有 2 种功能的生物体[117]。Bertran[113]发现 APS 还原酶的 β 亚基长 C 端的结构差异可以作为 SRPs 和 SDB 潜在标记工具。这个结果仅是基于一些 SRPs 和 2 株完全测序的 SDB 基因组得到的，存在一定的局限性，不过仍为寻找区分 SRPs 和 SDB 的分子标记提供了独特见解。

3　硫酸盐还原菌参与驱动其他元素循环的耦合机制

3.1　硫酸盐还原菌参与驱动碳循环

　　红树林生态系统中植物将大气中的 CO_2 固定后以生物量的形式储存，能够在深埋地底数百年之久后形成重要的"蓝碳"汇[118]，工业化快速发展以及人为因素的干扰严重威胁了红树林生态功能，影响着蓝碳储量和温室气体的动态变化[119]。SRPs 是驱动红树林湿地碳硫循环的

关键菌群之一[25]。放射性同位素研究显示，硫酸盐还原速率在表层沉积物和深层硫酸盐-甲烷过渡带出现 2 个峰值[120]，说明 SRPs 驱动的碳硫耦合过程主要分布在表层沉积物以及硫酸盐-甲烷过渡带。已有研究表明，SRPs 几乎贡献了海洋沉积物一半以上有机碳的矿化[121−122]、盐沼缺氧沉积层总呼吸作用的 70%−90%[97]以及红树林沉积物全部的 CO_2 排放[8]。在红树林湿地表层沉积物中 SRPs 通过氧化有机质产生 CO_2 使得 SO_4^{2-} 浓度下降[9]。湿地中的 CH_4 产生主要来自于沉积物中的产甲烷古菌，而 CH_4 的消耗则主要归因于甲烷厌氧氧化 (anaerobic oxidation of methane，AOM)过程[123]。海洋沉积物中的硫酸盐一半以上都通过 AOM 作用消耗[120]，Elvert 等[124]对 SRPs 的荧光原位杂交技术观察到它们在 AOM 的聚集物中大量存在，说明 SRPs 活动与厌氧甲烷氧化古菌密切相关。SRPs 与产甲烷古菌存在竞争关系，Xu 等[125]用五氯苯酚(pentachlorophenol，PCP)明显抑制了 SRPs 的活性后观察到厌氧产甲烷菌生长速率增加。Zhang 等[126−127]的研究进一步表明脱硫橄榄状菌属(*Desulfobacca*) SRPs 与产甲烷菌存在显著的非随机相关，SRPs 主要与氢营养型和乙酸营养型产甲烷菌竞争，但能与甲基营养型产甲烷菌共存。此外 SRPs 也表现出与产甲烷菌和甲烷氧化菌协同合作的一面，硫酸盐枯竭后，SRPs 会发酵有机酸和醇，产生氢、乙酸和二氧化碳，可以为产甲烷古菌提供氢、甲酸和乙酸等，进而为甲烷氧化菌提供充足的甲烷[128−130]。SRPs 从与产甲烷菌的竞争再到协同合作的厌氧甲烷氧化过程均体现了其在控制温室气体排放中的调控能力，作为"幕后英雄"在"双碳"目标的大趋势下具有巨大的应用潜力。

3.2　硫酸盐还原菌参与驱动氧循环

　　红树林湿地潮汐的周期性变化会使潮间带

表层沉积物中的 SRPs 经常暴露在氧气的胁迫中。已有研究报道 SRPs 在好氧区和缺氧区均有存在，其中，脱硫弧菌属成员具有较高的耐氧能力[131–132]。脱硫弧菌包含硫酸盐和氧气还原所需的酶系统，由于底物水平的磷酸化不足以支持它们的生长[133]，它们需要通过硫酸盐异化还原与电子耦合磷酸化产生能量用以维持生长[134]。纯培养实验进一步证实了还原氧气的酶系统只是一种耐氧的保护机制[135]。脱硫弧菌 *Desulfovibrio gigas* 会通过膜结合氧还原酶[136]和细胞质氧化还原酶 (rubredoxin: oxygen oxidoreductase，Roo)相结合的机制[137–138]将氧气还原为水(图 1)。细胞色素 *bd* 酶(cytochrome *bd* quinol oxidase，Cyd)和血红素铜细胞色素 *c* 氧化酶(haem-copper cytochrome *c* oxidase，Cox)是在脱硫弧菌科中发现的 2 种膜结合氧化还原酶[104,136]。在细胞质中，Roo 是一种同源二聚体酶，每个亚基含有一个黄素单核苷酸(flavin mononucleotide，FMN)和催化二铁中心(catalytic di-iron center)[139]。红素氧化还原蛋白 Rb (rubredoxin)通过氧化 NADH 为 Roo 蛋白提供电子供体将氧还原为水[137,139]。已有研究在脱硫弧菌属中发现了趋磁性的 SRPs，它们能将磁铁矿(Fe₃O₄)或灰铁矿(Fe₃S₄)生物矿化成细胞内的磁小体，从而可以向具有丰富营养的微氧区进行定向移动[140]，这些研究均揭示了脱硫弧菌属 SRPs 与氧代谢之间的密切关系。此外 Schoeffler 等[141]通过驯化得到的脱硫弧菌变异菌株能够呼吸氧气获得能量并生长，这使我们对 SRPs 的氧气适应机制有了新的认识。

3.3　硫酸盐还原菌参与驱动氮循环

红树林生态系统因高效的初级生产力以及反硝化作用造成的净氮损失常被认为是氮有限的生态系统[142]。氮进入红树林生态系统主要通过土壤微生物对 N₂ 的固定以及人为氮源的排

放[13,143]。具有固氮基因遗传历史的脱硫叶菌属、脱硫杆菌属、脱硫肠状菌属和脱硫弧菌属等 SRPs 成员广泛存在于海洋沉积物中[27,57]，因此 SRPs 对沿海生态系统氮输入发挥重要作用[144–145]。此外，固氮微生物的活性是影响红树林土壤中 N₂ 固定的主要因素[146]。红树林生态系统是典型的富碳环境，SRPs 如脱硫弧菌属成员还可以通过异化硝酸盐还原为氨过程(dissimilatory nitrate reduction to ammonium，DNRA)来维持生物可利用的氮含量[147]。Nie 等[13]通过鸟枪宏基因组测序和 qPCR 分析发现，脱硫杆菌目中的 SRPs 成员含有大量的硝酸盐还原基因，尤其是 DNRA 基因。

反硝化过程是红树林湿地生态系统消除外来氮污染物的主要过程[148]，也是沉积物厌氧环境中产生 N₂O 的主要来源[149]。N₂O 是反硝化过程中主要的中间产物也是大气中 N₂O 排放的重要来源，而红树林系统中因 SRPs 的存在使得滨海湿地只是 N₂O 排放的弱源[150–151]，这可能是 SRPs 与反硝化菌对硝酸盐底物竞争中胜出的结果。SRPs 是红树林生态系统中关键的环境友好型微生物，不仅是不容忽视的氮素初级生产力，还能降低温室气体 N₂O 的排放，为湿地的节能减排提供新策略。

3.4　硫酸盐还原菌参与驱动金属元素循环

红树林丰富的有机质和硫酸盐含量使得硫酸盐还原成为有机质矿化的主要路径，而在生物扰动下铁异化还原速率会明显提高[98]。Hyun 等[14]的研究表明，硫酸盐还原和铁(Ⅲ)还原在盐沼湿地中对有机质矿化的贡献较大并且存在此消彼长的现象,说明硫酸盐还原与铁(Ⅲ)还原是竞争性抑制关系。铁(Ⅲ)还原主要由 SRPs 以及地杆菌 (*Geobacter*) 和除硫单胞菌 (*Desulfuromonas*)等铁还原菌驱动[152]。SRPs 产生的 H₂S 会与重金属离子(如 Fe²⁺、Mn²⁺、Zn²⁺

和 Hg^{2+} 等)反应形成不溶性金属硫化物, 也能利用酶直接将金属还原为毒性较低或较难溶解的形式[153]。Lovley 等[154−157] 对 *Desulfovibrio vulgaris* 的系列研究表明, 细胞色素 c 在 Fe (III) 还原中发挥重要作用。*Desulfovibrio vulgaris Hildenborough*、*Desulfomicrobium norvegicum*、*Desulfovibrio gigas* 和 *Desulfovibrio desulfuricans Norway* 可以通过细胞色素 c_3 还原铁。Li 等[158] 向富集 SRPs 培养基加入氧化铁(III)后, 细胞色素 c 基因和硫酸盐还原相关基因均上调, 说明 SRPs 驱动的非生物还原铁和生物酶促还原铁能够协同发挥作用。SRPs 产生过剩的 H_2S 在向上扩散的过程中会被 Fe(III)氧化物氧化为中间价态硫($S_2O_3^{2-}$、S^0), 在降低 H_2S 的毒性同时也抑制铁还原菌的异化还原[159]。中间态硫通过歧化反应生成 SO_4^{2-} 和 H_2S 以及中间态硫[113], 在低温下可参与 FeS 向黄铁矿转化并稳定地存在环境中。红树林生态系统中硫酸盐还原的主要硫化合物是 FeS_2, 其次为 HS^-、FeS 和 S^0 等[8]。FeS、FeS_2 和 HS^- 会被氧气、铁锰氧化物和硝酸盐等不完全氧化生成元素硫 $S^{0[160−161]}$, 在微生物作用下元素 S^0 会被 Fe(III)和 Mn(IV)进一步氧化为 SO_4^{2-} 和 $SO_3^{2-[162]}$, 而这些溶解态的硫化物若长时间未被沉淀, 就会形成有机硫[163]。元素硫 S^0 可以与溶解硫化物耦合生成多硫化物(S_n^{2-}), 进而促进黄铁矿的形成[164]。沉积物中活性铁氧化物和铁硫化物仍可继续 吸附或共沉淀重金属离子, 还可改变磷的形态影响其生物有效性和活性[165]。在缺乏碳源时, 成熟的 SRPs 能够氧化单质铁[166], 甚至可以在没有硫酸盐的情况下利用 Fe(III)氧化物或硝 酸盐作为电子受体生长[129,167]。在氧化铁存在的情况下, 硫酸盐的异化还原总是伴随着硫歧化[168], 氧化铁会作为硫化物清除剂, 更利于硫

歧化反应的发生[169]。此外, 歧化作用还使黄铁矿形成的速度提高了 10^4–10^5 倍, H_2S 在促进 FeS 向黄铁矿转化的过程中会产生 H_2, 专性硫歧化微生物 *Desulfocapsa sulfoexigens* 可以利用 H_2 产生能量从中受益, 并可能协同进化出加速黄铁矿形成的机制[114]。而 SRPs 在黄铁矿形成中的机制仍然是未解之谜, 亟需更有力的研究证据。

红树林湿地沉积物中的甲基汞主要来源于微生物的甲基化作用, SRPs、铁还原菌和产甲烷菌是主要的汞甲基化细菌[170−172]。Choi 等[173−174] 的研究表明, *Desulfovibrio desulfuricans* LS 体内乙酰辅酶 A 生成时, 甲基转移酶会作用于丙酮酸盐的甲基并与 Hg^{2+} 结合生成甲基汞, 首次证实 SRPs 所采取的汞甲基化途径为乙酰辅酶 A 途径, 但这并不是所有能够进行甲基化过程的微生物的通用路径[175]。Parks 等[176] 发现 *hgcA* (编码某种类咕啉蛋白的基因)和 *hgcB* (编码铁氧化还原蛋白的基因)是汞甲基化相关过程的关键基因。甲基化和去甲基化在环境中同时发生, 环境条件的变化会影响平衡状态[177]。吴浩对中国多地红树林区域甲基化水平研究时发现 SRPs 的作用可能为去甲基化[178]。Chen 等[179] 发现在水稻中 SRPs 和产甲烷古菌分别参与了砷的甲基化和去甲基化, 影响着二甲基化砷的动态变化。浮游植物小球藻自身会与铁还原菌竞争底物, 进而抑制其甲基化过程, 但其分泌的藻类有机物却又能促进 SRPs 的甲基化作用[180]。SRPs 的还原产物 H_2S 能与 Hg^{2+} 形成 HgS, 因此低硫酸盐还原率有利于汞甲基化[181], 此外 SRPs 的歧化作用也会抑制甲基化过程[182]。这些研究表明 SRPs 的甲基化作用是复杂的, 目前在自然条件下甲基化过程的分子机制尚不明晰, SRPs 与其他生物之间互作以及与环境因子的联系仍需进一步研究。

4　总结与展望

　　SRPs 是红树林生态系统中驱动碳氮硫以及金属等元素耦合的中坚力量，但其对厌氧环境的苛刻要求以及不可忽视的微生物互作等复杂过程限制了我们对 SRPs 驱动的元素耦合机制的研究。因此，未来可以在以下 6 个方面展开进一步的研究：(1) 挖掘区分硫歧化过程和硫酸盐还原过程的关键基因，从分子演化学角度进一步揭示微生物驱动的硫循环在早期地球地质演化过程中的作用；(2) 探究硫代谢途径功能基因与环境因子之间的关联以及结合沉积物中碳硫等同位素组成变化，有助于阐明 SRPs 参与驱动的生物地球化学元素循环的耦合机制；(3) 阐明不同 SRPs 类群与不同重金属之间的分子响应机制是应用 SRPs 进行重金属生态修复的理论基础；(4) 促进传统纯培养技术与微流控、细胞分选、拉曼光谱等技术的交叉应用，发展高通量微生物分离培养系统。微流控技术每秒可以产生大量液滴，这不仅可以实现单个菌株的分离培养，还能消除菌株生长速率差异引起的物种竞争，有利于恢复复杂生态系统中稀有或生长缓慢的微生物，为获得更丰富的 SRPs 纯培养菌株的超高通量鉴定和筛选提供了可能；(5) 未培养古菌是红树林生态系统中驱动元素循环的重要类群，利用合成生物学技术研究难培养古菌对于硫酸盐的还原能力有利于 SRPs 家族的构建，为进一步探讨自然状态下 SRPs 与产甲烷古菌和甲烷氧化菌等互营合作过程提供基础；(6) 在国家"双碳"战略下，SRPs 日益凸显其在生态治理下的重要位置，因此 SRPs 对于红树林湿地"蓝碳"形成的作用及贡献也是未来重要的研究方向。

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