Sulfate-reducing bacteria unearthed: ecological functions of the diverse prokaryotic group in terrestrial environments

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ABSTRACT   Sulfate-reducing prokaryotes (SRPs) are essential microorganisms that play crucial roles in various ecological processes. Even though SRPs have been studied for over a century, there are still gaps in our understanding of their biology. In the past two decades, a significant amount of data on SRP ecology has been accumulated. This review aims to consolidate that information, focusing on SRPs in soils, their relation to the rare biosphere, uncultured sulfate reducers, and their interactions with other organisms in terrestrial ecosystems. SRPs in soils form part of the rare biosphere and contribute to various processes as a low-density population. The data reveal a diverse range of sulfate-reducing taxa intricately involved in terrestrial carbon and sulfur cycles. While some taxa like *Desulfitobacterium* and *Desulfosporosinus* are well studied, others are more enigmatic. For example, members of the Acidobacteriota phylum appear to hold significant importance for the terrestrial sulfur cycle. Many aspects of SRP ecology remain mysterious, including sulfate reduction in different bacterial phyla, interactions with bacteria and fungi in soils, and the existence of soil sulfate-reducing archaea. Utilizing metagenomic, metatranscriptomic, and culture-dependent approaches will help uncover the diversity, functional potential, and adaptations of SRPs in the global environment.

KEYWORDS   sulfate reduction, uncultured microorganisms, soil microbiology, sulfur cycle, rare biosphere, terrestrial environment

Existing trends in the study of certain taxa of microorganisms in modern science can lead to biases that distort our understanding of their place in nature. These biases can be associated with the location or ecological niche where representatives of the group were first discovered. An example of such bias can be seen in research on archaea, which for a long time were solely considered through the prism of extremophilic lifestyles. However, recent studies indicate the need to study mesophilic archaeal species and acknowledge the group's ubiquitous nature (1) and even its potential involvement in human pathological processes (2).

We believe that the study of sulfate-reducing prokaryotes (SRPs) has encountered a similar issue. Abundant new data, including metagenomic analyses, indicate that the involvement of SRPs in ecological cycles in soil habitats may be underestimated.

SRPs have been extensively studied since the 19th century, and these works concentrated predominantly on specific habitats where this group plays crucial roles, such as structuring of microbial community in paddy soils and wetlands, driving the carbon flux in the global marine environment, and the role in pathogenic processes in the intestinal tract. Moreover, the biotechnological importance of SRPs was realized, either as the primary corrosion agent (3, 4) or essential part of bioreactors and activated sludges (5, 6). However, the substantial amount of new information collected about this group for the last two decades allows one to suggest even more ecological functions mediated by SRPs in nature. It includes SRP contribution to microbial communities at different levels, existence of a large proportion of uncultured and unclassified taxa

related to SRPs, and, most importantly, the ecology of SRP in soils. The latter is the most important gap in studying the microbial turnover of sulfur: SRPs were reported in soils multiple times, but the actual role of this group is poorly understood.

The main reasons for this bias are as follows:

1. SRPs are more commonly studied in the context of marine ecosystems.
2. While planning research, a wrong assumption can emerge that anaerobic SRPs are exclusive for anaerobic environments, not aerated soils.
3. Sulfate-reducing bacteria in terrestrial environments do not represent a cohesive taxonomic group, which impedes comprehensive study of whole terrestrial SRP diversity.
4. This group encompasses many non-culturable forms, whose physiological understanding has only recently become accessible with the advancement of metagenomic, metatranscriptomic, and predictive metabolic pathway analysis methods.

Considering all the aforementioned points, we strongly believe that the current perspective on SRPs needs to be revised based on the latest data, which will enable the emergence of new trends in the study of the environmental role of SRPs.

Therefore, the primary aim of this review is to examine the present status of understanding regarding SRP ecology within terrestrial ecosystems and to bring together new and overlooked data. Additionally, we propose a model highlighting the role of SRPs in terrestrial environments, particularly in soils.

WHAT DO WE KNOW ABOUT SULFATE-REDUCING PROKARYOTES?

The ability to reduce sulfur compounds, especially using sulfate anions as the terminal electron acceptors coupled to sulfide generation [dissimilatory sulfate reduction (DSR)], is not connected to a specific taxonomic group. This is due to the lateral gene transfer events and the unique evolutionary trajectory of SR metabolism. Species of the same taxonomic unit (genus or family) may be able to reduce (i) sulfate solely, (ii) sulfate and other S compounds such as elemental sulfur or thiosulfate, (iii) only some compounds except sulfate, or (iv) even disproportionate S compounds. There is no strict linkage between phylogeny and physiology. Moreover, the preference of electron acceptor depends on the environmental conditions, which results in using ferrous iron, nitrates, or even oxygen and organics. These considerations make it impossible to limit the group of bacteria under discussion only to complete reducers to sulfide or only to those which reduce sulfate solely, not to mention specific taxa. Here, we will use "sulfate reducers" or "SRPs" as generalizing terms for microbes with dissimilatory metabolism of sulfur compounds.

Sulfate reduction is one of the most critical processes in known ecosystems since it is the main way sulfur compounds are reduced in modern ecosystems. DSR is often coupled with the oxidation of many organic substrates, from volatile fatty acids to recalcitrant aromatic hydrocarbons (7). Some estimates indicate that sulfate is the second most abundant anion in marine environments after chlorides (8). With low oxygen levels and high concentrations of dissolved organic matter (9), water environments provide preferable conditions for sulfate-reducing prokaryotes to flourish, which is why microorganisms capable of DSR are well studied in marine and freshwater environments. Sulfate reducers also populate flooded soils and deep soil horizons (10, 11). In some cases, microbial reduction of sulfur compounds can be one of the major drivers of biogeochemical turnover, which is especially true for wetlands (12), peatlands (13), paddy soils (14), and soils undergoing flooding-evaporation cycles. Polluted and harsh environmental sites with active soil formation processes, such as sludges and acid mines, also comprise niches for SRPs (15–17). At the same time, the role of SRPs in natural ecosystems is not restricted solely to participation in the sulfur cycle. Microbial metabolism intensely connects the sulfur and carbon cycle (18). For example, sulfate

reducers are responsible for a significant flux of CO_2 from organics, which is especially important in marine ecosystems (19), where they can oxidize up to 30% of dissolved organics. As for the nitrogen cycle, the most critical SRP process is the ability to reduce nitrites and nitrates if the sulfate anions are absent (20). Moreover, data that sulfate reduction can be coupled with nitrogen fixation by some SRPs existed for more than 70 years (21) and are confirmed by recent works (22, 23).

Furthermore, according to some estimations, SRPs can act as primary producers in crust microbiomes without relying on photosynthetic processes (24). Another remarkable SRP characteristic is their interaction with compounds that are often considered xenobiotics or presented in xenobiotic concentrations. Many pollutants of significant environmental concern can be metabolized or immobilized by sulfate reducers. It is well known that these microorganisms can degrade mono- and polyaromatics (7, 25–28) and chlorinated organics (29) and precipitate heavy metals (such as Zn, Ni, and Cu) in the form of poorly soluble sulfides or enhance precipitation indirectly, so they gain a selective advantage in ecosystems with polymetallic or combined pollution (30, 31). Sulfate reducers are specifically known for sphalerite (ZnS) and related minerals precipitation (32, 33) Moreover, SRP-immobilized zinc was suggested to be more stable than its abiogenic alternative (34). One unique group of SRPs, known as dissimilatory metal-reducing bacteria, can reduce most heavy metal (HM) ions, including uranium (35, 36). Currently, many sulfate reducers are known to be able to reduce extracellular metals directly or via shuttle molecules. Overall, sulfate-reducing bacteria are essential in metal biogeochemistry (37–39). The intricate cell biology and physiology of SRP, however, are beyond the scope of the review and can be explored in other recent publications (40).

Due to the ubiquitous distribution of SRPs in natural ecosystems, there are numerous gaps in our understanding of their ecology. This includes the phenomenon of dormancy in SRPs, their role in the rare biosphere, and the degree to which SRP metabolic capacities go beyond the reduction of sulfur species. The most prominent gaps are visible when considering terrestrial microbial communities with SRPs.

EVIDENCE FOR SRPs AS A VITAL PART OF TERRESTRIAL ECOSYSTEMS

Marine and aquatic conditions are favorable for SRPs, which is why our knowledge of this large and diverse group is limited to water habitats (41). To date, SRP population dynamics, diversity, and physiology are poorly understood in pristine and anthropogenically impacted terrestrial ecosystems, especially in soils (28, 42). Collected data are mostly restricted to areas where anaerobic conditions are sustained most of the time, such as paddy soils and subsurface water horizons. Despite the recognition of the urgent need for studies addressing the biogeochemical role of sulfate reducers in aerobic or hypoxic terrestrial zones (41, 42), little progress has been made in the last years. One can presume that the strictly anaerobic group of microorganisms will not be an active part of environments with the regular influx of oxygen (such as topsoils) or that its influence will be negligible and limited to anaerobic microniches. However, there are multiple aerotolerant and oxygen-respiring SRP genera, such as *Desulfovibrio*, *Desulfobulbus*, *Desulfomicrobium*, and *Desulfofaba* (43, 44), and even proliferation in aerated topsoil was reported (28). The understanding slowly emerges that DSR can substantially affect ecosystem productivity in terrestrial environments (12, 13, 41, 45). Moreover, low sulfate concentrations in soils, peatlands, and rice paddy fields are not constraints for either high sulfate reduction rates or sulfate reducer diversity (46).

Except for the extensively studied *Desulfovibrio* and *Desulfotomaculum*, plenty of other important SRPs inhabit soils, including those with occurring aerobic conditions (Fig. 1). The most demonstrative in-land sulfate reducers belong to the Bacillota phylum. The first example is *Desulfitobacterium* genus. More than 20 years ago, scientists showed that pollutant-degrading *Desulfitobacterium* species, initially isolated from the environment contaminated with chlorinated aromatics, are widespread throughout different soils with various levels of anthropogenic impact (47). The authors hypothesized that the studied *Desulfitobacterium* are a part of diverse natural microbial communities with
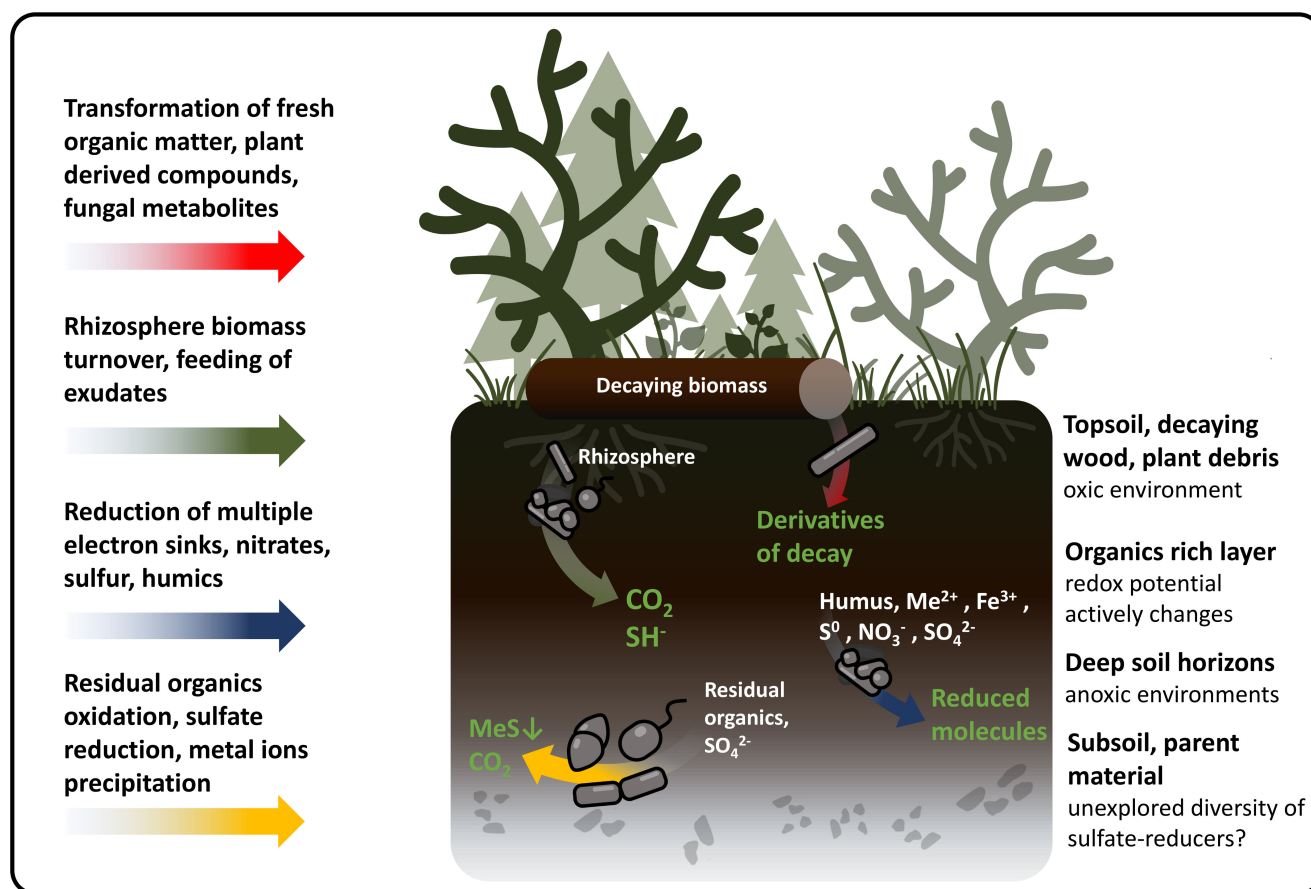
FIG 1 Summary of different ecological functions mediated by SRPs in soils.

the ability to degrade chlorinated organics as an accessory. Further studies reported the active role of SRP species in HM attenuation in contaminated soils (48–50), with *Desulfitobacterium* among such species (50, 51), because of their ability to form poorly soluble metal sulfides (52). The ubiquity of the genus was confirmed by the study of Mingo et al. (53), who showed that different phenyl methyl ether-demethylating *Desulfitobacterium* strains were isolated in great quantity from top horizons of different soils, and 16S rRNA gene copies were observed in each soil sample studied. In another study, deoxynivalenol was significantly de-epoxidized by a microbial consortium isolated from wheat topsoil, with *Desulfitobacterium* sp. as a significant actor in deoxynivalenol detoxification (54). Interestingly, phenyl methyl ethers and deoxynivalenol are products of fungal metabolism, suggesting another role of *Desulfitobacterium* spp. in soils, aside from the sulfur and iron reduction.

Recently, petroleum-degrading, thiosulfate-, and iron-reducing microbe was isolated from contaminated soil, which genetically clustered with *Desulfitobacterium aromaticivorans* but showed distinct physiological and phylogenetical traits (55). It was suggested to classify this strain to the new *Paradesulfitobacterium* genus and reclassify *Desulfitobacterium aromaticivorans* to it. An interesting study was performed by Huang et al. (56), where soil incubation experiments with glucose, lignin, and hemicellulose amendments and hypoxic conditions resulted in the enrichment of *Desulfitobacterium* and *Desulfosporosinus* genera. Furthermore, these two genera and *Desulfotomaculum* were the significant taxa emerging from approximately 60-cm depth of cryosols during long-term thawing experiments, which confirms that they are adapted to altering conditions in soils (57). All these findings widen our perspective on the SRP diversity and ecology in soils.

Desulfosporosinus genus appears to be another SRPs frequently met in hypoxic/oxic environments. It is usually captured from water-saturated soils such as paddy fields (56, 58), wetlands, peatlands, and other soils with anoxic conditions. However, the presence of the genus has been shown in more air-saturated soils too. These include enrichment cultures from As-Pb-contaminated soils near smelters in China (49), microcosms with alkane-contaminated soils (59), and natural communities of benzene-toluene-xylene-contaminated soils (60). A study of Gagliano et al. (61) describes a topsoil (0–3 cm) microbial community near the terrestrial hydrothermal vents with harsh conditions, including low pH and temperature >60℃. *Desulfosporosinus*, followed by *Desulfotomaculum*, were among the major dominating taxa. The authors did not specifically discuss that observation but reported a high level of water saturation in this soil and attributed it to the active condensation of the hydrothermal water vapor from below. It presumably should create hypoxic conditions, but intense water evaporation in hydrothermal vents and the vicinity to the surface air make this case especially interesting in the scope of this review.

Genera *Desulfosporosinus* and *Desulfotomaculum*, along with *Desulfovermiculus*, again have been reported as dominating groups in the deep horizon of colluvial soils (62). The authors mentioned that anoxic conditions for studied soils, even at the deep level, are rare and transient. Furthermore, a study on more temperate soils revealed the presence and the dominance of *Desulfosporosinus* operational taxonomic unit (OTU) (followed by *Desulfobulbus*) among SRPs in areas of intensive land use, such as arable soils and grasslands (42). One more SRP genus from Bacillota for which soil as an isolation source and habitat was reported is *Desulfonispora*. Iron-rich soils (63), soils from ice-free zones in the Arctic (64), and ornithogenic arctic soils (65) have been stated as the source where *Desulfonispora* was found to be isolated or detected in metagenomic studies. Although *Desulfonispora* instead metabolizes organosulfonates than actively reduces sulfate (66), its publicly available genome annotation contains *DsrAB* genes, suggesting the ability to reduce sulfite (BioProject accession number PRJEB20235).

Other phyla, such as Thermodesulfobacteriota, Acidobacteriota, Campylobacterota, and Thermotogota, also provide SRPs found in land ecosystems. A compelling and counterintuitive case is the metagenomic study undertaken in China wetlands, where the *Desulfuromonadaceae* family was significantly enriched in sediments during the dry season (67). Based on the network analysis, authors suggested this family to be one of the putative keystones shaping the dry season microbial community. Sequences affiliated with *Desulfuromonas*, a typical member of *Desulfuromonadaceae* family, were found to be abundant in an amplicon metagenomic survey of soils near the Roopkund Glacier, India, and the already mentioned *Desulfosporosinus* and *Desulfitobacterium* genera were present as well (68). Like *Desulfuromonadaceae* (67), *Desulfurellaceae* family was among the significant and active members of the soil microbiome, as reported by two independent studies. The first denotes the increased abundance of the family because of farm activities (69), and the second addresses the effects of tree species on adjusting soil's microbial communities (70). The microbial community of the latter study was completely in-land without flooding, and the authors managed to uncover significant differences in *Desulfurellaceae* abundance between soils under different tree coverage. The study by Miletto et al. (71) found that in experimentally flooded grassland soil, there was an increase in the abundance of *Desulfobulbaceae* family members compared to salt marsh soil, where *Desulfobacteraceae* members were the predominant sulfate-reducing bacteria. Finally, *Mesotoga* genus, which is the only mesophilic member of Thermotogota phylum, can reduce thiosulfate and molecular sulfur and can be found in soils (72, 73). Moreover, it was hypothesized that the genus is spreading across various terrestrial biomes as a result of human technogenic activity, since its presence is often accompanied by high content of polyaromatic hydrocarbons (PAHs) (73).

In contrast to soils, deep terrestrial subsurface is well recognized as a habitat for SRPs. These bacteria were repeatedly reported as the active members of deep crystalline bedrock microbial community (74–79) and can be found at more than 2-kilometer depth

(80). In deep subsurface, SRPs contribute to symbiosis with archaea or to metal corrosion. The latter is specifically studied in the context of radioactive waste disposal, since SRPs immobilize and absorb radioactive elements in deep fractures (81–85) as well as mobilize radioactive metals such as plutonium both directly (86) or indirectly by copper containers corrosion (87).

BIOTIC RELATIONS OF SRPs IN SOILS

Rhizosphere

Sulfate reducers are present in diverse ecological niches and habitats, including plant rhizosphere. However, most studies focus on the microbial community of seagrass and other plants inhabiting soil-water interfaces. Many papers are studying the SRP communities in paddy soils. A rather diverse SRP community characterizes rice fields. Among the genera identified in such soils are *Desulfobacca*, *Desulfovibrio*, *Syntrophobacter*, *Desulforhopalus*, *Desulfarculus*, and *Desulfobulbus* (88). The SRPs play a vital role in the rhizosphere of plants grown in soils contaminated by potentially toxic elements (PTEs). In paddy soils located in the zone adjacent to thallium sulfide utilization plant, thallium's geochemical fractionation is largely reliant on the activity of Fe-reducing *Geothrix* and sulphate-reducing *Anaerolinea* (89). Sulfur-cycling microorganisms also contributed to the mitigation of chromium toxicity by reduction of Cr(VI) to less toxic Cr(III). A recent study showed that in the rice rhizosphere, *Desulfovibrio* species reduced sulfate to sulfide utilizing citric acid from root exudates as electron donors. *Thiobacillus* used the resulting sulfide to reduce Cr(VI) (90). It has been shown that the addition of sulphate reduced Cd's translocation from soil to rice grain by 53.2%–63.2%, depending on moisture conditions. The mechanism involved CdS precipitation by *Desulfovibrio*, promoted by flooding (91). As for the influence of SRPs on the bioavailability of arsenic, the evidence is contradictory (92). It has been shown that SRPs can take part in direct and indirect reduction of As, leading to increased bioavailability (93). At the same time, other studies suggest that the microbially mediated formation of secondary mackinawite (FeS) leads to trapping As in its structure, decreasing the mobility of this toxic element (94).

SRPs were also found in other highly flooded yet in-land niches, such as coastal silt soils and salt marshes. In coastal silts, it was shown that functional bacteria enriched in *S. glauca* rhizosphere can enhance the driving effect of the sulfur cycle and promote the transformation and circulation of Fe, N, and C in the soil by enhancing the degradation of organic matter and sulfate reduction (95). Sulfate-reducing bacteria were thus thought to be particular hub bacteria for the growth of salt-tolerant plants. For salt marshes, a recent study revealed that the core rhizosphere microbiome of a typical salt marsh plant, *Spartina alterniflora*, is highly enriched with sulfate-reducing genera, such as *Desulfatiglans*, *Desulfocarbo*, *Desulfatitalea*, *Desulfobulbus*, *Desulfopila*, and *Desulfosarcina* (96). Thus, significantly higher rates of enzymatic organic matter decomposition as well as the relative abundances of putative sulfur (S)-oxidizing, sulfate-reducing, and nitrifying prokaryotes correlated with *S. alterniflora* productivity (96). Moreover, prokaryotic species from the *Desulfobulbus*, *Desulfatitalea*, *Desulfovibrio*, and *Sulfurospirillum* genera were shown to couple sulfate or sulfur respiration with nitrogen fixation (96–98), which expands their role in rhizosphere communities.

In the rhizosphere of plants in paddy soils, there are several driving factors determining the numbers and activity of the SRPs. Main factors include the availability of sulphates, dissolved organic matter, and their ratio. More than 30 years ago, it was shown that the optimal ratio of sulphates to available carbon sources is 2:1, and the maximum numbers of SRPs are observed in the rhizosphere during the tillering phase (99). This can be attributed to root exudation activity which differs significantly during plant development. Another important factor is the oxygen level, which should limit SRP growth. Studies of rice rhizosphere have shown that the conditions in rhizosphere soil are oxic and would theoretically be unsuitable for SRP activity. However, the presence of anoxic microsites ensures their survival and participation in geochemical processes (100). Furthermore, among SRPs, several species are tolerant to the presence of oxygen

to some degree (101, 102). Thus, we should expect SRPs to be present in the rhizosphere of plants growing in well-drained soils that are not subjected to regular flooding.

However, there are very few publications dedicated to SRP communities of such soils. In 2006, the black layer formation in the rootzone of *Agrostis stolonifera* was attributed to active biologically induced sulfate reduction (103). The studies of oak rhizosphere revealed that the abundance of particular genera was different in rhizosphere and bulk soil. The abundance of *Desulfacinum* was higher in bulk soil compared to oak rhizosphere. The abundance of *Desulfuromonas* was low in both rhizosphere and bulk soils (104). The influence of tobacco plants on the abundance of SRPs was different and dependent on the Cd contamination level. High Cd treatment (5.8 mg kg^{-1}) tended to enrich sulfate-reducing bacteria (such as *Desulfarculaceae*). In comparison, low Cd treatment (0.2 mg kg^{-1}) led to the enrichment of plant growth-promoting bacteria (*Bacillus*, *Dyadobacter*, *Virgibacillus*, and *Lysobacter*) (105). This observation demonstrates the potential role of SRPs in decreasing the bioavailability of PTEs in soils with normal water regimes. The SRP communities are also active in the rhizosphere of crop plants. For example, sulfate reducers are present in the rhizosphere of maize, and their abundance is more stable when the plants are colonized by mycorrhizal fungi (106).

To conclude, among the SRPs, the role in terrestrial plants' rhizosphere is shown for *Desulfovibrio*, *Syntrophobacter*, *Desulfobacca*, *Desulforhopalus*, *Desulfarculus*, *Desulfacinum*, *Desulfuromonas*, *Anaerolinea*, and *Desulfobulbus*. The representatives of the mentioned genera can take part in regulating PTE bioavailability and depend on plant root exudates as electron donors. Despite the potentially oxic conditions, their ecological niches are not limited to flooded soils and should be studied in more detail in all terrestrial ecosystems.

SRPs as part of the soil rare biosphere and the role of phages in their life strategy

The most demonstrative and cited studies about the SRP impact on an ecosystem concerning their low relative abundance have been conducted by Pester et al. (13). Results showed that SRPs, being the "rare" part of the particular microbial community, can still considerably contribute to the biogeochemical flow of carbon, with the effects going way beyond the community itself. Furthermore, the intriguing observation was made that sulfate reducers can increase ribosomal count and sustain some transcriptional activity even at zero-growth, comprising less than 0.01% of the microcosm community (107). Finally, the group showed that a small population of *Desulfosporosinus* in microcosms does not multiply its biomass by growth or proliferation but remains transcriptionally and metabolically active for more than a month (108). Such zero growth coupled with cellular activity was hypothesized to be the meaningful strategy in highly fluctuating niches, i.e., peat soils. Unfortunately, not so many studies of SRPs combining community profiling and cultural data have been conducted so far.

A survey of George et al. (42) has shown noticeable diversity of sulfate reducers in different soils at low levels of absolute abundance, which peaked in grassland soils and was not correlated strictly with the acidity or moisture level. Again, the most abundant SRP taxa were *Desulfosporosinus* and *Desulfobulbus*. The authors hypothesized that the low observable relative abundance of sulfate reducers can be explained by both SRP dormancy/rarity and the inappropriateness of general prokaryotic primers to amplify SRP ribosomal genes. This, in turn, can shed light on the other study of (109), where the amplicon metagenomic approach failed to reveal the presence of sulfate reducers in the flooded coal mine. However, plenty of sulfur oxidizers were found, hinting at some source of reduced sulfur compounds. Indeed, subsequent enrichment culturing revealed the presence of *Desulfotomaculum* and *Desulfomicrobium* species, and similarly, it was then hypothesized that they are rare biosphere members. It is the question of whether such results are caused by actual rarity or insufficient primers. It is perhaps both, especially since it is reported that microbial groups can be enriched from a sample inoculate while not showing in its metagenomic profile (109).

An interesting case was reported by Karnachuk et al. (110). The study focuses on the thermophilic *Desulfofundulus* species, which was isolated from soils and rocks near burning coal seams. This species produces spores capable of germinating into metabolically active sulfate-reducing cells, even in a mesophilic environment. However, these cells are unable to divide under such conditions. Based on this discovery, authors challenge the existing explanation that abundant thermophiles in mesophilic conditions are merely metabolically inactive biomass. It can be further hypothesized that at least part of reductive sulfur metabolism taking place in moderate soils is attributed to thermophilic bacteria, like *Desulfofundulus*, *Thermotoga*, *Caldisericum*, and many others.

Based on the above, we should consider it essential to conduct culture-dependent studies to characterize an SRP community. These observations are also interesting in the context of SRP virome. Viruses of sulfate reducers, presented especially as prophages, are numerous (111). They also can coinfect their metabolic and syntrophic partners (112) and contribute to the ecological role of SRPs (113, 114). For example, based on an analysis of soil-recovered SRP genomes, it was suggested by Li et al. (41) that SRP phages can participate in cell life by providing protection from oxidative stress and facilitating glycoside hydrolysis. Such participation can be achieved if SRP viruses are present as prophages, which, in turn, can be facilitated by a life strategy with low population density, rare cell division events, and high transcriptional activity.

Fungi

Fungal-SRP interactions are an even rarer topic in literature. Anaerobic fungi in deep granite fractures were hypothesized to be in syntrophic relationships with SRPs by supplying the latter with hydrogen and acetate (77). Both fungi and SRPs are known for colonization and degradation of metal or concrete materials, such as rocks, ceramics, metal statues, and several built environments (115), where they can coexist in a biofilm. This view is supported by the study of Nuppunen-Puputti et al. (116), where cross-kingdom interactions between fungi and SRPs were detected on schist surfaces, and by the survey of Edgcomb et al. (117), found collective hydrocarbon degradation by fungi and sulfate-reducing bacteria (SRB) in hydrothermal vents. Again, possible metabolic interaction can exist between SRB and fungi in soils, given the ability of *Desulfitobacterium* spp. to transform fungal metabolites (53, 54). Thus, arid soils, rocks, granite intrusions, and ore deposits provide potential spots for interactions between sulfate reducers and fungal species in terrestrial ecosystems. More studies are required for understanding fungal-SRP interactions.

Syntrophic interactions with other bacteria

Despite the long research history, little is known about syntrophic interactions between SRPs and other bacteria, especially in soils. It has been known for a long time (118) that sulfate reducers naturally develop relationships with sulfur-oxidizing (both lithoautotrophic and photosynthesizing) bacteria by providing them with reduced sulfur species such as sulfide or thiosulfate. Their co-occurrence can be found in multiple areas (96, 101, 119). However, the relationships between sulfate-reducing and sulfur-oxidizing bacteria (SOB) in soils are poorly understood. Since the high diversity of both SRPs and SOB groups as well as different sulfur compounds readily available in natural conditions, we should expect complex cooperative-competitive interactions between different members of sulfur-transforming community. This picture became even more sophisticated if oxidative-type Dsr pathway in SOB and sulfide oxidation metabolism in SRPs [like in *Desulfobulbus*, *Desulfovibrio*, see references (120, 121)] are considered. Many studies undertaken so far describe reducer-oxidizer relationship only in marine sediments (122, 123) or artificial systems, such as municipal wastewater treatment plants (124–127) and laboratory co-cultures (128). Direct syntrophic association was described by Yamamoto-Ikemoto et al. (125), where sulfur bacteria filamentous bulking and increased sulfide oxidation rates were observed after the elevation of microbial sulfate-reducing activity in an activated sludge system. Fukui et al. (122) reported close natural associations between

gliding filamentous sulfate-reducing *Desulfonema* spp. and giant filamentous sulfide-oxidizing *Tioploca* and *Beggiatoa* species in coastal and freshwater pond's sediments. The authors hypothesized in the first place that the capacity for gliding motility of *Desulfonema* is hindered in sediments and that *Tioploca* sheaths provide another substrate for gliding in such conditions. Recently, a close association between sulfide-oxidizing cable Desulfobulbaceae bacteria and *Desulfatiglans* was confirmed to take place in sediments suboxic zone (129). These interactions should take place in soils too, since such electroactive Desulfobulbaceae genera as *Electronema*, *Electrothrix*, and *Desulfobulbus* can be found in temperate and anaerobic soils (39, 42, 71). On the other hand, soils, as aquatic sediments, are solid-state heterogenic media, where filamentous species can provide not only nutritional but also spatial advantage for motile sulfate metabolizing bacteria. SRP potential interactions with fungal hyphae discussed above also hint on such type of symbiosis. Xia et al. (130), reported co-occurrence of SRPs and SOB in landfill cover soil layers. Uranium-bearing sandstone was also documented as a source with an active sulfate-reducing and sulfur-oxidizing microbial community (131). In the rhizosphere zone, the existence of SRPs depends on the activity with which aerobic species remove oxygen, although it is not a specialized type of interaction. More close interactions were reported multiple times in between SRPs and methanogens or methane oxidizers, as reviewed in references (132, 133). It was the subject of recent investigations (133–135). Almost all comprehensively studied syntrophy includes archaea in subseafloor, except for Candidatus *Acidiflorens* and methanogens in thawing permafrost (136), and the case of *Mesotoga prima*, a sulfur and thiosulfate-reducing microorganism that can establish interspecies hydrogen transfer with hydrogenotrophic sulfate reducers in oil reservoirs and, possibly, soils (137).

Finally, microbial interactions between SRPs and other representatives of natural microbial communities, particularly sulfur compound oxidizers, have been studied for many years. However, the studies have been heavily focused on aquatic or artificial ecosystems, while terrestrial habitats have largely been overlooked. The diversity of SRP morphology and life strategies (motile and attached, filamentous and single-celled, actively dividing and capable of maintaining activity at zero growth, microaerophiles and obligate anaerobes), metabolism types, available sulfur compounds, and potential symbiotic partners suggests that we have only scratched the surface in studying their relationships with other bacteria.

UNCULTURED AND UNCLASSIFIED REALM OF SULFATE-REDUCING MICROORGANISMS

Most of the knowledge about sulfate reducers was obtained by studying culturable representatives of the group. However, a vast gap exists between the cultured and observed diversity of dissimilatory sulfite reductase (*Dsr*) genes. As far back as in 2008 (11), unique phylotypes deeply divergent from common cultured sulfate-reducing bacteria were found. Since then, novel *Dsr* variants continued to emerge from multiple studies. In wetlands, for example, most sulfate reducers belong to unclassified and rare taxa (12) as well as in peatlands (138). The distribution of *Dsr* genes across various genomes suggests the presence of full gene clusters for sulfate, sulfite, or sulfur reduction in very different phyla (19). Interestingly, almost full clusters were found in typically aerobic bacteria such as Actinomycetota. More recently, the diversity of *Dsr* genes was estimated in arsenic-contaminated soils, and again, most variants were new at the genus and family levels (139). In the same year as the study of Anantharaman group, a high-coverage metabarcoding survey with more than 200 samples representing 14 habitats revealed even more hidden diversity of *Dsr* genes, with an amount of new species-level OTU reaching more than 150,000 (140). The authors stated that the *Dsr* copies of already cultivated sulfate reducers comprise less than 1% of the discovered quantity, even when we consider the existence of inactive copies of *Dsr* genes and those which are working in the opposite direction in the sulfur-oxidizing taxa. It was concluded that a "rare sulfate-reducing microorganisms' biosphere" exists that can serve as a seed

bank triggered by environmental changes. From the perspective of the current review, it should be noted that a limited amount of temperate terrestrial ecosystems has been taken into the study and no highly aerated representatives at all. Can it then be that even such high previously undetected diversity is underrated? The answer is likely yes, given that, in the study of Vigneron et al. (140), nearly 30% of uncovered gene copies were attributed to unknown and unclassified taxa and affiliated with different uncultured environmental superclusters. Finally, no *Dsr* clusters or sulfate-reducing taxa were found to be ubiquitous, which again shows how diverse and specialized SRPs can be, in terms of metabolic capacities and role in a community. The point is also supported by the variety of SRP stress coping mechanisms, defense systems, and syntrophic interactions (141) and by the reports of niche partitioning between different SRPs at the microscale in microbial mats (142) and macroscale in sediments (143). Considering all of this, one should ask what a rarefaction curve would look like for all known *Dsr* variants thus far. Are we even close to a plateau?

If such an enormous diversity of sulfate reducers exists in all environments and is hard to culture, we should rely on metatranscriptomic data. A limited number of studies have considered sulfate reduction taxa and activity based on metatranscriptomic data so far: in microbial fuel cells (144), in waters (145–147), and in artificial systems (148, 149); only a few has been soil oriented. Surprisingly, Acidobacteriota was reported as the active sulfate reducers in terrestrial ecosystems. To our knowledge, the first report of Acidobacteria contribution to the dissimilatory sulfur cycle was made by Pester et al. (13), where a minor but significant share of peatland sulfate reduction was affiliated with Acidobacteria subgroup 3. In recent years, acidobacterial sulfate reducers appeared periodically in studies of the marine environment (150, 151), while on the surface, only peatlands have shown a full set of SR genes in Acidobacteria genomes. A remarkable study of Li et al. (41) follows metatranscriptomic data obtained from revegetated acid soil near the acid mines. The authors recovered multiple high-quality metagenome-assembled genomes (MAGs) of *Deltaproteobacteria* and *Acidobacteria* lineages, which carry complete and actively expressing DSR pathways; revealed the role of viruses in their life strategy; and concluded that acidobacterial SRPs dominate over canonical SR deltaproteobacteria in studied sulfate-rich soils. Hausmann et al. (152) recovered MAGs of sulfite- and sulfate-respiring Acidobacteria from peatlands and confirmed the activity of DSR pathways both in soils and microcosm experiments.

Finally, MAGs of similar bacteria were obtained in seasonally thawed Sweden peatlands and was named Candidatus *Acidiflorens* (136). Although the study did not discuss a complete set of necessary genes for DSR, the MAG did have it. It later clustered with other SR acidobacteria in visualization by Flieder et al. (151). All four studies indicate usage of plant-derived oligo- or polysaccharides, namely, xylanes, by these Acidobacteria. Acidobacteria in peatlands perform a unique process of coupling complex organic matter's degradation to sulfate reduction. Besides that, a few studies were conducted. A clear increase in Desulfobacterota transcripts was observed for acid sulfate soils in unoxidized deep soil horizons (153). Contradictory metatranscriptomic results were reported regarding the effect of the increase in atmospheric CO_2 content on soil microbial communities and S cycle specifically. In the study of Padhy et al. (154), dissimilatory and assimilatory S pathways were upregulated as well as the abundance of sulfate-reducing genera, while in reference (155), sulfate reduction was significantly downregulated.

To sum up, metagenomics constantly reveals an unexpected diversity of sulfate reducers in all Earth habitats. At the same time, limited environmental transcriptomic studies show that this diversity can extend beyond the canonical SR taxa. Table 1 summarizes the data on SRP diversity in terrestrial habitats obtained with different omics approaches. More metatranscriptomic and culture-based studies are required to characterize such SRP diversity fully.

TABLE 1 SRPs that have been identified in different terrestrial ecosystems in the last 10 years and their contribution to sulfur cycling

Material	Habitat	Identified SRPs	Sulfur cycle contribution	Approach	Study
Soil	Revegetated acidic mine wasteland	Acidobacteria sb. 1, Deltaproteobacteria (Desulfovibrio, Syntrophobacteraceae)	Sulfate, sulfite reduction	Shotgun metagenomics, metatranscriptomics	(41)
Peat, soil	Thawing palsa and bog	Acidobacteria, Acidobacteriaceae family, Candidatus Acidiflorens spp.	Sulfate, sulfite reduction	Shotgun metagenomics, metatranscriptomics, metaproteomics	(136)
Soil	Acid sulfate soils	Desulfobacteria	Sulfate, sulfite, sulfur reduction	Shotgun metagenomics, 16S rRNA amplicon sequencing, metatranscriptomics	(153)
Peat, soil	Schlöppnerbrunnen II acidic peatland	Desulfosporosinus, Syntrophobacter, Desulfobacca acetoxidans, Acidobacteria sb. 1 and 3, Verrucomicrobia	Sulfate, sulfite reduction	Shotgun metagenomics, metatranscriptomics, stable-isotope probing	(152)
Rock and soil	Chagan-Uzun lignite open mountain pit	Desulfofundulus sp., Thermanaeromonas sp.	Sulfate, sulfite, thiosulfate reduction	Shotgun metagenomics, 16S rRNA amplicon sequencing, pure culture isolation	(110)
Soil	Soil contaminated with chloroethene near the Alameda Naval Air Station	Mesotoga spp.	Sulfur, thiosulfate reduction	Shotgun metagenomics	(73)
Sediments	Salt marsh sediments (S. alterniflora rhizosphere)	Desulfatitalea, Desulfopila, Desulfosarcina, Sulfurospirillum	Sulfate, sulfite, sulfur reduction	16S rRNA amplicon sequencing	(96)
Soil	Wales grasslands with different degree of land use	Desulfosporosinus, Desulfobulbus, Desulfobacca, Desulfomonile	Sulfate, sulfite reduction	16S rRNA amplicon sequencing	(42)
Soil	Hainich National Park Forest soil	Desulfurellaceae	Sulfate, sulfite reduction	16S rRNA amplicon sequencing	(70)
Dried out coastal sediments	Subtropical intertidal wetland	Desulfuromonadaceae	Sulfate, sulfite, sulfur reduction	16S rRNA amplicon sequencing	(67)
Soil	South Moravia colluvial chernozems	Desulfosporosinus, Desulfotomaculum, Desulfovermiculus	Sulfate, sulfite reduction	16S rRNA amplicon sequencing	(62)

WHY HAVE SULFATE-REDUCING ARCHAEA NOT BEEN DISCOVERED FROM COMMON SOILS?

Today, only four SR archaea genera are cultured: *Archaeoglobus*, *Caldivirga*, *Thermocladium* (40), and *Vulcanisaeta* (156), and none of them are from soil. All four thrive in oil deposits and hot springs. In metagenomic studies, two more sulfate-reducing candidate archaeal phyla, Hydrothermarchaeota and Aigarchaeota, were found to harbor sulfate-reducing machinery (19, 157). Also, some scarce evidence exists that Asgard archaea can be involved in the dissimilatory reduction of thiosulfate (158). Nevertheless, all mentioned archaea thrive or supposedly thrive in diverse extremophilic and/or deep ecosystems. Only one instance of Dsr-containing archaeal Thermoplasmatota MAG assembled from soil metagenome was reported by Diao et al. (46). So why evidence for sulfate-reducing archaea in terrestrial sites is so scarce, almost non-existent? The answer most likely lies in evolution. Recent findings suggest that the diversity of sulfur cycle microbiota in the ancient Earth was maintained mainly through intermediate sulfur compounds such as sulfite, rather than sulfate, due to the lack of the latter in the ancient atmosphere and hydrosphere (156, 159–161). Sulfate was initially present in negligible concentrations but began to accumulate only after the occurrence of the global oxidation event (GOE) (162). Given that archaea are intrinsically adapted to chronic energetic stress (163) and that reduction of sulfate, but not sulfite, is ATP dependent (156), it is possible to speculate on the following.

Before GOE, sulfate reduction was not an essential process on early Earth (159, 164). Sulfur cycle microbiota thrived on S intermediates. Among them are sulfite- and thiosulfate-respiring species of *Pyrobaculum*, sulfur-respiring members of Crenarchaeota (165), or the recently discovered sulfite-reducing Diaforarchaea (160) and, possibly, Korarchaeota (166). On the other hand, only a limited bacterial population supposedly metabolized sulfate and could transfer their DSR genes to archaea more than once (156). Furthermore, along with the elevation of oxygen and sulfate content during the GOE, bacteria were the first to take advantage of these electron acceptors. In such an environment, no energetic stress existed for a bacterium that couples the oxidation of a substrate to the reduction of sulfate, and most archaea could not compete with it. More than that, there is evidence that around GOE, another event took place, namely, the decrease in global Ni concentrations, which favored sulfate reducers over Ni-dependent methanogens (167) and probably led to the increase in the worldwide abundance of the former. The pathways of dissimilatory SR were able to evolve extensively and did that to a much more degree in bacteria than archaea. Eventually, the diversity of sulfate-reducing bacteria expanded and moved to the surface, and the first soils began to emerge. It is generally assumed that plants colonized the land surface around 400–500 mya and were the driving force for soil formation. It is then safe to assume that in pre-Devonian times, the diversity of prokaryotes forming (along with plants and fungi) and populating the first soils was mainly composed of bacteria. Bacterial species would inevitably dictate subsequent terrestrial turnover of sulfur. Thus, it is likely that bacteria monopolized dissimilatory sulfate reduction in soils from the very beginning. The exact moment can be set even earlier regarding the abovementioned fungi-SRP associates at rock surfaces and the fact that fungi preceded plants on land. Naturally, such a model could be biased because of insufficient attention of microbiologists to sulfate-reducing archaea in non-extreme environments. It requires rigorous investigation of the sulfur cycle evolution during the start of the Palaeozoic era as well as more intense efforts toward SR-archaea isolation.

LIFE STRATEGY OF SRPs IN SOILS WITH HIGH OR RAPIDLY CHANGING REDOX POTENTIAL

Based on the studies, it is possible to construct a picture of SRP ecology in soils. First, most SRPs thriving in aerated soils would belong to the bacterial domain. Even with the existence of aerotolerant species, we should expect that SRPs tend to fill anaerobic

microniches in soil, such as soil pores (28), soil pore water, deep horizons, and rhizo-spheric hotspots where most of the oxygen is readily consumed by aerobes. In these niches, SRPs are highly likely adapted to an oligotrophic, rare biosphere member strategy because the amount of sulfate ions is limited, the competition level among other species is high, and the redox potential is not always low enough. There, a typical sulfate-reducing bacterium (e.g., *Desulfitobacterium* sp., *Desulfosporosinus* sp., or *Desulfovibrio* sp.) probably maintains low-density population and assimilates products of organic matter decomposition, such as different short- and long-chain organic acids and also aromatics and molecular hydrogen. In soil matrix, SRPs will more likely be a part of a multispecies biofilm rather than planktonic form. So, it will be attached to soil particles or to plant roots if it is a part of the rhizosphere (such as species of *Desulfobulbus* and *Desulfovibrio* genera).

If the conditions change, the bacterium can sporulate or go into dormancy, depend-ing on the taxon, facilitating the distribution of its cells across the soil environment. Different mechanisms may promote spreading, such as encapsulation by movable soil particles, flooding events that connect isolated microniches, and traversing the gut of soil invertebrates. For example, Zhou et al. (168) studied iron reduction in earthworms' gut microbial communities during the soil microcosm experiment. They found *Desulfo-sporosinus*, *Desulfotomaculum*, and *Desulfovibrio* to be important iron reducers in worms' intestines. Once favorable conditions return, inactive cells awaken and start to assimilate the same electron and carbon sources, as it is less likely that their range has changed. What changes more often is the spectrum of available electron acceptors. Apparently, the diversity of acceptors is responsible for the fact that SRPs mediate the remarkable diversity of soil reductive processes. According to the many observations, SRPs are part of the microbial group that reduces a variety of compounds in soil organic matrix, especially humic residues, and a variety of metal cations, especially Fe^{3+}. Numerous examples exist of SRP-reducing humic substances (169–171), and sulfate reducers such as *Desulfosporosinus* are found in humic-enriched consortia as a minor but an inevitable part (172). Moreover, several SRP genera are capable of extracellular electron transfer, such as *Desulfuromonas*, *Desulfitobacterium*, *Desulfotomaculum*, *Desulfosporosinus*, and *Desulfobulbus* (39, 144). FeS nanoparticles synthesized by sulfate reducers can facilitate the acquisition and transport of electrons from solid donors (173).

Thus, typical soil sulfate reducers appear to act as an electron relay system between accumulated small molecular weight organics and multiple electron acceptors (Fig. 2). What differs soil SRPs from that of marine and sediment origin is another mode of life, which includes (i) very limited, compared to water, concentrations of sulfate; (ii) more frequent and prolonged exposure to oxygen; and (iii) availability of unique electron donors and acceptors; and (iv) different set of possible syntrophic partners. These constraints determine the small size (down to being the "rare" biosphere members) of SRP populations, high cellular activity without proliferation, the potential role of viruses, and increased metabolic flexibility.

A much more understudied group is microbes capable of dissimilatory sulfate reduction but not constrained by oxygen or other factors due to another taxonomic position. The most prominent are acidobacteria. Almost all sulfate reducers oxidize volatile organics such as short-chain fatty acids, some can process more complex compounds, and it seems that acidobacterial members can couple sulfate reduction to plant-derived polysaccharide catabolism. It is plausible to say that peat soil sulfate reducers are active participants in diverse biomass decomposition and provide nutrients and conditions for other microorganisms. Nothing, however, is known about different lineages in an ecological sense. According to ecophysiological and metagenomic-orien-ted studies (19, 46), the genetic basis for sulfate reduction has such soil-occurring taxa as Verrucomicrobiota, Armatimonadota, Nitrospirota, Nitrospinota, Planctomycetota, and even Actinomycetota. The actual presence and ecological role of sulfate reduction in the metabolism of these taxa should be the focus of future studies in soil microbial ecology.
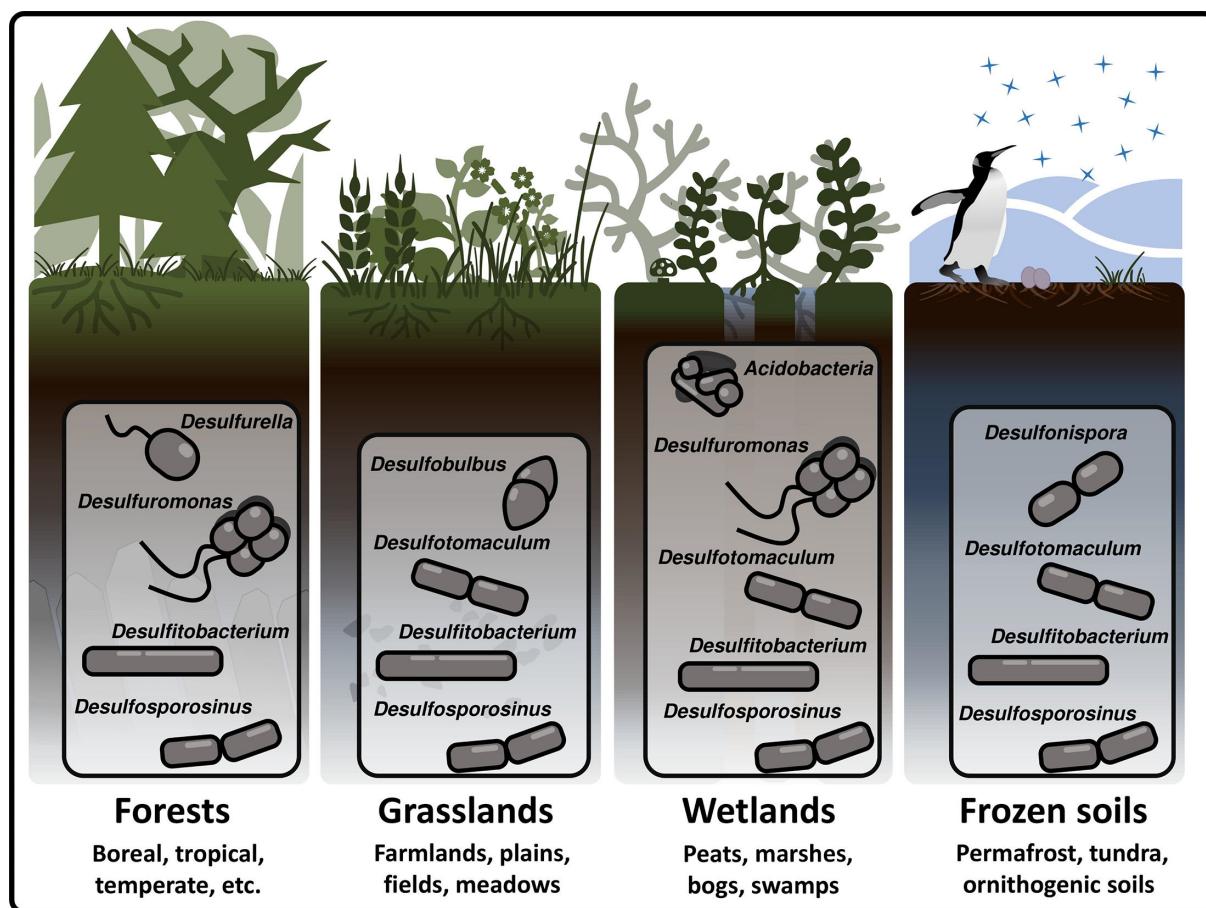
FIG 2 Overview of terrestrial ecosystems where different SRP genera occur according to numerous studies.

CONCLUSION AND FUTURE PERSPECTIVES

Sulfate-reducing bacteria are a diverse group of prokaryotes that mediate a remarkable number of processes in ecosystems at the global scale. Based on the studies reviewed in this manuscript, it becomes evident that SRPs actively contribute to terrestrial environments as rare soil microorganisms. The four most prevalent soil sulfate-reducing taxa are *Desulfitobacterium*, *Desulfosporosinus*, *Desulfuromonas*, and *Desulfotomaculum*. It seems that these taxa have adapted to various soil types, regardless of contaminants, aeration levels, or vegetation cover. Their ecological role in soils can be summarized as the ability to transfer the electrons from various donors to various acceptors. SRPs contribute to soil organic matter turnover and tightly connect carbon and sulfur cycles. Recent advances in metagenomic and metatranscriptomic approaches let us step forward in the study of sulfate reducers and realize that due to lateral gene transfer, the ability to reduce sulfur compounds spans way beyond previously known species.

We believe that future research in the field of SRPs should focus on the following aspects:

1. The specific mechanisms through which soil SRPs contribute to soil biogeochemical cycling and soil organic matter decomposition.
2. The habitat preferences and ecological behaviors of non-canonical sulfate reducers, such as Acidobacteriota, Verrucomicrobiota, and Planctomycetota.
3. The existence and role of sulfate-reducing archaea in temperate soil ecosystems.

The results may broaden our understanding of microbial processes involved in sulfate transformation in soil and pave the way for more efficient utilization of soil resources and bioremediation practices.

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