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ARTICLE

Cable bacteria extend the impacts of elevated dissolved oxygen into anoxic sediments

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Abstract

Profound biogeochemical responses of anoxic sediments to the fluctuation of dissolved oxygen (DO) concentration in overlaying water are often observed, despite oxygen having a limited permeability in sediments. This contradiction is indicative of previously unrecognized mechanism that bridges the oxic and anoxic sediment layers. Using sediments from an urban river suffering from long-term polycyclic aromatic hydrocarbons (PAHs) contamination, we analyzed the physicochemical and microbial responses to artificially elevated DO (eDO) in the overlying water over 9 weeks of incubation. Significant changes in key environmental parameters and microbial diversity were detected over the 0–6 cm sediment depth, along with accelerated degradation of PAHs, despite that eDO only increased the porewater DO in the millimeter subfacial layer. The dynamics of physicochemical and microbial properties coincided well with significantly increased presence of centimeter-long sulfide-oxidizing cable bacteria filaments under eDO, and were predominantly driven by cable bacteria metabolic activities. Phylogenetic ecological network analyses further revealed that eDO reinforced cable bacteria associated interspecific interactions with functional microorganisms such as sulfate reducers, PAHs degraders, and electroactive microbes, suggesting enhanced microbial syntrophy taking advantage of cable bacteria metabolism for the regeneration of SO_4^{2-} and long-distance electron transfer. Together, our results suggest cable bacteria may mediate the impacts of eDO in anaerobic sediments by altering sediment physiochemical properties and by reinforcing community interactions. Our findings highlight the ecological importance of cable bacteria in sediments.

Introduction

Rapid industrialization and urbanization have led to greatly increased waste discharge into waterways causing widespread pollution. The degradation of these pollutants consumes dissolved oxygen (DO), which leads to hypoxia in the water column and even results in black appearance and odor problems. Meanwhile, persistent hydrophobic

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compounds such as polycyclic aromatic hydrocarbons (PAHs) tend to adsorb onto suspended particles and eventually settle to the sediment to form endogenous pollution [1, 2]. Therefore, contaminated rivers have become one of the most important issues for aquatic ecosystems and have aroused widespread concern [3].

In order to reduce high-load pollutants, aeration is a common strategy in the remediation of contaminated rivers as it elevates DO and promotes aerobic degradation. Due to the limited permeability of oxygen in sediments, the effects of aeration on sediment bioremediation are thought to be constraint within the millimeter surficial layer [4], paradoxically biogeochemical responses to DO fluctuation in the overlaying water are often observed in subfacial layers where oxygen is undetectable [5–9]. Enhanced oxic formation and downward diffusion of oxidants such as nitrite (NO_2^-), nitrate (NO_3^-), and sulfate (SO_4^{2-}) under elevated DO (eDO) could not fully explain such phenomenon especially as that muddy sediments generally have a low diffusion capacity of solutes [10]. The underlying mechanisms linking DO and biogeochemical responses in anoxic sediment require further study.

Sulfide-oxidizing "cable bacteria" are recently discovered centimeter-long multicellular filamentous bacteria of the family Desulfobulbaceae [11]. They make a living through the so-called long-distance electron transfer (LDET), which harvests electron donors such as hydrogen sulfide (H_2S) or iron sulfide (FeS) in anoxic sediments while depositing electrons on acceptors such as oxygen or nitrate at the water–sediment interface [12, 13]. By coupling the two spatially separated redox half-reactions, cable bacteria LDET has the potential to accumulate SO_4^{2-} in sediments [14, 15], and simultaneously drive the acidification of the sulfidic layer (down to pH 6.1), exerting large effects on the sediment biogeochemistry [11, 12, 16, 17]. In addition, due to their ubiquitous presence in sediments including those ones contaminated by complex organic matters, cable bacteria have been reported to promote the anaerobic carbon degradation such as the removal of alkanes in marine sediment [18] and toluene in freshwater aquifers [15]. Given their genomic inability in dihydroxylation of aromatic rings and beta oxidation of fatty acids [19], a direct involvement of cable bacteria in complex organic compounds degradation is unlikely. Rather, enhancement of microbial syntrophic interactions in association with cable bacteria LDET may have indirectly promoted the cascade degradation of complex organic compounds. Yet, how community diversity and the interspecific characteristics of complex sediment microorganisms, particularly their role in PAHs degradation, are shaped along with the dynamic of cable bacteria remain unexplored.

In this study, we aim to compare sediment physicochemical patterns followed by 16S rRNA gene Illumina sequencing-based microbial profiling under eDO and ambient DO (aDO) in overlaying waters thereby gaining insights into the potential role of cable bacteria in mediating the influence of eDO in anaerobic freshwater sediments, especially the biodegradation of PAHs. We hypothesized that higher oxygen availability under eDO will enhance cable bacteria growth which would (i) induce a sulfate replete condition in sediment, fueling PAHs oxidation couple to sulfate reduction and (ii) significantly alter indigenous microbial diversity and reinforce cable bacteria associated community interactions, and thus promote the cascade degradation of sediment PAHs.

Material and methods

The following is the summary of methods used in this study. More detailed information is provided in Supplementary Information.

Experimental setup

Sediment (0–30 cm in depth) was collected from a creek experiencing long-term aromatic organic compounds contamination in the Pearl River Delta, China, (22°45′31.7″N, 113°16′22.0″E), where cable bacteria presence had been visually confirmed. Sediment was sieved and homogenized, and put in glass beakers (80 mL sediment, 100 mL total in the beaker, $n = 60$) and divided between two reservoirs with deionized water kept at 25 °C. One reservoir was gently aerated to achieve a DO saturated state (roughly 7.80 mg L^{-1}) at the water–sediment interface, while the other received no aeration keeping it at ambient conditions at the sample site (roughly 2.94 mg L^{-1}).

As shown by several previous studies, cable bacteria have an opportunistic lifestyle that peak within 2–4 weeks after sediment disturbance, and decline in population size thereafter possibly with the depletion of reduced sulfur compounds [20, 21]. Therefore, microprofiles of the incubation systems were recorded at six time points (after weeks 0, 1, 2, 3, 4, and 9) to closely monitor the thriving of cable bacteria and effects after the peak. Six beakers were removed at each time point from each reservoir and subsamples were taken vertically every 2 cm from top to 6 cm depth from the sediments in each of the beaker for DNA extraction, PAHs, and other chemical measurements. During the incubation time, deionized water was added every 48 h following water evaporation from the incubation reservoirs. The addition of deionized water did not create significant impact on the overall DO state of the incubation system, particularly in the sediment, as no significant change in DO at the superficial water–sediment interface was detected during water addition in both incubation reservoirs.

Chemical analysis

High-resolution depth microprofiles of oxygen and pH were measured using commercialized in situ microsensor operated with a motorized micromanipulator (Unisense, Denmark) as described previously. Several sets of additional environmental parameters were measured to better understand the geochemical properties of sediment and porewater samples, including: (i) ammonium (NH_4^+), nitrate (NO_3^-), nitrite (NO_2^-), sulfate (SO_4^{2-}), total carbon (TC), total organic carbon (TOC), total nitrogen (TN), and available phosphorus (AP) in sediments and porewaters and (ii) the contents of PAHs and the partitioning of heavy metal species in sediments.

Visual identification and quantification of cable bacteria

To ascertain the presence of cable bacteria in sediment samples, conventional bright-field microscopy, scanning electron microscopy (SEM), and fluorescence in situ hybridization (FISH) identification with a Desulfobulbaceae-specific probe were performed to visualized the cable bacteria filaments in sediment samples by following previously published protocols [13, 20]. Abundance estimation were conducted base on the number of reads of previously reported cable bacteria species (e.g., *Candidatus* Electronema palustris and *Candidatus* Electronema species) identified in the high-throughput sequence pool of this study, FISH-based cable bacteria filaments density measurement, in concert with real-time quantification using an in-house qPCR assay for Desulfobulbaceae. More details can be found in Supplementary Information.

DNA isolation and Illumina sequencing analysis

Microbial genomic DNA was isolated using DNeasy PowerSoil Isolation Kit (Qiagen, Hilden, Germany). DNA quality was assessed based on absorbance ratios of 260/280 nm and 260/230 nm, and DNA concentrations were quantified with a PicoGreen method. Illumina sequencing of PCR amplicons targeting V3–V4 hypervariable regions of microbial 16S rRNA gene was performed with the Illumina HiSeq 2500 platform (Illumina, Inc., San Diego, CA, USA). Details of amplicon preparations, sequencing, and data analysis (e.g., raw reads processing, ASV identification) are described in Supplementary Information.

Phylogenetic microbial ecological network (pMEN) analyses

Moving beyond conventional descriptive analysis of microbial community that commonly infer microbial interactions from species richness and abundance, the emerging ecological network analysis interrogates interspecific relationship base on the co-occurrence pattern and dynamic changes in abundances over multiple samples, providing more thorough and robust depiction of microbial interactions [22, 23]. In this study, interactions between cable bacteria and co-occurrence taxa were measured through a recently developed pMEN analyses, which bases on high-throughput metagenomic data and has been demonstrated to be an effective approach to approximate complex interspecific relationships of microbial communities [23–27]. The pMEN analysis was performed using the MENA pipeline (http://ieg4.rccc.ou.edu/mena/main.cgi) [24, 28] and network topology was visualized by Gephi 0.9.2. Details are described in Supplementary Information.

Statistical analysis

The microbial α-diversity of each sample was evaluated using ASV richness, Shannon diversity, and Evenness indices. The ordination pattern of samples under eDO and aDO were determined by nonmetric multidimensional scaling (NMDS) [29]. Adonis (permutational multivariate analysis of variance), multiresponse permutation procedure (MRPP), and analysis of similarities (Anosim) using Bray–Curtis distance were performed to examine the differences in microbial community composition and structures [30]. The Pearson correlation and Mantel tests were used to measure the correlations between PAH residuals and the structure of cable bacteria in sediment layers [31]. Redundancy analysis (RDA) and Spearman's rank correlation coefficients were used to identify the effect of sediment environmental variables on the microbial community composition [32]. All the above analyses were performed in R (version 3.4.4; http://www.r-project.org/) using the vegan [33], ieggr, and ecodist packages [34]. The effects of eDO on the relative abundances of microbial populations were measured by computing the response ratio using the formula described previously [35].

Results

Effects of eDO on sediment chemical properties

Across the incubation period, oxygen penetrated up to 3.98 ± 0.56 mm in sediments under eDO treatment, but extended to much lesser depth (1.57 ± 0.63 mm) under aDO treatment ($p < 0.001$, $n = 30$, Student's t test, Fig. 1A). This meant that only the top sediment layer (0–2 cm depth) was exposed to oxygen in any of the incubations. Porewater pH

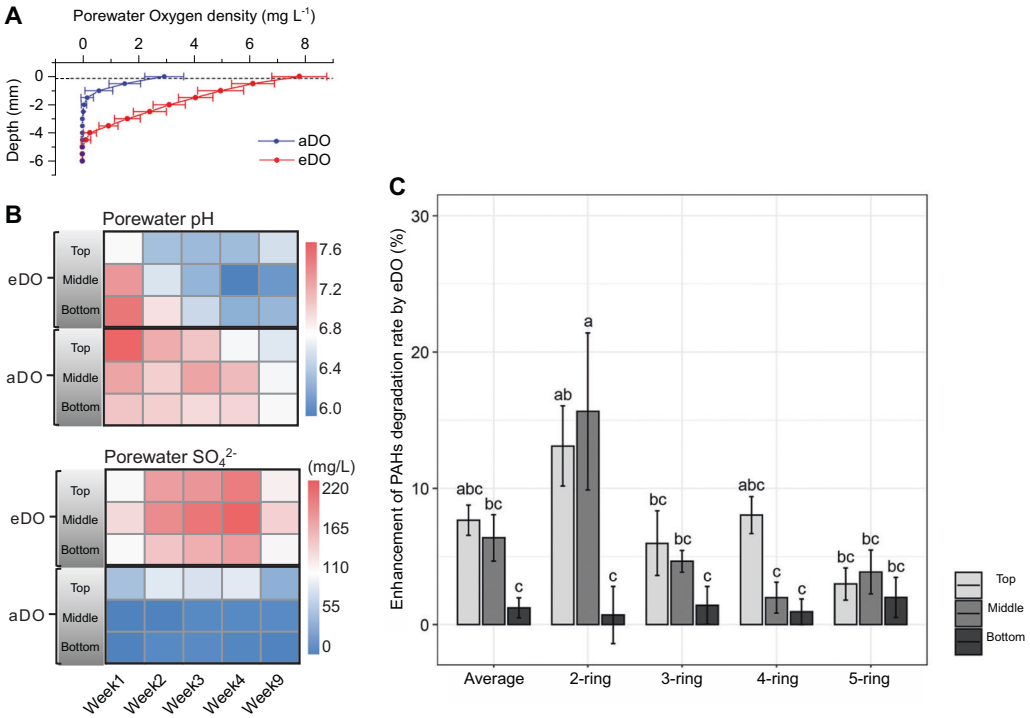

Fig. 1 Effects of eDO on sediment variables and PAHs degradation. **A** Close-up of the oxic zone with microprofile of oxygen in sediment; mean ± SD were calculated based on six replicates across five sampling time points ($n = 30$). **B** Depth distribution of pH and sulfate (SO_4^{2-}). **C** The effect of eDO on the enhancement of PAHs degradation rate over nine weeks of incubation. 2_ring: naphthalene, acenaphthene, acenaphthylene, fluorene; 3_ring: phenanthrene, anthracene, fluoranthene; 4_ring: pyrene, chrysene, benzo[a]anthracene, benzo[b]fluoranthene, and benzo[k]fluoranthene; 5_ring: benzo[a]pyrene, dibenzo[a,h]anthracene, indeno[1,2,3-cd]pyrene, benzo[g,h,i]perylene. Significance was determined by two-way ANOVA followed by Tukey's HSD test at $p < 0.05$. Values marked with different letters are significantly different. Error bars represent the standard deviation of the mean ($n = 6$).

in sediments gradually declined from initially neutral to about 6.01 after 4 weeks of incubation under eDO ($p < 0.01$, $n = 6$, ANOVA, Fig. 1B). The acidification of porewater occurred at all three sediment layers where the largest pH reduction was observed in the middle layer (2–4 cm depth). In contrast, the pH of porewater under aDO remained generally unchanged (Fig. 1B). For the first 4 weeks under eDO, porewater SO_4^{2-} concentrations increased gradually in all layers then decreased in week 9 ($p < 0.001$, $n = 6$, ANOVA, Fig. 1B), while no significant change was observed for samples under aDO. Decrease of the SO_4^{2-} concentrations from week 4 to week 9 in eDO sediments could be ascribed to diffusion loss to the overlying water after depletion of the FeS pool stopped sulfate generation. Consistently lower concentration of porewater NH_4^+ concentrations were observed in all sediment layers across the incubation period ($p < 0.05$, $n = 6$, ANOVA, Fig. S1). Furthermore, porewaters TN, TC, and TOC and sediments TC, TOC, and AP reduced gradually over time in both treatments, and lower concentrations were often observed under eDO than under aDO, particularly in the top and middle layers ($p < 0.05$, $n = 6$, ANOVA, Fig. S1).

PAHs degradation was accelerated under eDO by 7.7% at the top layer, 6.4% at the middle layer, and 1.2% at the bottom layer, relative to aDO. The enhancement of PAHs degradation under eDO depended on the individual and interactive effects of sediment depth and the structural complexity of PAHs ($p < 0.05$, $n = 6$, ANOVA, Fig. 1C). The degradation of 2-aromatic-ring PAHs (e.g., naphthalene, acenaphthene, acenaphthylene, fluorene) increased by 13.1 and 15.6% relative to aDO in the top and middle layers, significantly higher than those at the bottom layers (Fig. 1C). Compared to the middle and bottom layers, the degradation of 4-aromatic-ring PAHs (e.g., pyrene, chrysene, benzo[a]anthracene, benzo[b]fluoranthene, and benzo[k]fluoranthene) was significantly higher at the top sediment layers in response to eDO (Fig. 1C).

Effects of eDO on overall pattern of sediment microbial communities

Over 14.1 million qualified 16S rRNA gene sequences were obtained via Illumina sequencing. After data processing including singleton removal and rarefaction at 48,000 sequences per sample, 22,635 ASVs remained (13,844 for eDO samples, 13,414 for aDO samples). Phylogenetic diversity reduced significantly under eDO, with the greatest response observed at the middle layer (Fig. S2).

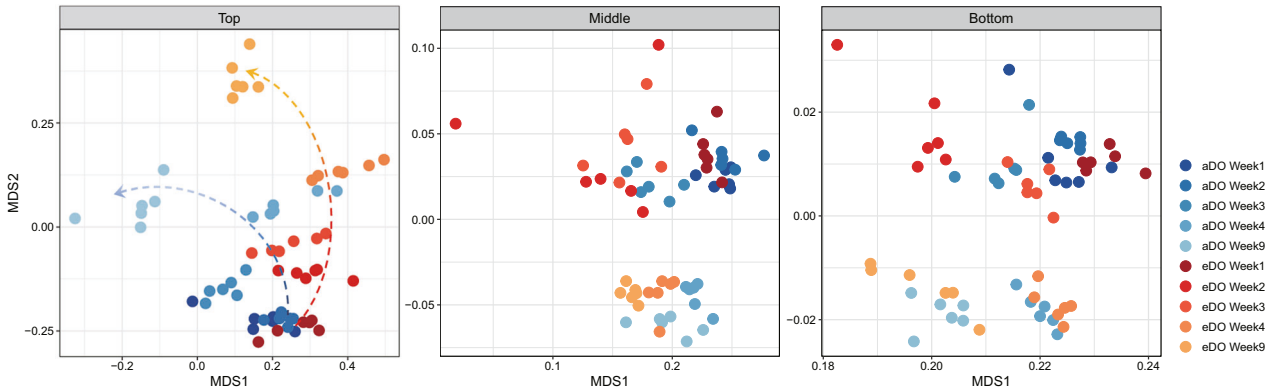

Fig. 2 Nonmetric multidimensional scaling (NMDS) analyses showing the influences of eDO on sediment microbial community composition and structures. From left to right: NMDS ordination plots of the top, middle, and bottom layers.

The microbial community structures changed constantly over time under both aDO and eDO but followed different trajectories, as visualized by the NMDS ordination based on the Bray–Curtis dissimilarity, indicating gradual accumulation of variations between communities of both treatments (Fig. 2). Moreover, the three complementary nonparametric multivariate statistical tests (Adonis, Anosim, MRPP) further revealed that the microbial community structures of top, middle, and bottom layers across the incubation period were significantly different ($p < 0.05$) between eDO and aDO treatments (Table 1). These results indicated that, despite only having a direct influence on porewater oxygen concentration at the millimeter-range water–sediment interface, the eDO treatment significantly altered sediment microbial community composition and structure across all the sediment layers in this study.

A total of 57 known phyla were detected in this study among which more than half (42, 36, and 34 at the top, middle, and bottom layers, respectively) were significantly altered by eDO in terms of the abundances, including the dominant phyla (e.g., Proteobacteria, Firmicutes, Actinobacteria, and Acidobacteria) (Fig. 3 and Fig. S3). Most of the significantly changed phyla were reduced in the top and middle layers (31 and 24, respectively), whereas a larger number of phyla (18) were increased in the bottom layer under eDO (Fig. S3). Notably, the abundances of α-, β-, and γ-proteobacteria were significantly increased in the top layer in response to eDO, and δ-proteobacteria were increased at the middle layer (Fig. S3). As δ-proteobacteria contain the major lineages of gram-negative sulfate reducers, their relative proportions were further explored in detail. The putative sulfate-reducing genera tended to decrease in relative abundance under eDO in the top layer reflecting their intrinsic nature of oxygen sensitivity, but became more abundant under eDO in the middle and bottom layers (Fig. S4). Similarly, there was a distinct response of Firmicutes-affiliated genera (e.g., *Clostridium, Intestinibacter*, and *Syntrophomonas*) to eDO across sediment layers with consistent reduction of these genera at the top layer but generally increment at the middle and bottom layers (Fig. 3 and Fig. S3). In addition, greater abundances of putative electroactive microorganisms (e.g., *Geobacter, Pseudomonas*) that can exchange electrons with extracellular matters (e.g., electrodes, minerals) via extracellular electron transfer were also observed in the middle and bottom layers under eDO (Fig. S5).

Table 1 Pairwise dissimilarity test of 16S rRNA gene data sets among any pairs of samples under eDO and aDO.

eDO vs. aDO	Adonis		Anosim		MRPP	
	R^2	p	R	p	Delta	p
Top						
Week 1	0.309	**0.002**	0.791	**0.004**	0.170	**0.003**
Week 2	0.518	**0.002**	1.000	**0.003**	0.309	**0.002**
Week 3	0.365	**0.004**	0.991	**0.003**	0.209	**0.003**
Week 4	0.391	**0.005**	0.744	**0.004**	0.357	**0.003**
Week 9	0.503	**0.002**	1.000	**0.002**	0.448	**0.003**
Middle						
Week 1	0.215	**0.007**	0.926	**0.005**	0.172	**0.005**
Week 2	0.380	**0.007**	0.870	**0.004**	0.279	**0.006**
Week 3	0.179	**0.002**	0.461	**0.006**	0.014	0.240
Week 4	0.243	**0.003**	0.629	**0.002**	0.159	**0.002**
Week 9	0.219	**0.005**	0.744	**0.002**	0.097	**0.010**
Bottom						
Week 1	0.166	**0.027**	0.367	**0.003**	0.099	**0.024**
Week 2	0.448	**0.005**	0.332	**0.004**	0.414	**0.004**
Week 3	0.136	**0.004**	0.239	**0.010**	0.063	**0.005**
Week 4	0.125	**0.002**	0.519	**0.003**	0.016	0.130
Week 9	0.126	**0.031**	0.344	**0.020**	0.013	0.247

$p < 0.05$ (in bold).

Adonis permutational multivariate analysis of variance, *Anosim* analysis of similarities, *MRPP* multiresponse permutation procedure.

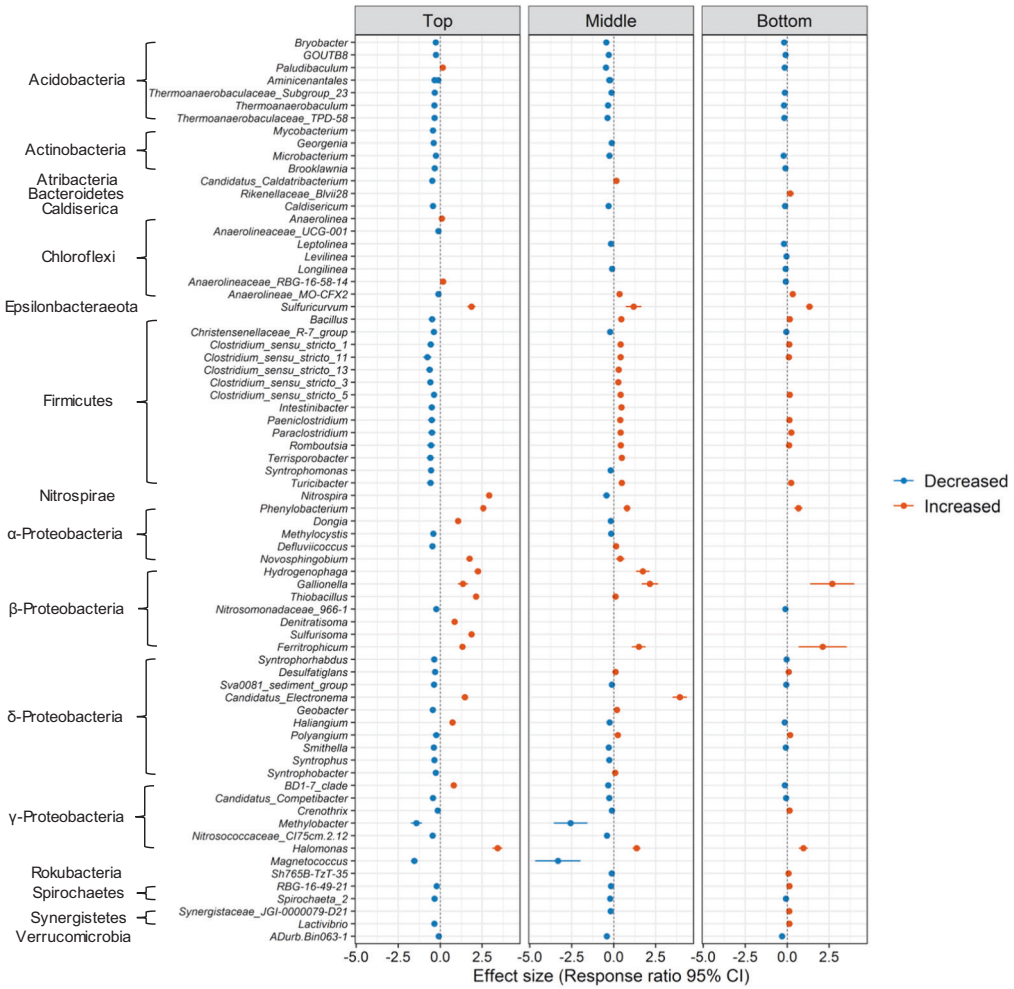

Fig. 3 The significantly changed genera at the top, middle, and bottom layer sediments in response to eDO. Only abundant genera (relative abundance > 0.1%) with known phylogeny are shown. The relative abundance of bacteria was represented by the reads of 16S rRNA gene sequences at the genus level, and was measured as sum of the same genus across all sampling time for each sample. A response ratio (RR) of a variable is the natural log of the ratio of the average value in the treatment group (eDO in this case) to the average value in the control group (aDO in this case), and the significance was tested at the 95% confidence interval (CI). The vertical line was drawn at RR = 0.

Dynamic of cable bacteria and their interaction with other populations in sediments

Cable bacteria sequence variants aligning to the freshwater *Candidatus* Electronema palustris were abundant in both aDO and eDO treatments, as well as sequences clustering together adjacent to the two known *Candidatus* Electronema species, suggesting that these ASVs are potentially novel cable bacteria species. Filamentous cable bacteria were identified using SEM and FISH (Fig. 4A). The relative abundance of cable bacteria increased from an initial 0.012% to a peak level of 1.35% under eDO at the fourth week and 0.37% under aDO at the ninth week (Fig. 4B). Over the entire incubation period, the relative abundances of cable bacteria were almost doubled at the top and bottom layers, and increased by nearly 5.3 times at the middle layer, in response to eDO (Fig. 4B), whereas there were generally no differences for the abundances of overall bacteria between treatments (Fig. S6). The dynamic of cable bacteria was further verified by qPCR quantification targeting the cable bacteria-specific *dsrB* genes. A large amount of *dsrB* genes were observed ranging from 3.14×10^5 to 6.79×10^7 copies per gram dry sediment across the incubation period, among which there were 8.76×10^6 copies per gram on average under eDO, about 4.5 times higher than that under aDO conditions (Fig. 4C). Consistent with the Illumina sequencing results, top and middle layers harbored most of the cable bacteria. The largest enrichment of cable bacteria was observed on the fourth week, which increased by 8.1, 6.1, and 2.9 times in the top, middle, and bottom sediments, respectively, in response to eDO (Fig. 4C). In addition, after 4 weeks of incubation, FISH showed 309.16 ± 29.25 and

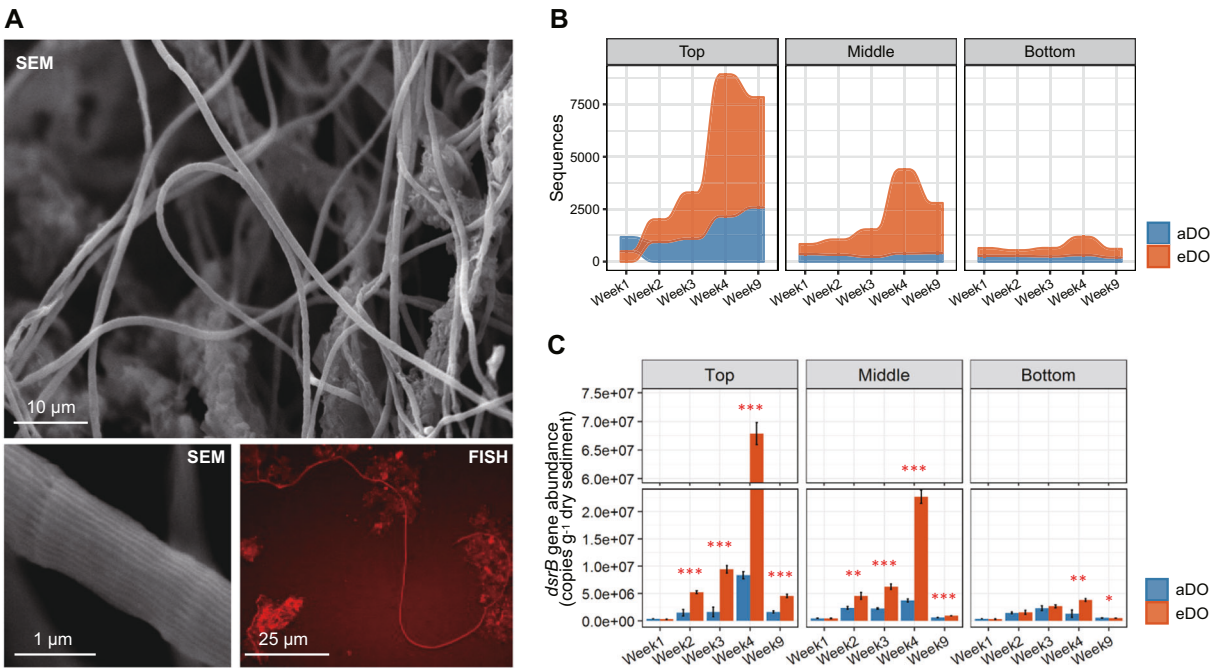

Fig. 4 Visualization and quantification of cable bacteria. A Filaments of cable bacteria measured by SEM and FISH. **B** The abundances of cable bacteria measured by the 16S rRNA sequencing reads. **C** The abundance of cable bacteria-specific *dsrB* genes copies per gram of dry sediment. Data are presented as mean ± SD ($n = 6$). Significance was determined by Student's t test. An asterisk (*) denotes $p < 0.05$, double asterisks (**) denote $p < 0.01$, and triple asterisks (***) denote $p < 0.001$.

$97.80 \pm 13.55\ m\ cm^{-2}$ cable bacteria filaments in the top and middle layer sediments under eDO, respectively, which were 10.6 and 7.4 times greater than those of aDO. No filament of cable bacteria was observed in the bottom layer. Together, these results showed comparable levels of increases in cable bacteria abundance under eDO treatment.

The co-occurrence patterns of microorganisms under eDO and aDO were evaluated based on the pMEN networks with a focus on cable bacteria associated interactions. Overall, sediments under eDO exhibited simplified co-occurrence networks than those of aDO, coinciding with the lower microbial diversity in eDO sediments. Subnetworks including cable bacteria and closely associated microbial populations were further established. In contrast to the overall microbial co-occurrence pattern, cable bacteria tended to form much more complex pMEN topological structures with associated populations under eDO than under aDO (Fig. S7). Meanwhile, the reinforced complexity of cable bacteria subnetworks under eDO appeared to be stable over time. Further community composition analysis on these microbial populations showed ample taxonomic diversity, which composed of 16 phyla and dominated by Proteobacteria, Acidobacteria, and Chloroflexi (Fig. S7 and Table S1). Predominantly positive interactions (74.6%) were established between cable bacteria and these populations, indicative of prevalent mutually cooperative relationships among these microorganisms. More than half (60.6%) of the ASVs being mutually interacted with cable bacteria were found in previously reported PAHs degrading communities or have been demonstrated to be PAHs degraders, and many (32.4%) featured a sulfur metabolism. Noticeably, a group of putative electroactive microorganisms (26.8%, e.g., *Clostridium*, *Smithella*, and *Anaerolinea*) that commonly found in microbial fuel cells (MFCs) was also observed (Table S1).

Linkages between microbial dynamics and environmental factors

To link the alteration and successional dynamics of microbial communities under eDO to key environmental properties measured in this study, RDA and Spearman's rank correlation coefficient were performed. Both analyses showed that, apart from porewater oxygen availability, other environmental properties significantly shaped the composition and structures of the sediment microbial communities (specifically SO_4^{2-}, pH, NH_4^+, TN, TC, TOC, and AP, $F = 4.823$, $p < 0.001$) (Fig. 5 and Fig. S8). Of these properties, SO_4^{2-} concentration and pH were apparently the most important attributes to drive community differentiations between aDO and eDO treatments. The temporal variation of microbial communities were explained more by the porewater TC and TN status, NH_4^+, and sediment AP, indicating the consumption of sediment nutrients drove community shifts over time. In addition, significant correlations were detected between the abundance of cable bacteria and porewater pH and SO_4^{2-} concentrations,

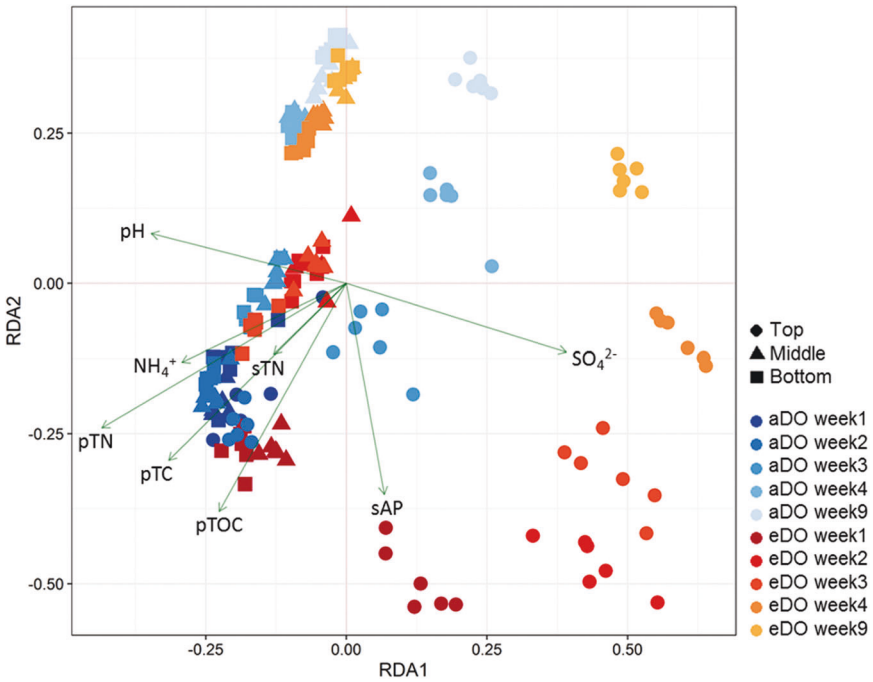

Fig. 5 Redundancy analysis (RDA) of 16S rRNA gene sequence data and environmental attributes. pTN porewater total nitrogen, pTC porewater total carbon, pTOC porewater total organic carbon, sAP sediment available phosphorus.

confirming the key role of cable bacteria LDET in changing these properties in these sediments ($p < 0.001$, Fig. S9).

Possible linkages between the sediment PAHs residues at the end of incubation and the abundances of cable bacteria were explored using Pearson correlation and Mantel test. Pearson correlation analysis detected a significant negative correlation between the abundances of cable bacteria and the remaining concentrations of overall PAHs and several individual PAH compounds ($p < 0.001$, Fig. S10), indicating accelerated removal of these compounds in company with higher growth of cable bacteria. Consistent with the Pearson correlation results, Mantel test also revealed significant correlations between the abundances of cable bacteria and overall PAHs, naphthalene, acenaphthylene, acenaphthene, fluoranthene, benzo[a]anthracene, benzo[b]fluoranthene, and benzo[k]fluoranthene ($p < 0.05$, Table S2).

Discussion

The discrepancies between our general understanding and empirical observations on the responses of chemical and biological processes in anoxic sediments to eDO are indicative of previously unrecognized mechanism that bridges the oxic and anoxic sediment layers. By comparing physicochemical and microbial community patterns in sediments under contrast overlaying water DO and in relation to the dynamics of cable bacteria metabolisms, we showed that the cable bacteria LDET could be the missing link that facilitates the propagation of eDO influence along sediment depth, which significantly alters the co-occurring microbial diversity, interspecific interactions, and associated biogeochemical processes (Fig. 6). Particularly, enhanced cable bacteria LDET under eDO could accelerate in situ PAHs degradation in sediments likely due to a generation of sulfate replete condition favoring the functional activities of sulfate reducers specialized in PAHs degradation, and reinforcing interspecific interactions for efficient degradation of PAHs. Given the high toxicity and persistence of PAHs, accelerated removal of these compounds by cable bacteria could be of great environmental significance. This study provides new insights into understanding the potential role of filamentous electrically conductive cable bacteria in the sediment biogeochemical cycling.

Aeration promotes cable bacteria LDET

The unique LDET enables cable bacteria to oxidize reduced sulfur compounds more efficiently than other sulfide-oxidizers do, giving them a competitive advantage in response to elevated oxygen availability [14, 21]. As expected, the additional oxygen supply under eDO led to much faster growth of the cable bacteria population than that under aDO. Noticeably, such stimulation effect of eDO on cable bacteria abundances lasted for over 9 weeks, indicating intensified LDET under eDO across the incubation period. Supporting previous suggestions, elevated oxygen availability also drove intensive downward growth of cable bacteria in sediments of this study possibly due to a pursuit for a deepening sulfidic front [18, 21]. The peak densities of cable bacteria filaments under eDO are similar to the recent report from wetland soils (400 ± 100 m cm^{-2})

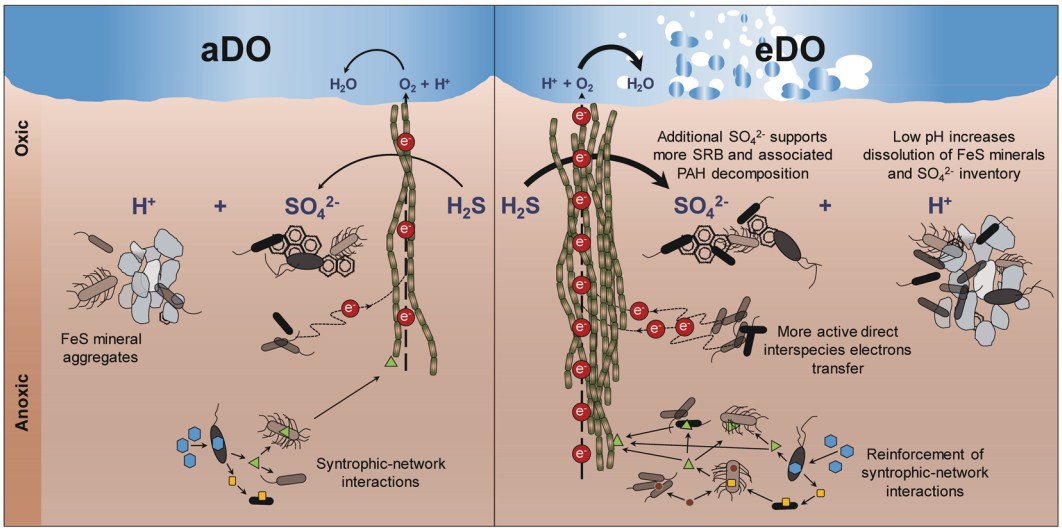

Fig. 6 Conceptual summary of the influence of eDO on sediment biogeochemical processes mediated by cable bacteria. eDO stimulation of cable bacteria growth and LDET activities increases the production and overall inventory of sediment SO_4^{2-}, generating a novel niche for functional microorganisms such as the SRB, PAH-degraders, and electroactive microbes that take advantage of the additional SO_4^{2-} as metabolic substrate or the enhancement of cable bacteria LDET. Meanwhile, eDO reinforces syntrophic-network interactions between cable bacteria and the co-occurring microbes. Consequently, sediment biogeochemical processes, such as the recalcitrant organic matter degradation, accelerate under eDO mediated by cable bacteria.

[36], but higher than the observations of freshwater streambank (40 m cm^{-2}) [37].

Sulfate repletion by cable bacteria LDET promotes PAHs degradation

In the subfacial layer where sulfate is abundant, degradation of organic compound is predominantly coupling with the reduction of SO_4^{2-} carried out by specialized anaerobes such as sulfate-reducing bacteria (SRB) [38, 39]. The accelerated degradation of hydrocarbon contaminations, e.g., toluene [15] and petroleum hydrocarbons [40] in sediments harboring a larger abundances of cable bacteria, has been related to the cable bacteria LDET-related promotion in sulfate availability and anaerobic biodegradation by SRB. However, enhanced hydrocarbon degradation did not always coincide with the pattern of sediment sulfate concentration. In a recent study, the occurrence of cable bacteria accelerated alkane degradation by 24% in marine sediments where no net increase in SO_4^{-2} was detected, instead the authors proposed that H_2S toxicity alleviation as a result of sulfide oxidation by cable bacteria may play a role in favoring microbial degradations [18]. In our system, eDO sediments maintained a higher concentration of sulfate (about 2–116 times) in comparison to those of aDO sediments. The spatial and temporal profile of sulfate coincided well with dynamics of cable bacteria abundances, indicating a major contribution of cable bacteria in the regeneration of sulfate. Our results are consistent with the recent study which showed that cable bacteria LDET led to more than threefold higher sulfate inventories in sediments subjected to air-saturated water column comparing to the air-free controls [14]. In addition, sulfate availability was increased to a larger extent (roughly ten times on average) in response to eDO in our system. Such difference may attribute to the lower pH value in eDO sediments (Fig. 6), which has been suggested to increase dissolution of FeS minerals and thus increase the bioavailable sulfate inventory upon oxidation [18].

Furthermore, the extra sulfate in eDO sediments appeared to invest greater abundances of SRB, e.g., *Desulfovibrio* [41], *Clostridium* [42], and Epsilonbacteraeota [43], which were more abundant in samples in which SO_4^{2-} were more abundant. Our result contrasts with those of Sandfeld et al. [14], who observed higher sulfate reduction rates in association with higher SO_4^{2-} by cable bacteria LDET, but no significant change in sulfate reducers after 6 weeks of incubation. We believe that inherent variations in biogeochemical features of the sediments between these studies and sampling time may contributed to the different observation, as we did detect constantly varied increment of SRB under eDO than aDO over time and even slight reductions of SRB in response to eDO, for example, in the week 9 middle layer sediments. As microbial sulfate respiration dominates the degradation of PAHs in sulfate-reducing conditions [38, 44], upswing of the number of SRB and sulfate respiration by elevated sulfate availability would favor the PAHs removal in sediments. Our observations, therefore, provide evidences supporting our first hypothesis that sulfate repletion by cable bacteria being one of the major causes of an enhancement of PAHs degradation (Fig. 6).

Cable bacteria LDET alters indigenous microbial diversity and reinforces community interactions

The eDO treatment markedly reduced the diversity of the bacterial communities, and the reduction could be accounted for by strong restriction for oxygen sensitive populations, such as *Geobacter* [45] and *Clostridium* [46] in the oxidized water–sediment interface. As suggested by the RDA result, however, driven by increased SO_4^{2-} and low pH under eDO, selections for populations featuring sulfur metabolism and/or adapting to mildly acidic conditions, e.g., Firmicutes [47] and Proteobacteria [48, 49], could also contribute to a larger extent to the reduction in community diversity. Within the eDO sediments, a large number of Firmicutes- and Proteobacteria-affiliated taxa were selectively enriched, most of which have either been demonstrated to carry PAHs catabolic properties, e.g., *Novosphingobium* [50–52], *Hydrogenophaga* [53, 54], and *Ferritrophicum* [55], or commonly found in PAHs degrading communities contributing to the PAHs breakdown or subsequent degradation of intermediates, e.g., *Phenylobacterium* [56, 57], *Gallionella* [58], *Thiobacillus* [59, 60], and *Halomonas* [61, 62]. Therefore, the selective enrichment of these populations within eDO sediments is suggestive of a shift of environment favoring biodegradation of PAHs driven by cable bacteria LDET.

Genomic evidences have demonstrated that cable bacteria possess limited organotrophic potential by assimilating simple organic acids and alcohols, ruling out its possibility of being an active PAHs degrader [19]. Hence, how do cable bacteria interact with the coexisting microbial populations in the context of complex organic carbon degradation remains a crucial question. A few studies have revealed substantial community shifts in association with cable bacteria LDET such as selective enrichment of oil degraders, e.g., *Sulfurimonas*, *Desulfocapsa*, and *Arcobacter* [18], codevelopment of chemoautotrophs, e.g., *Thiomicrospira frisia* and *T. halophile* [63], and competitive suppression of methanogens [36], indicating changes in complex microbial interactions and ecosystem functions involve in carbon cycling. By employing pMEN network analysis, we were able to pinpoint microbial populations from the complex sediment microbial communities that mutually interacts with cable bacteria. Meanwhile, the enhanced network complexity under eDO than aDO is indicative of reinforced mutual interactions between cable bacteria and co-occurring microbial populations. Among populations identified in the cable bacteria subnetworks, mutualistic interactions between *Dehalococcoidia, Anaerolineaceae*, and cable bacteria were prevalent although they remained in constantly low levels of relative abundances across the incubation period. Interestingly, these microorganisms were also observed in a recent study on petroleum hydrocarbon contaminated marine sediments, which represented the two most enriched OTUs as an effect of cable bacteria LDET [18]. Our finding, therefore, highlighted the robustness of close interactions between cable bacteria and these populations. *Dehalococcoidia* are particularly widespread in the marine subsurface and were suggested for PCB and PCE degradation potential through sulfate respiration [64]. *Anaerolineaceae* are commonly found in syntrophic environments such as anaerobic digestors and are responsible for the degradation of fatty acids and carbohydrates to syntrophic intermediates [65]. Along with these microorganisms, the large pool of anaerobic complex organic matter degraders and/or SRB that was detected in the cable bacteria subnetworks provided a strong indication of a sulfur syntrophy, taking advantage of cable bacteria LDET for the regeneration of SO_4^{2-} and promote degradations of PAHs and presumably other organic compounds (Fig. 6).

Noticeably, microorganisms featuring extracellular electron transfer capability (e.g., *Clostridia*, *Caldisericum*, and *Syntrophaceae*) accounted for a large portion of the total microbial populations that closely interact with cable bacteria. Electroactive microorganisms are typically selected near the anode of MFCs for their competitive advantages of transferring electrons across the cell membrane and using electrode as an effective electron acceptor [66, 67]. Particularly, in our previous study using sediments of the same site, *Caldisericum* and *Anaerolineaceae* were identified as keystone microbes to the electricity generation of a sediment MFC system [68]. In the current study, the similar enrichment of electroactive microorganisms in association with cable bacteria and the detection of their close interactions raise an intriguing possibility that the cable bacteria filamentous network across the oxic-anoxic sediment interface function as a wire, resembling MFCs, harvesting electrons from electroactive microorganisms and depositing them to oxygen or nitrate in the oxic layer. If so, a network of microbes-microbes connection in sediment may function as electron conductive cables, “hardwiring” the sediment environment and extending the impacts of oxygen to anoxic sediments than previously thought (Fig. 6).

It is noteworthy that, aside from cable bacteria LDET, conductive minerals may also mediate electron fluxes in sediments and potentially contribute to the propagation of eDO influence in anoxic sediments. It has been shown that additional conductive materials such as pyrite, biochar, or carbon fibers can improve soil/sediment conductivity [69, 70]. However, no evidence has appeared of conductive minerals in natural sediments mediating electron currents beyond the length of the mineral grains. More importantly, the long-distance filament conductivity of cable bacteria has been verified using resonance Raman microscopy to analyze cytochrome redox states in the living cells [71] and

cable bacteria can form a highly conductive network to bridge the electron transfer from anaerobic sediment to overlaying water [72, 73]. Through different approaches, previous studies have shown repeatedly that cable bacteria filaments are the main contributor to the long-distance electron transfer in sediments [20, 74, 75]. Comparatively, the chemical and biological shifts in eDO sediments could be largely attributed to enhanced cable bacteria LDET.

Data availability

DNA sequences of 16S rRNA gene amplicons are available in NCBI Sequence Read Archive under project no. PRJNA609391.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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