Adaptive Evolution of *Geobacter sulfurreducens* in Coculture with *Pseudomonas aeruginosa*

Lucie Semenec, Ismael A. Vergara, Andrew E. Laloo, Steve Petrovski, Philip L. Bond, Ashley E. Franks

**ABSTRACT** Interactions between microorganisms in mixed communities are highly complex, being either syntrophic, neutral, predatory, or competitive. Evolutionary changes can occur in the interaction dynamics between community members as they adapt to coexistence. Here, we report that the syntrophic interaction between *Geobacter sulfurreducens* and *Pseudomonas aeruginosa* coculture change in their dynamics over evolutionary time. Specifically, *Geobacter* sp. dominance increases with adaptation within the cocultures, as determined through quantitative PCR and fluorescence *in situ* hybridization. This suggests a transition from syntrophy to competition and demonstrates the rapid adaptive capacity of *Geobacter* spp. to dominate in cocultures with *P. aeruginosa*. Early in coculture establishment, two single-nucleotide variants in the *G. sulfurreducens* fabI and tetR genes emerged that were strongly selected for throughout coculture evolution with *P. aeruginosa* phenazine wild-type and phenazine-deficient mutants. Sequential window acquisition of all theoretical spectra-mass spectrometry (SWATH-MS) proteomics revealed that the tetR variant cooccurred with the up-regulation of an adenylate cyclase transporter, CyaE, and a resistance-nodulation-division (RND) efflux pump notably known for antibiotic efflux. To determine whether antibiotic production was driving the increased expression of the multidrug efflux pump, we tested *Pseudomonas*-derived phenazine-1-carboxylic acid (PHZ-1-CA) for its potential to inhibit *Geobacter* growth and drive selection of the tetR and fabI genetic variants. Despite its inhibitory properties, PHZ-1-CA did not drive variant selection, indicating that other antibiotics may drive overexpression of the efflux pump and CyaE or that a novel role exists for these proteins in the context of this interaction.

**IMPORTANCE** *Geobacter* and *Pseudomonas* spp. cohabit many of the same environments, where *Geobacter* spp. often dominate. Both bacteria are capable of extracellular electron transfer (EET) and play important roles in biogeochemical cycling. Although they recently in 2017 were demonstrated to undergo direct interspecies electron transfer (DIET) with one another, the genetic evolution of this syntrophic interaction has not been examined. Here, we use whole-genome sequencing of the cocultures before and after adaptive evolution to determine whether genetic selection is occurring. We also probe their interaction on a temporal level and determine whether their interaction dynamics change over the course of adaptive evolution. This study brings to light the multifaceted nature of interactions between just two microorganisms within a controlled environment and will aid in improving metabolic models of microbial communities comprising these two bacteria.

**KEYWORDS** competition, evolution, mutualism, syntrophs
**Geobacteraceae**, a family within the *Deltaproteobacteria*, predominantly reside in anaerobic environments, such as aquatic sediments, anaerobic wastewater, contaminated aquifers, and rice paddy soils, where they play a key role in the biogeochemical cycling of metals, sulfur, and carbon (1–8). Their relatively high abundance in these environmental niches (9–12) demonstrates their competitiveness in complex microbial communities. This stems from their metabolic flexibility which allows them to thrive under electron donor and nutrient-poor conditions (11, 13–16) and their adaptive ability to navigate toward metals via chemotaxis using flagella and pili (17). Furthermore, their enhanced ability to reduce insoluble electron acceptors of high redox potential via extracellular electron transfer (2, 6, 11), made possible by their hundreds of encoded c-type cytochromes and electrically conductive pili (18, 19), equip them with a competitive advantage to survive within mixed communities and conditions unfavorable for most organisms.

Although these physiological traits allow them to establish a dominant foothold in many of their environments, bacteria of this family, *Geobacteraceae*, are also adept at forming syntrophic interactions with other microorganisms. These can be formed via direct interspecies electron transfer (DIET), which utilizes c-type cytochromes and pili, hydrogen interspecies transfer-utilizing hydrogenases, or formate interspecies transfer utilizing formate dehydrogenase (20–23). Some of the studied interactions between *Geobacter* spp. and other species include *G. sulfurreducens* and *G. metallireducens* (23), *G. sulfurreducens* and *Rhodoferax ferrireducens* (24), *G. metallireducens* and *Clostridium beijerinckii* (25), *G. sulfurreducens* and *Escherichia coli* (26), *G. sulfurreducens* and *Clostridium pasteurianum* (27), and *G. sulfurreducens* and *Wolinella succinogenes* (28). Such studies aid in improving metabolic models of microbial communities.

Similar to *Geobacter* spp., *Pseudomonas aeruginosa* strains have also been found to participate in interspecies electron transfer, where *P. aeruginosa* endogenously produced phenazine shuttles electrons to electron-accepting bacteria (29, 30). Besides electron shuttling, *Pseudomonas* sp. phenazines are also known for their antibiotic properties, as are a multitude of other molecules they secrete (31, 32). *P. aeruginosa* and *G. sulfurreducens* have been found to coexist in many of the same environments, such as salt marsh estuaries, aquatic sediments, wastewater, and contaminated groundwater (33–38). Their potential for interaction, however, has only recently been investigated. Our recent adaptive evolution study on cocultures of *G. sulfurreducens* and *P. aeruginosa* found that several electron transfer processes were possible with the evolution of serially transferred cocultures, which progressively increased in fitness (39). Initially, DIET was the predominant form of syntrophic interaction. As they underwent 13 serial transfers, *G. sulfurreducens* upregulated its formate dehydrogenase (FdnG) and hydrogenase (HybA) enzymes, allowing for formate or hydrogen to be utilized as electron donors and supporting an increase in its metabolic flexibility.

This study sought to understand the impact on the dynamics of interaction and the genetic basis of these observed changes. Fluorescence in situ hybridization (FISH) and quantitative PCR (qPCR) revealed an increase in the dominance of *Geobacter* spp. over coculture evolution, indicating a shift from syntrophy to competition. Whole-genome sequencing showed rapid selection for genetic variants in the *Geobacter fabi* and *tetR* genes. A frameshift mutation in *tetR* was coincident with significant upregulation of an adenylate cyclase-hemolysin transporter gene (*cyaE*) and a resistance-nodulation-division (RND) efflux pump (GSU0949), both located in a predicted TetR-regulated operon (40). TetR family transcriptional repressors are known for their role in regulating efflux pumps and transporters of antibiotics or toxic chemicals (41). Here, we find that *G. sulfurreducens* growth is inhibited by *P. aeruginosa*-derived phenazine-1-carboxylic acid (PHZ-1-CA). Selection of *tetR* and *fabi* variants is not explained by PHZ-1-CA. In agreement with this, we observe these variants to be present in *phz*-deficient cocultures. This suggests that other phenazine derivatives or nonphenazine antimicrobials secreted by *P. aeruginosa* drive the selection of these variants or, alternatively, there is an as-yet-unidentified role for RND efflux pump and adenylate cyclase upregulation in these cocultures.
RESULTS

**Geobacter** spp. increasingly dominate coculture populations through adaptation. Previously, we observed that **Geobacter** spp. became more metabolically flexible with coculture adaptation. We also found that the abundance of **Geobacter** proteins was greater than that of **Pseudomonas** proteins in extracted coculture proteomes (39). To determine whether the increase in **Geobacter** metabolic flexibility changed coculture population dynamics over time, we directly quantified the abundance of each microbe in the population by performing qPCR on all cocultures (PAO1/H11001 DL-1, PA14/H11001 DL-1, and **phz** mutant/H11001 DL-1) for both initial (subculture 0 [s0]) and adapted (subculture 13 [s13]) cocultures. In both the initial and adapted cocultures, the **Geobacter** copy number significantly outnumbered that of **Pseudomonas** spp. (Fig. 1).

The dominance of **G. sulfurreducens** became more pronounced with adaptive evolution over 100 generations by s13, with the highest proportion of **Geobacter** to **Pseudomonas** spp. found in the adapted **phz** mutant + DL-1 cocultures (Table 1). This result shows that **Geobacter** spp. may be more likely to dominate **Pseudomonas** spp. in the absence of phenazine secretion and suggests a possible inhibitory role of phenazines on **Geobacter** spp. (see below). Overall bacterial abundance increased through successive coculture generations (Fig. S1), and **Geobacter** spp. became the most abundant community members by S13. This corresponds with its enhanced metabolic flexibility as it adapts (39), and hence its diminished reliance on **Pseudomonas** spp. for providing electron donors through DIET.

Due to the inability of qPCR to distinguish viable from nonviable cells (42), FISH was performed using probes (Table S1) targeting 16S rRNA, visualizing only the metabolically active population (43). FISH confirmed the dominant presence of **Geobacter** spp. (Fig. 2) in both the initial and adapted cocultures (Fig. S2 to S5). However, the **Pseudomonas** population as visualized by FISH was lower than that found by qPCR, and

### Table 1

| Coculture                | Log copy no. | G. sulfurreducens | G. sulfurreducens/P. aeruginosa ratio |
|--------------------------|--------------|-------------------|--------------------------------------|
| PAO1 + DL-1 s0          | 6.6E+04      | 2.2E+05           | 3:1                                  |
| PAO1 + DL-1 s13         | 4.8E+04      | 2.8E+07           | 589:1                                |
| PA14 + DL-1 s0          | 1.0E+05      | 7.7E+06           | 75:1                                 |
| PA14 + DL-1 s13         | 4.7E+04      | 1.5E+07           | 316:1                                |
| **phz** mutant + DL-1 s0| 2.8E+05      | 1.6E+07           | 57:1                                 |
| **phz** mutant + DL-1 s13| 1.7E+04    | 6.7E+07           | 3,980:1                              |

**FIG 1** Proportion of **G. sulfurreducens** to **P. aeruginosa** in cocultures. Black and gray bars represent log copy numbers of DNA from early-stationary-phase cocultures using **G. sulfurreducens**-specific primers (Gsulf_F and Gsulf_R) and **Pseudomonas**-specific primers (Pse435F and Pse686R), respectively, via qPCR. Solid bars represent initial (s0) cocultures, and dotted bars represent adapted (s13) cocultures. *, P ≤ 0.05.
therefore, the majority of the Pseudomonas population identified by qPCR is likely to represent a subpopulation of either slow-growing/dormant cells, metabolically inactive cells, or extracellular DNA (44). Intriguingly, despite the larger population of Geobacter spp. and their increased metabolic flexibility over time, isolation of G. sulfurreducens from the cocultures where it was plated on Nutrient broth supplemented with acetate and fumarate (NBAF) agar under anaerobic conditions (see the Supplemental Methods) was not successful. Conversely, *P. aeruginosa* was easily isolated from the cocultures on LB agar under aerobic conditions (Fig. S6 and S7).

**Genetic selection of tetR and fabI variants in early and late stages of coculture evolution.** Whole-genome sequencing of all cocultures and the original inoculum pure cultures was conducted to detect whether any mutations were selected for in the initial (s0) and adapted (s13) cocultures. Given the significantly lower abundance of *P. aeruginosa* in all cocultures, the genomic reads corresponding to *P. aeruginosa* were insufficient for statistically significant data analysis and variant calling. A comparison of the cocultures to the original inoculate of *G. sulfurreducens* revealed the presence of two genetic variants gained through coculture adaptation, a frameshift insertion in the tetR gene (GSU0951) and a missense single-nucleotide variant in the fabI gene (GSU1008), that were absent from the inoculate DL-1 genome (Fig. 3).

The fabI missense single-nucleotide variant was rapidly selected for early in coculture adaptation, possibly during lag phase, where an average of 83% of the reads across replicates from initially established cocultures had already acquired it (Fig. 3). Further...
selection occurred with evolution, whereby an average of 99% of the reads across replicates contained this mutation by the 13th transfer. This variant is characterized by a single nucleic acid substitution at genetic coordinate 1089002, resulting in a missense mutation that substitutes a serine for a proline at amino acid position 122. This gene encodes FabI, an enoyl-acyl-carrier protein (enoyl-ACP) reductase which catalyzes the last step in fatty acid biosynthesis (45, 46). FabI is a target for several antibiotics, including diazaborine (47), isoniazid (48), and triclosan (49), and a single amino acid substitution within it is sufficient to confer resistance to these antibiotics (48, 50–54).

Early selection was also observed for a genomic variant of the GSU0951 (here referred to as tetR) gene, which was found in an average of 22% of the initial coculture reads across replicates. Similar to the fabI variant, the tetR variant was strongly selected for through coculture adaptation, becoming present in an average of 98% of the adapted coculture reads. This variant was characterized by a single-nucleotide polymorphism (SNP) involving an insertion at genetic locus 1023986. This SNP resulted in a frameshift mutation, changing the identities of 43 amino acids downstream of this position, followed by an early stop codon, leading to premature truncation of the protein. The absence of this protein from all coculture proteomes suggests that this mutation is likely deleterious. Although G. sulfurreducens pure cultures grown in syntrophic NB(formate + fumarate) medium were not evolved through serial transfers due to their poor growth in this medium, we recently observed that adaptively evolved PAI-A-deficient mutants of G. sulfurreducens (via 13 serial transfers) in NB(formate + fumarate) medium do not acquire any mutations in tetR or fabI (55). Therefore, these two mutations appear to be specifically acquired in response to the presence of P. aeruginosa.

**Evidence for TetR regulation of CyaE and an RND efflux pump.** tetR encodes a predicted transcriptional regulator of the TetR family, the members of which are known to behave as repressors of transcriptional activity (40). TetR is situated upstream of a predicted operon composed of genes GSU0950 and GSU0949, which putatively encode an outer membrane adenylate cyclase transporter (CyaE) and an RND efflux pump, respectively, and predicted ABC transporter genes, GSU0948 and GSU0947 (40). As TetR is predicted to negatively regulate this operon, we looked at the protein abundances of these gene products within our proteomics data previously obtained by sequential window acquisition of all theoretical spectra-mass spectrometry (SWATH-MS) (39). Both GSU0950 (herein referred to as CyaE) and GSU0949 (RND family efflux pump) were found in significantly higher abundances in cocultures than in G. sulfurreducens pure cultures. As the genetic frequency of the tetR variants increased from 22% (range, 17 to 31%) to 98% (range, 95 to 100%) with adaptive evolution, the log2 fold change (log2FC) (coculture versus DL-1) of CyaE protein abundance increased from an average of 1.4 (range, 1.31 to 1.62) to 2.7 (range, 2.71 to 2.76) (Fig. 4). Similarly, GSU0949 increased in abundance, with adaptation from initially absent to a log2FC of 2.46 (range, 2.30 to 2.75). Interestingly, GSU0948 and GSU0947 were not found in the extracted proteomes, suggesting a lack of control of these genes by TetR under the conditions of this study.

**Antimicrobial activity of PHZ-1-CA does not select for tetR and fabI genetic variants.** Due to the ability of RND efflux pumps to export antibiotics like *Pseudomonas* phenazines (56) and our finding that *Geobacter* dominance over *Pseudomonas* spp. was highest in the absence of phenazines, we sought to test the antimicrobial activity of phenazines on *G. sulfurreducens*. We measured the MIC of PHZ-1-CA, a precursor to PYO, phenazine-1-carboxamide, and 1-hydroxyphenazine (57), for *G. sulfurreducens* in adapted cocultures versus that of the *G. sulfurreducens* DL-1 wild type (not previously exposed to *P. aeruginosa*). The MIC of cocultures with PAO1 and PA14 was 250 mg/liter (Table 2), whereas the MIC of phz mutant cocultures was 125 mg/liter after 38 days. The MIC of the DL-1 wild type was 125 mg/liter, the same as for the phz mutant coculture, and after one serial transfer (s1), it increased to 250 mg/liter. This result confirms a partial inhibitory activity of PHZ-1-CA on *G. sulfurreducens* and suggests that the various phenazine derivatives may be secreted by the PAO1 + DL-1 and PA14 + DL-1 cocul-
duced given their higher MICs over that of the phz mutant + DL-1 coculture. Since the tetR and fabI mutations were acquired already in s0 cocultures, we assessed whether DL-1's1 acquired mutations in tetR or fabI after one serial transfer in PHZ-1-CA. Targeted next-generation sequencing of these genes at high coverage (~27,000×l) found no variants with an allelic frequency of 2% or greater that were absent in G. sulfurreducens not treated with PHZ-1-CA. This result indicates that tetR and fabI mutations are not selected for due to the presence of PHZ-1-CA in particular. This suggests that other P. aeruginosa antibiotics and phenazine derivatives, such as anthranilate, PYO, and 1-hydroxyphenazine, may be driving the selection of these mutations. In agreement with this, PHZ-1-CA was below the detection limits in all cocultures (see Supplemental Methods), as previously observed for P. aeruginosa PAO1 pure cultures grown in minimal medium (57).

DISCUSSION

Geobacter and Pseudomonas spp. are electrochemically active bacteria found to cohabit many of the same environments of ecological significance, including contaminated sites and wastewater streams (35, 38). In this study, assessment of their adaptive evolution using serial transfers in vitro enabled observations of real-time interaction dynamics and survival strategies, something not easily acquired through in situ experiments given the complexity of their environments and the presence of other community members.

For all three Pseudomonas strains, PAO1, PA14, and the phz mutant, tested in cocultures with G. sulfurreducens, the Geobacter sp. population was dominant. Throughout time, Geobacter sp. dominance increased with coculture evolution. The increasing dominance of Geobacter spp. resembles a transition from initial syntrophy to a com-

---

**TABLE 2** Phenazine-1-carboxylic acid MIC after 38 days

| Culture                  | MIC (mg/liter) |
|--------------------------|----------------|
| PAO1 + DL-1 s13         | 250            |
| PA14 + DL-1 s13         | 250            |
| phz mutant + DL-1 s13   | 125            |
| DL-1 s1                 | 125            |
| PAO1                    | 250*           |
| PA14                    | 500            |
| phz mutant              | 500            |

*MIC after 30 days.
petitive interaction, where Geobacter spp. may be benefiting at the cost of Pseudomonas spp. Interestingly, isolation of G. sulfurreducens from the cocultures was not possible despite its dominance, suggesting a reliance on Pseudomonas spp. This was the case for both initial s0 and adapted s13 cocultures. Not only was G. sulfurreducens more dominant than was P. aeruginosa, but it also appeared to be more metabolically active, as indicated by FISH. Bacteria enter dormancy as a bet-hedging strategy and in response to various environmental factors, including nutrient limitation (58), competition (59), and antibiotics (60). Alternatively, their growth can be inhibited through contact-dependent inhibition or predation as an extreme response to limited nutrients (61, 62). It is yet unclear whether G. sulfurreducens inhibits P. aeruginosa growth, which would suggest possible predation, or whether P. aeruginosa ushers itself into dormancy in order to protect itself from the limited and competitive conditions (63, 64). This warrants further investigation, especially given the close relation of Geobacter spp. to the prokaryotic predators Bdellovibrio spp. that reside in similar environments and can prey on various Pseudomonas species (65, 66). Given that Geobacter and Pseudomonas spp. coexist in many oligotrophic and contaminated environments where Pseudomonas spp. are often less abundant than Geobacter spp. (33, 35, 37), we believe that their coculture interaction dynamics observed in this study may have ecological relevance.

This study provides the first account for selection of tetR and fabl mutations in Geobacter spp. as a response to coculture evolution with P. aeruginosa. The consistent selection for tetR and fabl variants observed across all three cocultures and three biological replicates strongly suggests an adaptive evolutionary role of these mutations to the fitness of Geobacter spp. in cocultures with P. aeruginosa. Furthermore, the observation that increased genetic frequency of the tetR frameshift variant mirrored the increased expression of downstream genes, GSU0950 and GSU0949, is in agreement with the predicted regulatory role of tetR within the TetR operon (40). The results described here show the propensity of G. sulfurreducens to undergo rapid adaptive evolutionary changes that may play a role in protection against competition with stresses created by P. aeruginosa, as Geobacter spp. become more metabolically versatile during coculture adaptation (39). Strong and rapid selection driven by a limited number of mutations has been observed in other work, where a single-nucleotide mutation of a regulatory gene confers rapid adaptive resilience to stress (23, 67, 68).

TetR-regulated RND efflux transporters are important for antibiotic or toxic chemical efflux (41). Pseudomonas spp. are known to produce a vast array of antibiotics, including phenazines and quinolones, that have various antimicrobial properties on different bacterial species (31, 32). Recently, it was shown that P. aeruginosa itself uses the RND family efflux protein complex MexGHI-OpmD to secrete the PYO intermediate 5-methylphenazine-1-carboxylate (5-Me-PCA) and thus enables self-resistance to this highly reactive compound (56). Besides phenazines, this same efflux pump can also export the toxic Pseudomonas quinolone signal (PQS) precursor anthranilate (69), the antibiotic norfloxacin, and the toxic dye acriflavine (70), which demonstrates the wide range of substrates for this efflux pump. We found that one serial transfer of unadapted Geobacter spp. in PHZ-1-CA resulted in an increased MIC but did not correspond with the selection of tetR and fabl variants. Hence, it is likely that posttranscriptional or posttranslational modifications allowed for adaptation to Pseudomonas sp. PHZ-1-CA. In agreement with this, coculture of Geobacter spp. with a phenazine-deficient Pseudomonas mutant still resulted in the selection of tetR and fabl mutations. In future work, a comprehensive panel of P. aeruginosa antibiotics needs to be screened for their potential to drive selection of the tetR and fabl variants in order to rule out whether these variants arise as an antimicrobial response. In addition to GSU0949 RND efflux pump upregulation, the adenylate cyclase transporter CyaE (GSU0950) is also upregulated in response to adaptation with P. aeruginosa. Adenylate cyclases catalyze the synthesis of the second messenger, CAMP, and are commonly attributed to their toxic effects on eukaryotic hosts, as in the case of Bordetella pertussis and Vibrio cholerae (71). Their role in interactions with P. aeruginosa, however, requires further investigation.
especially given the inability to isolate *G. sulfurreducens* from *P. aeruginosa* in the cocultures.

This work demonstrates the complex interplay between syntrophy and competition that can occur between just two microbial species in a defined medium. Microbial communities can adapt mutually beneficial interactions often involving cross-feeding or exchange of electrons (72). Such interactions have commonly been found in methanogenic communities where syntrophy between methanogens, fermentative bacteria, and acetogens takes place (73). Furthermore, DIET allows the exchange of reducing equivalents between syntrophic microbial partners and has been found to occur in various environments and under lab culture conditions (2, 12, 23, 74). Although DIET appears as an initial form of syntrophy between *G. sulfurreducens* and *P. aeruginosa*, this interaction transitions to competition as *G. sulfurreducens* increases its utilization of formate. Our finding corresponds well with previous hypotheses that in a majority of cases, adaptation of two culturable microbial species leads to competitive rather than cooperative interactions, even in a medium designed for syntrophy (75). In this coculture, competition eventually supersedes syntrophy as *Geobacter* spp. adapt to utilize hydrogen and formate as electron donors. This can be a valuable lesson when evaluating the immense array of interactions that occur at the microbial community level in natural environments.

**MATERIALS AND METHODS**

**Strains and media.** *G. sulfurreducens* DL-1 (PCA strain, ATCC 51573) was grown under strictly anaerobic conditions in NB supplemented with acetate and fumarate (NBAF) medium, as previously described (76), except no resazurin was added. For growth of the pure culture, 20 mM acetate and 40 mM fumarate were used as the electron donor and acceptor, respectively. *P. aeruginosa* PA01, PA14, and PA14 Δphz1 Δphz2 (here referred to as the phz mutant) (57) strains were grown under strictly anaerobic conditions in NB medium containing 20 mM formate and 20 mM nitrate as the electron donor and acceptor. The two strains of *P. aeruginosa* differ in their phenazine production under different conditions, where PA01 produces 4-fold higher pyocyanin (PYO) than does PA14 in medium that mimics the cystic fibrotic lung (77), while PA14 produces 10-fold higher pyocyanin PAO1 in Luria-Bertani (LB) medium (57). For growth of the cocultures, 20 mM formate and 40 mM fumarate were provided as the electron donor and acceptor, the former of which is preferentially utilized by *Pseudomonas* spp., and the latter of which is only utilized by *Geobacter* spp. To initiate s0 cocultures, each bacterial species from pure cultures grown to late-log phase was inoculated at a concentration of 3.4 × 10^7 cells/ml as determined via a hemocytometer to ensure equal representation of *Geobacter* and *Pseudomonas* spp. when establishing the coculture. Adaptation of the cocultures involved transferring 1% of culture to fresh NB(formate/fumarate) medium once they reached stationary phase, the growth stage when *P. aeruginosa* begins producing phenazines (57), as determined by the optical density at 600 nm (OD600). The cultures were adapted to up to 13 transfers. The initial culture is referred to as culture 0 (s0), and the 13th transfer culture is called subculture 13 (s13). In total, 13 transfers were made, and stocks of cultures were flash frozen in liquid nitrogen and stored at −80°C.

**SWATH-MS proteomics.** All cell harvesting, protein extraction, proteomics, and statistical analyses were performed as previously reported (39).

Genomic DNA extractions and next-generation sequencing. Each coculture comprised three biological replicates. For each biological replicate, there were an additional eight pooled technical replicate cultures. One milliliter of culture was harvested from each replicate at early stationary phase and centrifuged at 14,000 relative centrifugal force (rcf) for 10 min. The supernatant was removed, and cell pellets were snap frozen in liquid nitrogen and stored at −80°C until genomic DNA extraction. Genomic DNA extractions were done using the Isolate II genomic DNA kit from Bioline, according to the manufacturer's instructions. DNA concentrations were measured on the Implen NanoPhotometer P330, and samples were normalized to the same concentration before pooling all technical replicates to obtain an even representation of each replicate. Whole-genomic libraries were made with the Nextera XT kit (Illumina Inc., Australia), and library concentration and mean fragment lengths were measured using a Qubit fluorometer (Invitrogen) and Bioanalyzer (Agilent Technologies). Next-generation sequencing with the Illumina Hiseq2500 platform by the Australian Genome Research Facility (Parkville, Victoria, Australia). Genomic DNA extractions and next-generation sequencing. Each coculture comprised three biological replicates. For each biological replicate, there were an additional eight pooled technical replicate cultures. One milliliter of culture was harvested from each replicate at early stationary phase and centrifuged at 14,000 relative centrifugal force (rcf) for 10 min. The supernatant was removed, and cell pellets were snap frozen in liquid nitrogen and stored at −80°C until genomic DNA extraction. Genomic DNA extractions were done using the Isolate II genomic DNA kit from Bioline, according to the manufacturer's instructions. DNA concentrations were measured on the Implen NanoPhotometer P330, and samples were normalized to the same concentration before pooling all technical replicates to obtain an even representation of each replicate. Whole-genomic libraries were made with the Nextera XT kit (Illumina Inc., Australia), and library concentration and mean fragment lengths were measured using a Qubit fluorometer (Invitrogen) and Bioanalyzer (Agilent Technologies). Next-generation sequencing with the Illumina Hiseq2500 platform by the Australian Genome Research Facility (Parkville, Victoria, Australia).

Assigning reads in sequenced coculture genomes. Adapter sequences were trimmed from paired-end reads using Cutadapt v1.13 (78), with a required minimum length (m) of 30 and a quality cutoff (q) of 15. Trimmed reads were aligned against the GCF_000007985.2 assembly of the Geobacter sulfurreducens PCA genome, the GCF_0000067665.1 assembly of Pseudomonas aeruginosa PAO1, and the GCF_000404265.1 assembly of Pseudomonas aeruginosa PA14 using SMALT v0.7.6 (http://www.sanger.ac.uk/science/tools/smalt-0). The SMALT index for each genome was built using a k-mer (k) size of 11 and a step size (s) of 1. For each coculture of Geobacter sulfurreducens PCA and a Pseudomonas strain, the alignment of paired-end reads against each reference genome was used to categorize each read pair using SAMTools (78–81) as properly mapped (+F 0 × 2), or not (+F 0 × 2) distinguishing reads unmapped...
Given the two genomes (here referred to as species A and B), reads were assigned as originating from genome A if they were (i) mapped to genome A and unmapped to genome B, or (ii) mapped to both genomes, with a sum of the SAMT alignment for both reads in the pair in genome B being less than 80% of the sum of the alignment score in genome A. Read pairs not fulfilling these criteria or with a mapping quality score of less than 30 were excluded from further analysis. Using the above-described categorization, reads assigned to each genome were marked for duplicates with picard (v2.9.3 [http://broadinstitute.github.io/picard/]) and realigned with the Genome Analysis Tool Kit (GATK) v3.5-0 (80). Single-nucleotide variants (SNVs) and small insertions/deletions were called using the HaplotypeCaller function of GATK, with an indel size (indelSizeToEliminateInRefModel) of 20, a minimum mapping quality (mmq) score of 30, and ploidy of 2 to allow for detection of mutations occurring in a subset of the cell population. The impact of mutations on protein-coding transcripts was assessed using CooVar v0.07 (81).

Harvesting for FISH and cell fixation. During harvesting of cocultures at early stationary phase, as described above, 2 ml of each culture was harvested for FISH. Harvesting at early stationary phase for pure cultures of each bacteria was also performed and used for positive- and negative-control tests. Cells were pelleted at 4,000 rcf for 10 min, resuspended in 1× phosphate-buffered saline (PBS), and then fixed in 4% paraformaldehyde for 12 h at 4°C. The cells were pelleted and washed two times in 1× PBS, followed by resuspension in a 1:1 ratio of 100% ethanol with 1× PBS, after which they were stored at −20°C until hybridization was performed within 1 month of storage.

Hybridization and microscopy. Hybridization was carried out according to the protocol by Erhart et al. (82), with minor modifications. Hybridizations were carried out at 46°C for 2 h in a humidity chamber using a hybridization buffer, as previously described (82); after testing a range of formamide concentrations, a 40% formamide concentration was found to give the most specific binding of the probes used, allowing distinct detection of each bacterial species compared to negative controls with no probe bound. Following hybridization, a 25-min wash step at 48°C was performed in a washing buffer, as previously described (82). The EUB338 FISH probe (83), which labels most bacteria, was used as a positive label for both G. sulfurreducens and P. aeruginosa and 5′ labeled with ATTO633. P. aeruginosa FISH probe (84) targeting the 16S rRNA was 5′ labeled with ATTO488. The G. sulfurreducens (23) FISH probe targeting the 16S rRNA was 5′ labeled with ATTO565. Labeled probes were obtained from Integrated DNA Technologies Pte. Ltd. (IDT, Baulkham Hills, NSW, Australia). All cells were also stained with the DNA binding dye 4′,6-diamidino-2-phenylindole (DAPI) to visualize all cells and ensure there were not any contaminant microorganisms in the cocultures not belonging to P. aeruginosa or G. sulfurreducens. Cells were visualized on a Zeiss confocal LSM780 microscope with a 63× and 100× oil immersion objective (Carl Zeiss MicroImaging GmbH, Germany) at the LIMS Bioimaging Facility (La Trobe University, Australia).

Cloning standards and quantitative PCR. Gene fragments of G. sulfurreducens and P. aeruginosa 16S rRNA were PCR amplified using Taq DNA polymerase (Qiagen, Australia) and the primers listed in Table S1. G. sulfurreducens has a 16S rRNA gene copy number of 2, and P. aeruginosa has a copy number of 4. The reaction conditions were as follows: 94°C for 2 min, followed by 32 cycles at 94°C for 1 min, 60°C for 1 min, and 72°C for 1.5 min. The fragments were then cloned into the TOP10 TA Cloning kit for subcloning with One Shot TOP10 chemically competent E. coli cells (Invitrogen), according to the manufacturer’s instructions for the transformation of One Shot Mach-1 competent cells. The transformed clones were picked for plasmid miniprep using the PureYield plasmid miniprep system (Promega, Australia). Plasmids pLS1 and pLS2, containing cloned P. aeruginosa 16S rRNA and G. sulfurreducens 16S rRNA gene fragments, respectively, were confirmed with sequencing by the Australian Genome Research Facility (AGRF). Quantitative PCR was performed to determine the ratio of G. sulfurreducens to P. aeruginosa in the cocultures. This quantification was done using the cloned 16S rRNA gene fragments to produce a standard curve. Their concentration was determined on the Implen NanoPhotometer P330, from which the copy number was calculated, and a 5-fold dilution series was made (109 to 102 genes/μl) to generate a standard curve. The primers (Table S1) used for the quantification of G. sulfurreducens gene copy numbers were Gsulf_F and Gsulf_R, and Pse435F and Pse686R were used for P. aeruginosa quantification, generating amplicons of 108 bp and 251 bp, respectively. Reactions were performed in a total volume of 20 μl with 3.3 μl SensiFAST SYBR and fluorescein mix (Bioline, Australia), 133 nM each primer, and 2 μl of DNA template. The qPCR cycle settings started with an initial denaturation at 94°C for 3 min, followed by 40 cycles of 94°C for 10 s and 60°C (G. sulfurreducens) or 58°C (P. aeruginosa) for 30 s, with a melting curve of 60°C for 30 s and temperature increasing to 95°C, with data readings at increments of 0.5°C.

Phenazine-1-carboxylic acid MIC. The MICs of PHZ-1-CA were determined using a broth dilution method where 2-fold serial dilutions (from 500 mg/liter to 2 mg/liter) of PHZ-1-CA (Merck) were made in anaerobic Hungate tubes and inoculated with cocultures (DL-1 + PAO1, DL-1 + PA14, and DL-1 + phz mutant) and pure cultures of DL-1, PAO1, PA14, and the phz mutant. The dilutions were made in 10% ethanol of either NB (formate + fumarate) medium (for cocultures), NBAF medium (for DL1 pure cultures), or NB (formate + nitrate) medium (for PAO1, PA14, and phz mutant pure cultures). Positive-control and ethanol control tubes were also inoculated with culture and contained medium only or 10% ethanol medium, respectively, with no PHZ-1-CA. Once the cultures reached early stationary phase, they were diluted to a turbidity equivalent to 0.5 McFarland standard (OD625, 0.1) corresponding to ~1 × 106 to 2 × 107 cells (85), and 1% of the culture was added to the dilution series tubes. The tubes were incubated at 30°C for 30 to 38 h. The MIC was established as the lowest concentration of PHZ-1-CA that inhibited growth.
Targeted sequencing of tetR and fabI. Targeted next-generation sequencing of the tetR and fabI regions was performed on G. sulfurreducens DL-1 pure cultures grown in sodium-1-carboxylic acid (Merck) at various concentrations for MIC testing. Primers were designed to amplify 350-bp regions of each gene and contained Illumina overhang adapter sequences (Table S1). For each 1-kb gene, three primer pairs were used to cover the entire length of the gene. Genomic DNA extractions were done using the Isolate II genomic DNA kit from Bioline, according to the manufacturer’s instructions. DNA concentration was measured on the Implen NanoPhotometer P330, and samples were normalized to 5 ng/μL and used to generate amplicon libraries with the MiSeq reagent kit V3 (Illumina, Inc., Australia). The tetR and fabI primers with appropriate Illumina adapters for the forward and reverse primers (Table S1) were used to generate amplicons according to the 16S rRNA metagenomic sequencing library preparation protocol (part no. 15044223 rev. B; Illumina). PCR cleanup was performed using AMPure XP beads, following the manufacturer’s instructions, and subsequent PCR was performed to add Illumina flow cell adapters and Nextera XT indices. DNA concentration and mean fragment lengths were measured using a Qubit fluorometer (Invitrogen) and Agilent 4200 TapeStation (Agilent Technologies). Next-generation sequencing with 300-bp paired-end reads and 600 cycles was performed on the Illumina MiSeq platform.

Data availability. All raw sequences are deposited in the Sequence Read Archive under BioProject number PRJNA544640 and BioSample numbers SAMN11792103 to SAMN11792109. The mass spectrometry proteomics data have been deposited to the ProteomeXchange Consortium via the PRIDE partner repository (86) with the data set identifier PXD013990.

SUPPLEMENTAL MATERIAL

Supplemental material is available online only.

TEXT S1, DOXC file, 0.1 MB.
FIG S1, TIF file, 1.6 MB.
FIG S2, TIF file, 1.3 MB.
FIG S3, TIF file, 2.5 MB.
FIG S4, TIF file, 2 MB.
FIG S5, TIF file, 2.2 MB.
FIG S6, TIF file, 2.2 MB.
FIG S7, TIF file, 2.4 MB.
TABLE S1, DOXC file, 0.1 MB.

ACKNOWLEDGMENTS

We thank Derek Lovley and Lars Dietrich for their generous gift of the Geobacter strains and mutants and PA14 and PA14 Δphz1 Δphz2 strains of P. aeruginosa, respectively. We acknowledge Vanessa Lee Hocken and Steven Batinovic for their assistance with laboratory work and facilitating sequencing. We also acknowledge Peter Lock for his support with the Bioimaging Platform at the La Trobe Institute for Molecular Science.

This research has been partially financially supported by the Human Protection and Performance Program of the Defense Science Institute. The Applied and Environmental Microbiology Laboratory receives support from the Defense Science and Technology Group (DSTG), Office of Naval Research Global (award N626909-13-1-N259), Asian Office of Aerospace Research and Development (AOARD; award FA2386-14-1-4032), and the Australian Research Council (ARC; award LP140100459).

We declare no conflicts of interest.

REFERENCES

1. Bond DR, Holmes DE, Tender LM, Lovley DR. 2002. Electrode-reducing microorganisms that harvest energy from marine sediments. Science 295:483–485. https://doi.org/10.1126/science.1066771.
2. Caccavo F, Jr, Lonergan DJ, Lovley DR, Davis M, Stolz JF, McNerney MJ. 1994. Geobacter sulfurreducens sp. nov., a hydrogen-oxidizing and acetate-oxidizing dissimilatory metal-reducing microorganism. Appl Environ Microbiol 60:3752–3759. https://doi.org/10.1128/AEM.60.10.3752-3759.1994.
3. Coates JD, Bhupathiraju VK, Achenbach LA, McNerney MJ, Lovley DR. 2001. Geobacter hydrogenophillus, Geobacter chapellei and Geobacter grbiciae, three new, strictly anaerobic, dissimilatory Fe(III)-reducers. Int J Syst Evol Microbiol 51:581–588. https://doi.org/10.1099/00207713-51-2.581.
4. Coates JD, Phillips EJ, Lonergan DJ, Jenter H, Lovley DR. 1996. Isolation of Geobacter species from diverse sedimentary environments. Appl Environ Microbiol 62:1531–1536. https://doi.org/10.1128/AEM.62.5.1531-1536.1996.
5. Deng DD, Zhang YC, Liu Y. 2015. A Geobacter strain isolated from rice paddy soil with higher bioelectricity generation capability in comparison to Geobacter sulfurreducens PCA. RSC Adv 5:43978–43989. https://doi.org/10.1039/C5RA06211J.
6. Lovley DR, Giovannoni SJ, White DC, Champine JE, Phillips EJ, Gorby YA, Goodwin S. 1993. Geobacter metallireducens gen. nov. sp. nov., a microorganism capable of coupling the complete oxidation of organic compounds to the reduction of iron and other metals. Arch Microbiol 159:336–344. https://doi.org/10.1007/bf00290916.
7. Prakash O, Ghring TM, Dalton DD, Chin KJ, Green SJ, Akob DM, Wanger G, Kostka JE. 2010. Geobacter daltonii sp. nov., an Fe(III)- and uranium(VI)-reducing bacterium isolated from a shallow subsurface ex-
posed to mixed heavy metal and hydrocarbon contamination. Int J Syst Evol Microbiol 60:546–553. https://doi.org/10.1099/ijs.0.01843-0.
8. Sung Y, Fletcher KE, Ritalahti KM, Apkarian RP, Ramos-Hernández N, Sanford RA, Mesbah NM, Löffler FE. 2006. Geobacter lovleyi sp. nov. strain SZ, a novel metal-reducing and tetrachloroethene-dechlorinating bacterium. Appl Environ Microbiol 72:2775–2782. https://doi.org/10.1128/AEM.72.4.2775-2782.2006.
9. Hori T, Muller A, Igarashi Y, Conrad N, Friedrich MW. 2010. Identification of iron-reducing microorganisms in anoxic rice paddy soil by “C-acetate probing. ISME J 4:467–278. https://doi.org/10.1038/ismej.2009.100.
10. Knief C, Delmonte N, Chaffron S, Stark M, Innerbeiner G, Wassmann R, von Mering C, Vorholt JA. 2012. Metaproteogenomic analysis of microbial communities in the phyllosphere and rhizosphere of rice. ISME J 6:1378–1390. https://doi.org/10.1038/ismej.2011.192.
11. Lovley DR, Holmes DE, Nevin KP. 2004. Dissimilatory Fe(III) and Mn(IV) reduction. Adv Microb Physiol 49:219–286. https://doi.org/10.1017/S0065-29110040005-5.
12. Morita M, Malvankar NS, Franks AE, Summers ZM, Giloteaux L, Rotaru AE, Rotaru C, Lovley DR. 2011. Potential for direct interspecies electron transfer in methanogenic wastewater digester aggregates. mBio 2:e00159-11. https://doi.org/10.1128/mBio.00159-11.
13. Anderson RT, Vrionis HA, Ortiz-Bernad I, Resch CT, Long PE, Davyad R, Kang YS, Maustzuckler DR, Plasser P, Lowie PS, Lovley DR. 2003. Stimulating the in situ activity of Geobacter species to remove uranium from the groundwater of a uranium-contaminated aquifer. Appl Environ Microbiol 69:5884–5891. https://doi.org/10.1128/AEM.01884-08.
14. Esteve-Núñez A, Núñez C, Lovley DR. 2004. Preferential reduction of FeII over fumarate by Geobacter sulfurreducens. J Bacteriol 186:2897–2899. https://doi.org/10.1128/JB.186.9.2897-2899.2004.
15. Holmes DE, Nevin KP, Lovley DR. 2004. In situ expression of mld in Geobacteraceae in subsurface sediments. Appl Environ Microbiol 70:7251–7259. https://doi.org/10.1128/AEM.70.12.7251-7259.2004.
16. Yang TH, Coppi MV, Lovley DR, Sun J. 2010. Metabolic response of Geobacter sulfurreducens towards electron donor/acceptor variation. Geomicrobiol J 27:408–415. https://doi.org/10.1080/01490451003518212.
17. Chifferes SE, Deboy RT, Dill LM, Lovley DR. 2002. Tunable metallic-like conductivity in microbial nanowire networks. Science 298:1967–1970. https://doi.org/10.1126/science.1076767.
18. Malvankar NS, Vargas M, Nevin KP, Franks AE, Leang C, Kim BC, Inoue K, Mester T, Covalla SF, Johnson JP, Rotello VM, Tuominen MT, Lovley DR. 2011. Tunable metallic-like conductivity in microbial nanowire networks. Nat Nanotechnol 6:573–579. https://doi.org/10.1038/nnano.2011.119.
19. Mawatari MA, Nevin KP, Newbold IA, Paulsen IT, Lovley DR, Fudenberg HH, Hartmann EM, Hsu T, Justice NB, Paulino-Lima IG, Luongo JC, Lymperopoulou DS, Gmez-Silvan C, Rothchild-Mancinelli B, Balk M, Huttoner
63. Akiyama T, Williamson KS, Schaefer R, Pratt S, Chang CB, Franklin MJ. 2017. Resuscitation of Pseudomonas aeruginosa from dormancy requires hibernation-promoting factor (PA4463) for ribosome preservation. Proc Natl Acad Sci U S A 114:3204–3209. https://doi.org/10.1073/pnas.1700659114.

64. Müller S, Strack SN, Ryan SE, Keams DB, Kirby JR. 2015. Predation by Myxococcus xanthus induces Bacillus subtilis to form spore-filled megagranules. Appl Environ Microbiol 81:203–210. https://doi.org/10.1128/AEM.02448-14.

65. Rice TD, Williams HN, Turg B. 1998. Susceptibility of bacteria in estuarine environments to autochthonous bdellovibrios. Microb Ecol 35:256–264. https://doi.org/10.1007/s00018-009-8704-7.

66. Stolp H, Starr MP. 1963. Bdellovibrio bacteriovorus gen. et sp. n., a predatory, ectoparasitic, and bacteriolytic microorganism. Antonie Van Leeuwenhoek 29:217–248. https://doi.org/10.1007/bf02466064.

67. Summers ZM, Veki T, Ismail W, Haveman SA, Lovley DR. 2012. Laboratory evolution of Geobacter sulfurreducens for enhanced generation DNA sequencing data. Genome Res 20:1297–1303. https://doi.org/10.1101/gr.107524.110.

68. Zhou AF, Hillesland KL, He ZL, Schackwitz W, Tu QC, Zane GM, Qu YY, Stahl DA, Wall JD, Hazen TC, Fields MW, Arpin AK, Zhou JZ. 2015. Rapid selective sweep of pre-existing polymorphisms and slow fixation of new mutations in experimental evolution of Desulfovibrio vulgaris. ISME J 9:2360–2372. https://doi.org/10.1038/ismej.2015.45.

69. Aendekerk S, Diggle SP, Song Z, Holby N, Cornelis P, Williams P, Camara M. 2005. The MexGHI-OmpD multidrug efflux pump controls growth, antibiotic susceptibility and virulence in Pseudomonas aeruginosa via a quinolone-dependent cell-to-cell communication. Microbiology 151:1113–1125. https://doi.org/10.1099/mic.0.27831-0.

70. Sekiya H, Mima T, Morita Y, Kuroda T, Mizushima T, Tsuchiya T. 2003. Functional cloning and characterization of a multidrug efflux pump, MexHl-OmpD, from a Pseudomonas aeruginosa mutant. Antimicrob Agents Chemother 47:2990–2992. https://doi.org/10.1128/aac.47.9.2990-2992.2003.

71. Ahuja N, Kumar P, Bhattacharjee R. 2004. The adenylate cyclase toxins. Crit Rev Microbiol 30:187–196. https://doi.org/10.1080/10408410490468795.

72. Kouzuma A, Kato S, Watanabe K. 2015. Microbial interspecies electron flow mediated by Bacillus subtilis to Myxococcus xanthus induces Bacillus subtilis to form spore-filled megagranules. Proc Nat Acad Sci USA 112:5488–5493. https://doi.org/10.1073/pnas.1500461112.

73. Foster KR, Bell T. 2012. Competition, not cooperation, dominates inter- and intraspecies interactions among culturable microbial species. Curr Biol 22:1845–1850. https://doi.org/10.1016/j.cub.2012.08.005.

74. Coppi MV, Leang C, Sandler SJ, Lovley DR. 2001. Development of a genetic system for Geobacter sulfurreducens. Appl Environ Microbiol 67:3180–3187. https://doi.org/10.1128/AEM.67.9.3180-3187.2001.

75. Han J, Soe CZ, Rose B, Harbour C, Codd R, Manos J, Cordwell SJ. 2012. Proteomics of Pseudomonas aeruginosa Australian epidemic strain 1 (AES-1) cultured under conditions mimicking the cystic fibrosis lung reveals increased iron acquisition via the siderophore pyochelin. J Proteome Res 11:776–785. https://doi.org/10.1021/pr200659h.

76. Martin M. 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. EMBnet J 17:10–12. https://doi.org/10.1186/1471-2164-17-100.

77. Li H, Handsaker B, Wysoker A, Fennell T, Ruan J, Marth G, Abecasis G, Durbin R, Genome Project Data Processing Subgroup. 2009. The Sequence Alignment/Map format and SAMtools. Bioinformatics 25:2078–2079. https://doi.org/10.1093/bioinformatics/btp352.

78. McKenna A, Hanna M, Banks E, Sivachenko A, Cibulskis K, Kernytsky A, Garimella K, Altshuler D, Gabriel S, Daly M, DePristo MA. 2010. The Genome Analysis Toolkit: a MapReduce framework for analyzing next-generation DNA sequencing data. Genome Res 20:1297–1303. https://doi.org/10.1101/gr.107514.110.

79. Verghese IA, Frech C, Chen N. 2012. CooVar: co-occurring variant analyzer. BMC Res Notes 5:615. https://doi.org/10.1186/1756-0500-5-615.

80. Erhart R, Bradford D, Seviour RJ, Amann R, Blackburn LL. 1997. Development and use of fluorescent in situ hybridization probes for the detection and identification of “microaerophilic” clostridia in adult human faeces. FEMS Microbiol Ecol 20:313–318. https://doi.org/10.1111/j.1574-6941.2006.tb01880.x.

81. Amann R, Binder BJ, Olson RJ, Chisholm SW, Devereux R, Stahl DA. 1990.
Combination of 16S rRNA targeted oligonucleotide probes with flow cytometry for analyzing mixed microbial populations. Appl Environ Microbiol 56:1919–1925. https://doi.org/10.1128/AEM.56.6.1919-1925.1990.

84. Hogardt M, Trebesius K, Geiger AM, Hornef M, Rosenecker J, Heesemann J. 2000. Specific and rapid detection by fluorescent in situ hybridization of bacteria in clinical samples obtained from cystic fibrosis patients. J Clin Microbiol 38:818–825. https://doi.org/10.1128/JCM.38.2.818-825.2000.

85. Balouiri M, Sadiki M, Ibnsouda SK. 2016. Methods for in vitro evaluating antimicrobial activity: a review. J Pharm Anal 6:71–79. https://doi.org/10.1016/j.jpha.2015.11.005.

86. Vizcaíno JA, Csordas A, del-Toro N, Dianes JA, Griss J, Lavidas I, Mayer G, Perez-Riverol Y, Reisinger F, Ternent T, Xu QW, Wang R, Hermjakob H. 2016. 2016 update of the PRIDE database and its related tools. Nucleic Acids Res 44:D447–D456. https://doi.org/10.1093/nar/gkv1145.
Minerva Access is the Institutional Repository of The University of Melbourne

Author/s:
Semenec, L; Vergara, IA; Lalock, AE; Petrovski, S; Bond, PL; Franks, AE

Title:
Adaptive Evolution of Geobacter sulfurreducens in Coculture with Pseudomonas aeruginosa

Date:
2020-03-01

Citation:
Semenec, L., Vergara, I. A., Lalock, A. E., Petrovski, S., Bond, P. L. & Franks, A. E. (2020). Adaptive Evolution of Geobacter sulfurreducens in Coculture with Pseudomonas aeruginosa. MBIO, 11 (2), https://doi.org/10.1128/mBio.02875-19.

Persistent Link:
http://hdl.handle.net/11343/246032

File Description:
published version

License:
CC BY