



Metal resistance systems in cultivated bacteria: are they found in complex communities?

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Metal resistance systems found in complex bacterial communities by shotgun metagenomic approaches were reviewed. For that, 6 recent studies investigating 9 metal-contaminated environments (water or sediments) were selected. Of the 22 possible metal-resistance systems, only 14 were found in complex communities. These widespread and easily detected metal-resistance systems were mainly biogenic sulfide production (*dsr* genes), resistance mediated in the periplasm (CopK and multicopper oxidases such as PcoA/CopA), efflux proteins (HME-RND systems, P-type ATPases, and the cation diffusion facilitator CzcD) as well as proteins used to treat oxidative damages (e.g., SodA) and down-regulation of transporters. A total of 8 metal-resistance systems were not found in the complex communities investigated. These rare systems include metal resistance by phosphatases, ureases, metallophores, outer membrane vesicles, methylation genes and cytoplasmic metal accumulation systems. In this case rarity may also be explained by a lack of knowledge on the specific genes involved and/or analytical biases.

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Introduction

Bacterial adaptations to excessive concentrations of metals have been described in many cultivated species [e.g., 1[•]]. A total of 22 systems are known and concern the extracellular environment, the outer membrane, the periplasm, the cytoplasmic membrane and the cytoplasm (Figure 1, Table 1). However, microbial ecosystems are often complex, with many uncultivated bacteria. As a consequence, resistance systems described in cultivated strains are not necessarily used or widespread in complex communities. The knowledge of the most widespread

systems is important, particularly in the field of ecotoxicology where metal resistance genes may be used as bioindicators of metal pollution [2]. To get a clearer picture, recent studies focused on metal-contaminated bacterial communities were reviewed. Only studies using shotgun metagenomics (6 studies) and metatranscriptomics (1 study) were selected because these approaches circumvent PCR biases [3]. These studies encompass 9 sites (Table S2). Two of the considered studies also used metaproteomics. Below, the possible resistance systems are listed and in each case it is indicated if their characteristic genes (when known) were found in the selected studies (Table 1, B).

The extracellular environment

Biogenic sulfides and other extracellular minerals

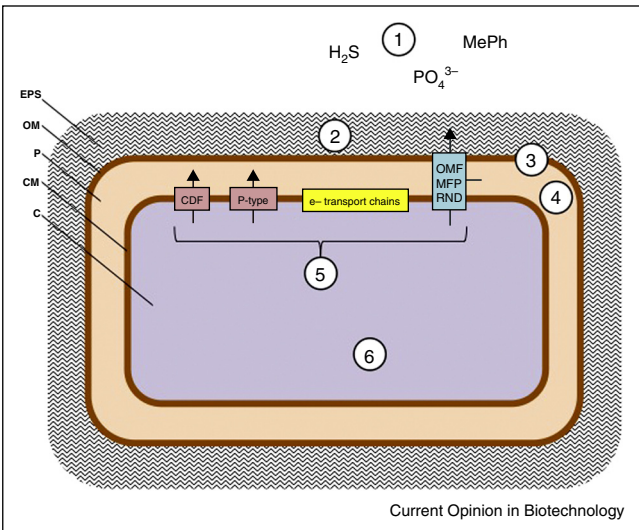
It is known for a long time that dissolved metals may be removed from solution by the production of biogenic sulfides. For instance, in a metal-contaminated salt marsh it was shown that the most active zone of sulfate-reduction controlled metal speciation [4]. At the community level, it was recently observed in lake sediments that sulfate reduction genes (*dsr*) were more abundant than other gene categories and were highly correlated with metal contamination [5]. Similarly, in a metal-contaminated marine sediment shotgun metagenomics indicated that genes related to dissimilatory sulfate reduction were over-represented [6^{••}]. Clearly, *dsr* genes appear as important markers of metal contamination in the field.

Microbially induced calcite precipitation (MICP) is a widespread phenomenon, particularly in the presence of ureolytic bacteria [7]. MICP may protect cells as extracellular calcite is able to trap various toxic metals [8]. But so far, MICP and high urease levels were not found in the examined metal-contaminated bacterial communities [6^{••}, 9^{••}, 10^{••}, 11^{••}, 12^{••}, 13^{••}]. Other extracellular biominerals have been reported in communities [14]; however, specific genes have not yet been identified.

Extracellular phosphatases and metallophores

Phosphatase-positive bacteria are often isolated from metal-contaminated environments and it was suggested that phosphatase activity decreases metal toxicity by causing precipitation of metal phosphates like $\text{NH}_4\text{UO}_2\text{PO}_4$ [15]. Although phosphatases have been identified in metagenomes [16], high levels were not found in the examined metal-contaminated bacterial communities [6^{••}, 9^{••}, 10^{••}, 11^{••}, 12^{••}, 13^{••}].

Figure 1



Location of the main metal-resistance systems in a typical Gram-negative cell (the same notation is used for Gram-positives lacking the outer membrane). 1, extracellular environment in which metallophores may be found (MePh); 2, exopolymeric substances (EPS); 3, outer membrane (OM); 4, periplasm (P); 5, cytoplasmic membrane (CM) with cation diffusion facilitators (CDF), P-type ATPases (P-type), electron transport chains and tripartite efflux pumps (composed of an RND pump in the CM, a membrane fusion protein (MFP) in the periplasm, and outer membrane factors (OMF) in the outer membrane); 6, the cytoplasm (C).

Siderophores and metallophores are low molecular weight metal-chelating agents [17,18]. Although their principal role is to chelate ferric iron in the extracellular environment, they can also chelate many other metals [19]. Siderophores bound to iron moves into the cell adequately but siderophores bound to other metals do not enter the cell efficiently [17]. In *Delftia acidovorans* a cluster of 7 genes is involved in the excretion of a metallophore that ultimately leads to gold precipitation [18]. But to the present state of knowledge metallophore genes were not found as more abundant in the investigated metal-contaminated communities [6^{**},9^{**},10^{**},11^{**},12^{**},13^{**}].

The extracellular polymeric substances (EPS)

The EPS of bacteria are known to complex metals [20] and protect them from excessive metal stress [21,22]. Once complexed, particular minerals may nucleate [23,24] a process that gives additional protection, particularly for Fe/Mn oxyhydroxides [25,26]. At the community level, it was shown that the most significant difference between a metal-contaminated sediment and a less contaminated site concerned the SEED gene category [27] ‘cell wall and capsule’ that included among others a glycosyl transferase and a UDP-N-acetylglucosamine epimerase [9^{**}]. Glycosyl transferases are enzymes involved in the export of extracellular polysaccharides [28]. However, genes involved in the formation of EPS were not found as more abundant in other metal-genomic studies [6^{**},10^{**},11^{**},12^{**},13^{**}].

Table 1

Metal-resistance systems detected in isolated bacterial strains and in metal-contaminated bacterial communities

Localization	A. In isolated bacterial strains [reference]	B. In metal-contaminated bacterial communities [reference]
Extracellular environment	Sulfide production [2,3] Calcite precipitation [5,6 ^{**}] Extracellular phosphatases [12 ^{**}] Extracellular metallophores [14–16] EPS [17–23]	<i>dsr</i> genes [4] — — — Glycosyl transferase, epimerase [7]
Outer membrane	LPS [12 ^{**}] Outer membrane vesicles [12 ^{**} ,26] Proteins [28–30] Downregulation of transporters	KDO-8-P synthase [7] — <i>pilA</i> [7] —
Periplasm	Metal-binding proteins [38–41] Redox enzymes [40,42*,44,45*,46,47] Cell wall [53,54]	<i>copK</i> [8] Multicopper oxidases [9 ^{**} ,43] Cell Wall SEED category [7]
Cytoplasmic membrane	Electron transport chains [55,56] Lipid phosphatases [57] P-type ATPases [59] Cation diffusion facilitators [61] HME-RNDs [62] Downregulation of transporters	Respiration SEED category [7] — <i>copA</i> [8] <i>czcD</i> [7,10 ^{**}] <i>czcA</i> [7,8,10 ^{**}]; <i>cusA</i> [9 ^{**}]; <i>arsA</i> [10 ^{**}] Pst sytem [6 ^{**} ,13 ^{**}] <i>arsH</i> [4,11 ^{**}] —
Cytoplasm	Redox changes [64–67] Methylation-volatilization [69,70] Metal accumulation [71,72,73*,74–78] ROS production, DNA repair and protein hydrolysis [1*,86*,87*]	<i>sodA</i> , <i>ahpC</i> , <i>dnaX</i> [12 ^{**} ,13 ^{**}]

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