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Insights into the bacterial synthesis of metal nanoparticles

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Metal nanoparticles have attracted considerable attention due to their astounding potential for a wide range of commercial applications. From targeted drug delivery and antimicrobial agents to electronics, metal nanoparticles seem to have immeasurable prospects in all areas of science. However, modern industrial production frequently involves complex procedures, large amounts of energy, utilizes strong chemical solvents, or produces hazardous waste. Biological synthesis has been proposed as an alternative for simpler, inexpensive, and more eco-friendly metal nanoparticle production. Microorganisms possess multiple mechanisms to transport, regulate and bind metal ions that may result in the biosynthesis of nanoparticles. They can synthesize even complex bimetallic nanoparticles, which are difficult to produce with normal chemical and physical processes. A better understanding of bacteria-metal interactions might thus pave the way for a wide array of industrial applications. This review will summarize the current methods for metal nanoparticle synthesis, with a focus on the microbial (bio) synthesis of nanoparticles. We will describe the general mechanisms of bacteria-metal ion interactions, including cellular uptake and the subsequent reduction into nanoparticles. Protocols for the production of metal-based nanoparticles of relevant elements with different bacterial strains are compiled and the current challenges in bacterial synthesis of metal nanoparticles in the industry are discussed.

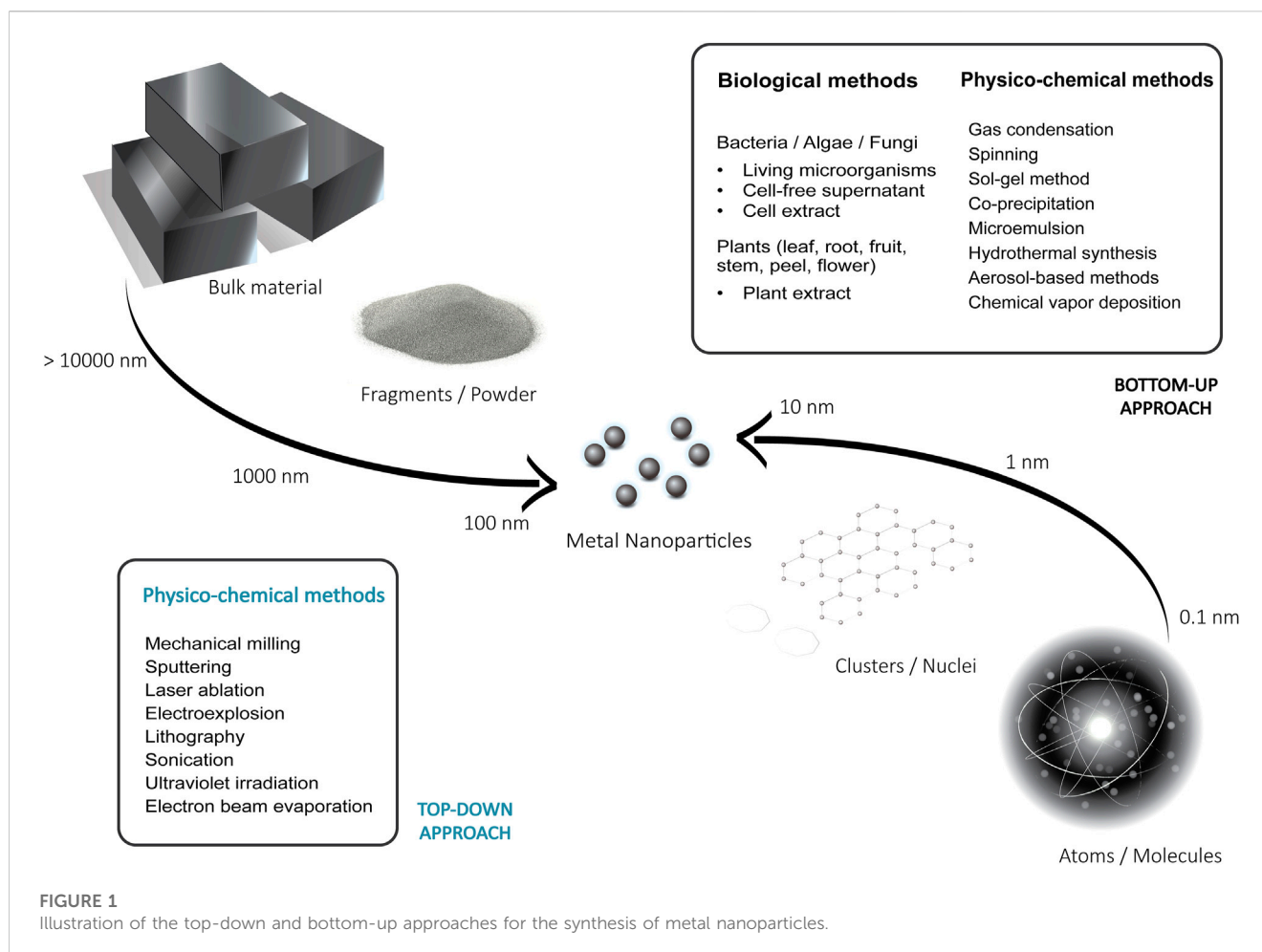
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1 Introduction

Nanoparticles (NPs) are defined as nano-structures with dimensions of 1–100 nm that can be comprised of a variety of materials such as carbon, metal, or organic substances. At the limits of this dimensions in the range of 1–10 nm, some literature may also referred to them as nanoclusters which are typically composed of up to 100 atoms and possess relevant physicochemical properties (Jimenez-Sandoval et al., 2023). Metal-based nanoparticles (MNPs) contain at least one metallic element and can display diverse shapes. Most of them have different properties compared to bulk metals due to their large surface-to-volume ratio, unique electromagnetic behavior, and high catalytic activity (Gao et al., 2021). In this review, a variety of MNPs is described, which not only comprise pure metals nanoparticles (e.g., Au, Ag, Pd, Pt, Fe), but also minerals or metal oxides NPs (e.g., Fe₂O₃, Co₃O₄, TiO₂), metal sulfides (e.g., Fe₃S₄, CdS), doped metal/metal compounds, and metal-organic complexes (Yaqoob et al., 2020).

The unique behavior of nanoparticles and other nanostructured materials is strictly size-dependent and can provide improved functional performance in a variety of technical



applications. Examples of industrial applications of MNPs include their use in chemical catalysis, cosmetics, detergents, water remediation, and even medical applications. The particular electromagnetic properties of Fe-based nanoparticles have secured their place as one of the most frequently used contrast agents in medical imaging (Javed et al., 2017; Makela et al., 2022) while the antibacterial properties of Ag have been effectively enhanced when it is used in the nanoparticle form (Nanda and Saravanan, 2009; Jaidev and Narasimha, 2010; Oves et al., 2019; Das et al., 2020). The large active surface of MNPs makes them highly reactive, and therefore, nanoparticles based on Ag, Ni, Pt, Pd, and others, are distinctly effective in heterogeneous catalysis (Bogireddy et al., 2016; Weng et al., 2017; Stephen et al., 2019; Krebsz et al., 2021). Pd nanoparticles are an example of an efficient catalyst of Suzuki-Miyaura reactions, in which carbon-carbon single bonds are formed to produce a complex variety of molecules that are especially important for the pharmaceutical industry (Søbjerg et al., 2009). Other useful potential applications include the degradation of a variety of toxic Azo dyes present in the wastewater produced by the textile industries (Bogireddy et al., 2016; Narasaiah and Mandal, 2020; Krebsz et al., 2021), and their use in anticancer treatments (Patil et al., 2022).

The targeted production of nanoparticles with specific properties such as defined shapes or size distributions requires strict control of the experimental conditions. Small changes in

the production process can have a strong effect on the size, crystallinity, porosity, roughness, and the shape of the produced nanoparticles (Vijayakumar et al., 2013; Jamkhande et al., 2019). Current methods for MNP synthesis are based on different chemical, physical, or biological methods, which can be classified into two major categories: (a) top-down and (b) bottom-up approaches (Figure 1). The preferred approach is dependent on the desired particles characteristics, the size of production, cost of operation, and the applications intended for the produced nanoparticles (de Jesus et al., 2021).

Top-down methods involve physical or chemical processes that aim to reduce or decompose large substrates or bulk materials. Preparation of MNPs by these methods allows the large-scale production of the high purity nanoparticles, which is crucial for many applications. It includes methods such as mechanical milling (Shojaei et al., 2021), sputtering (Orozco-Montes et al., 2021), chemical etching (Butterfield et al., 2020), laser ablation (Menazea, 2020), electroexplosion (Lozhkomoev et al., 2021), lithography (Fu et al., 2018), sonication (Tang et al., 2019), ultraviolet irradiation (Henglein, 1999), and electron beam evaporation (Nomoiev and Bardakhanov, 2012). Traditional top-down methods can produce particles with well-controlled shapes and uniform sizes, however, they usually require specialized fabrication facilities, large amounts of energy, produce hazardous waste and entail high production costs (Fu et al., 2018). Additionally,

most of them are not suitable for the preparation of extremely small-sized nanoparticles (<10 nm) (Fu et al., 2018; Jamkhande et al., 2019).

In the bottom-up approaches, dissolved or evaporated substances are used as the basis for growth and synthesis of the particles. Using a variety of chemical reactions and physical processes, the building blocks are assembled by controlled precipitation, crystallization and condensation with a low energy input to result in the nanoparticles (Chan and Kwok, 2011). These bottom-up approaches are widely used, as they tend to be more accessible and cheaper compared to the top-down methods. Among them are gas condensation (Zheng and Branicio, 2020), spinning (Stoller and Ochando-Pulido, 2020), sol-gel method (Parashar et al., 2020), co-precipitation (Andrade Neto et al., 2020), microemulsion technique (Mangaiyarkarasi et al., 2020), hydrothermal synthesis (Vinay et al., 2020), aerosol-based methods (Quintanilla et al., 2010; Yang et al., 2020; Gautam et al., 2021), plasma arcing (Tavares et al., 2008), and chemical vapor deposition (Katsui and Goto, 2021). Frequently, they are referred to as wet methods since most of them involve solvents, stabilizers, reducing agents and other chemicals. Nanomaterials produced by these methods often must be capped to restrict the particle growth and to obtain homogeneous nanoparticle populations. Capping agents are stabilization molecules widely employed to control the material's particle size, agglomeration, and morphology. They attach to the surface of the nanoparticle and reduce the surface energy, which has a direct effect on the dispersion of the NPs in wet media. Examples include gums, cationic surfactants, polymers, and plant extracts (Restrepo and Villa, 2021). The toxicity of some of the capping agents and other chemicals involved in this process has proven to be an important disadvantage of the techniques, along with the lack of precise control of particle shape, size and dispersity (Fu et al., 2018). As an alternative, bio-based methods have received increasing attention, as they promise a more reliable, non-toxic and eco-friendly synthesis of MNPs (Iravani, 2014).

The production of metal nanoparticles using biological methods belongs to the bottom-up approaches. A great variety of organisms such as plants, bacteria, fungi, and algae have been explored for their potential to synthesize for example silver, gold, iron, palladium, selenium, zinc, and platinum-based nanoparticles (Iravani, 2014; Ahmad et al., 2019; Li et al., 2021; Li et al., 2022). In addition, not only living organisms, but also many chemical substances derived from the metabolism of microbes and plants, such as biopolymers and biological extracts have been proposed as agents for the biological synthesis of MNPs (de Jesus et al., 2021; Soni et al., 2021). The natural reduction and stabilization agents in these reactions result in a potentially more sustainable synthesis compared to current chemical and physical methods. In general, these biological methods are considered to be more inexpensive, non-toxic, and environmentally benign as most reactions occur at room temperature and with a low energy input (Prasad et al., 2021). However, it is pertinent to note that these bio-nanoparticles tend to be polydisperse and difficult to purify. Some of the most significant challenges of nanoparticle biosynthesis include the control of size distribution and dispersity. In addition, it is important to understand the pathways of reduction that may lead to efficient nanoparticle production, and to develop suitable purification protocols (Khalil et al., 2022).

Reports on the synthesis of nanoparticles with bacteria can be categorized into three main methodologies, where NP production is mediated by intact living cells, by bacterial cell-free supernatants, or by cell lysate supernatants (cell extracts). In contrast to NPs formed by intact bacterial cells, supernatant-based synthesis has the advantage of a simpler downstream purification, characterization, and easy visualization of the produced NPs. Most importantly, this biosynthesis is not directly mediated by the metabolic processes of the bacteria, but only by the functional groups of the bacterial proteins or other biomolecules present in the reaction mixture and can be more directly influenced by the experimental conditions. Nanoparticles produced by biological methods are usually capped with non-toxic biomolecule coatings. These bio-coatings can enhance bio-compatibility of the particles e.g., in medical applications, and can also work as stabilizers that promote the formation of homogeneous small-size nanoparticles by preventing their aggregation (Ahmad et al., 2019). An example is the reduced toxicity of iron oxide nanoparticles by the addition of a biocompatible coating of polysaccharides that enables targeted delivery of materials for cancer therapy (Kianpour et al., 2019). The biological synthesis of metal nanoparticles has many potential uses not only in biomedical applications, but also in bioremediation, bioleaching, and biocorrosion (Narayanan and Sakthivel, 2010).

This review provides a comprehensive description of the biological synthesis of metal nanoparticles by bacteria, both in nature and in technical processes. We focus not only on the general interaction of metal ions with bacteria, but also include the findings on the pathways that lead to their reduction and subsequent nanoparticle formation. Examples of recent advances in MNP synthesis using different bacterial strains are presented and their potential applications are reviewed. Finally, the current challenges of the industrial production of metal nanoparticles by bacteria are discussed.

2 Bacteria-metal interactions

Bacteria have ubiquitous interactions with metals. They can be classified into the homeostasis of essential metals, and (heavy) metal resistance to harmful metals. Some metals are important as micronutrients whereas other (heavy) metals (such as Al, Pd, Cd, Au, Hg, Ag) are toxic to living organisms and do not have specific biological roles (Igiri et al., 2018). The essential metals are nutrients and trace elements for key metabolic processes, such as metals in the bacterial respiratory chain. Therefore, microbes have developed a variety of often highly specific mechanisms for metal transport, oxidation/reduction, or detoxification. Nevertheless, the unintentional uptake of high concentrations of metal ions or toxic heavy metals can occur, and microorganisms have developed different strategies to cope with heavy metal stress. Microbial populations can survive in metal-polluted locations by, directly or indirectly, modifying the metal availability through physical or biochemical mechanisms to protect their integrity (Iravani, 2014). The complex mechanisms developed by different species and strains vary and depend both on the native environment and on the heavy metal content. The basic mechanisms of bacteria-metal interactions can be divided into the following four categories:

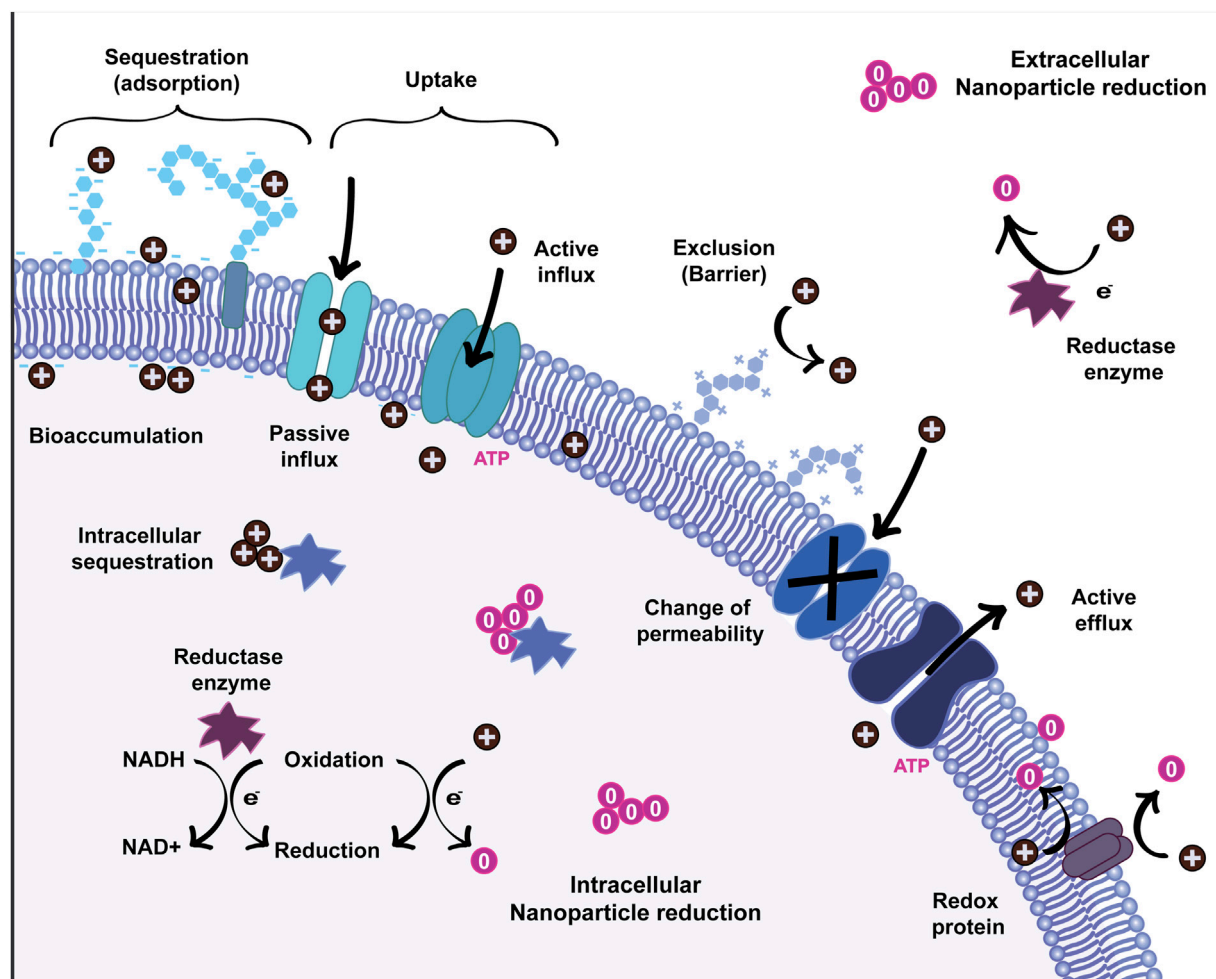


FIGURE 2 Schematics of bacteria interaction with heavy metals and mechanisms of nanoparticle formation.

2.1 Metal sequestration

Many essential biological processes involve metal ions, and in particular, redox active transition metals like manganese, iron, cobalt, copper and magnesium. For instance, divalent ions such as Mn^{2+} and Fe^{2+} , are indispensable for oxidative stress resistance or as cofactors for the respiratory chain in bacterial core metabolism (Palmer and Skaar, 2016). Hence, microorganisms have evolved pathways of metal sequestration to transport ions and to regulate ion availability. In the simplest case, the sequestration of metal ions occurs by adsorption. In Figure 2, metal ions are depicted as positively charged entities interacting with the bacterial membrane and other biomolecules. During adsorption, deprotonated functional groups (carboxyl, phosphonate, amine, and hydroxyl groups) on the cell surface result in a net negative charge which attracts metal cations and leads to non-specific binding of the metal to the cell surface (Saravanan et al., 2021). This process is independent of the cell metabolism, and it is mainly influenced by factors such as temperature, pH, ionic strength, concentration and by the complex composition of the microorganism's surface. As an example, Gram-positive bacteria

expose a large amounts of carboxyl groups in their peptidoglycan-rich cell walls, making them efficient metal chelators (Pham et al., 2022). As a consequence of this sequestration, these metals are enriched on the cell surface and can be taken up by specific transport processes (discussed below).

However, the extracellular sequestration of heavy metals not only allows to accumulate relevant metabolic cofactors, it is also a defense mechanism against toxic metals, by reducing the availability of unwanted metal ions. Polymers secreted by bacteria such as the exopolysaccharide (EPS) coatings of some species, have the ability to adsorb and bind metals extracellularly, thus acting as a protective layer that prevents the uptake of toxic metals (Bruins et al., 2000). Bacteria are likely to sequester non-essential metal ions, such as Au and Pd, by adsorption mechanisms. Compared to other microorganisms, Gram-negative bacteria such as *Acinetobacter calcoaceticus*, *Erwinia herbicola*, *Pseudomonas maltophilia* and *Pseudomonas aeruginosa* have the highest ability to accumulate metals such as gold (Tsuruta, 2004). This is a result of the surface charge present on the Gram-negative bacterial membrane, which promotes the gold adsorption from aqueous solutions. In the same way, the biosorption of Pd is presumably a result of the

chemical affinity of metal complexes such as $[\text{PdCl}_4]^{2-}$ for protonated groups on the cell surface at an acidic pH (Deplanche et al., 2010).

Free metal ions passively or actively transported from outside of the membrane into the cytoplasm can pose a danger to the cell and must be immobilized or transformed. Bacteria can produce metabolites, like metallothioneins, phytochelatins and glutathione with high affinity for metals for the intracellular sequestration of metal ions. Metallothioneins are small, cysteine-rich proteins that are directly involved in the homeostasis of different metal ions, including Cu^+ and Zn^{2+} . These proteins have been reported in bacteria such as *Bacillus altitudinis* MT422188 and *Mycobacterium tuberculosis* where they are expressed under Zn^{2+} and Cu^+ induced stress, respectively (Johnstone and Nolan, 2015; Khan et al., 2022). The immobilization of the ions decreases the toxicity; however, the metal sequestration mechanisms are limited by the saturation of the binding sites in the extracellular and intracellular matrix (Bruins et al., 2000).

2.2 Metal uptake

The metal ions in proximity to the extracellular layers can be imported by passive or active influx through the different layers of the cell wall, using non-specific transporters, metal-specific channels or passive diffusion (Figure 2) (Bruins et al., 2000). The indispensable uptake of essential metals is highly regulated and typically mediated by specific, energy-dependent uptake systems. In *E. coli*, *Alcaligenes eutrophus* and many other enterobacteria, essential trace elements such as Ni^{2+} , Co^{2+} , and Zn^{2+} ions are transported into the cell by constitutive Mg^{2+} transport systems (Nies, 1992; Komeda et al., 1997). These relatively unspecific uptake systems allow the “cost-effective” accumulation of macronutrients such as Mg and of trace metal ions in environments with habitual metal concentrations. In extreme conditions, with deficits in trace metals, bacteria can upregulate genes related to specific, ATP-dependent uptake systems for these elements in order to transport the ions against the concentration gradient. The TonB-dependent transporter, OprC, is repressed in *P. aeruginosa* by high exogenous Cu ion concentrations and expressed in anaerobic conditions to bind and transport $\text{Cu}^{+/2+}$ (Bhamidimarri et al., 2021). In environments with low availability of essential metals, many bacteria also secrete metal-sequestering proteins or other chelators to bind the biologically relevant ions and to specifically import them (Palmer and Skaar, 2016). An example of this mechanism are iron siderophores, which are low molecular weight compounds known for their high affinity for Fe ions. Siderophores are frequently used by pathogenic bacteria to chelate Fe^{2+} and Fe^{3+} in host environments that are otherwise deprived of free Fe ions (Johnstone and Nolan, 2015). The siderophores with bound ions are then recognized by specific outer membrane receptors that guide the chelated ions through energy-dependent ATP-binding cassette (ABC) transporters (Krewulak and Vogel, 2008; Ma et al., 2009). Because of the different chemical properties of Fe^{3+} and Fe^{2+} , bacteria utilize different specific transport systems (and siderophores) for each ion (Lau et al., 2016; Crespo et al., 2017). Examples of different transport systems involved in bacterial Fe uptake, include MntH, ZupT, YfeABCD, FutABC, EfeUOB and Feo (Lau et al., 2016).

The uptake of precious metals like Au, Ag, Pt, and Pd ions into bacteria is not well understood, as cells do not possess inherent active, specific transport mechanisms to regulate non-essential ion uptake. The absorption of toxic heavy metals is presumably a process carried out by passive mechanisms such as diffusion. Therefore, at elevated concentrations, non-essential metals can interact with the cell, cross into the cytoplasm and accumulate there (Lusa et al., 2016). However, some authors suggest that heavy metals like Pd may also accidentally be absorbed and imported into living cells through systems specific for essential metallic metabolites, such as Fe, Ni, Cu or Zn (Omajali et al., 2015). Metal ions with comparable properties and ion radius, due to their similar conformations, can out-compete essential ions in binding to proteins. As an example, the high affinity of Hg and Cd ions to cysteine-rich sites in Zn-binding proteins results in translocation of these toxic metals. A similar effect is found in Cu-binding proteins with Au and Ag as competing metal ions (Waldron and Robinson, 2009). A special case of non-essential metal uptake is the homeostasis mechanism of specialized metal-resistant bacterial strains for some toxic heavy metal ions. In the case of *Cupriavidus metallidurans*, genes in the *gig* (gold-induced genes) operon are strongly upregulated after sequestration of Au ions in the membrane. The proteins encoded by this operon are suggested to be directly involved in the import of Au ions into the cytoplasm to prevent the harmful action of Au^{3+} in the periplasm. The reduced complexes there are later removed from the cytoplasm (Wiesemann et al., 2013; Zammit and Reith, 2013).

2.3 Metal detoxification

If not regulated, high concentrations of metals would have adverse effects in the metabolic processes of the cell. In metals such as Cu, their redox activity favors the formation of active oxygen species, which explains their toxicity. Excess of essential metals or toxic, non-essential heavy metals also leads to mismetallation of proteins which results in their inactivation (Andrei et al., 2020). The exposure to high concentrations of heavy metals activates a mechanism of defense called metal exclusion, in which the permeability of the cell membrane, the envelope, or the surface layer is modified to prevent or reduce the further influx of metal ions (Figure 2). Bacteria can alter the composition of the cell wall in an attempt to form a barrier for ions. A well-known example of this mechanism is the reduction of the expression of Porin channels in heavy-metal resistant mutants of *E. coli*. In this case, pore proteins such as OmpF are expressed at a reduced rate, leading to increased Cu and Ag resistance (Lutkenhaus, 1977; Rouch et al., 1995; Li et al., 1997). In a complementary mechanism, the active efflux of metal ions involves the use of highly specific membrane transport systems. This process to decrease the concentration of harmful metal ions inside the cell is wide-spread among bacteria. The transport of cations and anions from the cytoplasm against a concentration gradient requires energy. The involved efflux pumps can be broadly classified by their energy source into ATP-dependent and proton-gradient-based systems. Further classifications are based on sequence similarity, transport function and substrate specificity (Nies and Silver, 1995; Hynninen, 2010; Delmar et al., 2014).

TABLE 1 List of relevant standard reduction potential (E_0) in respect to the standard hydrogen electrode at 298.15 K (25°C), 101.325 kPa (1 atm). The list is in alphabetical order, according to the symbol of metal element. Taken from Haynes, (2014).

Reaction	E_0 (Volts)
$Ag^+ + e \rightleftharpoons Ag$	0.7996
$AuCl_4^- + 3 e \rightleftharpoons Au + 4 Cl^-$	1.0020
$Cd^{2+} + 2 e \rightleftharpoons Cd$	-0.4030
$Co^{2+} + 2 e \rightleftharpoons Co$	-0.2800
$Co^{3+} + e \rightleftharpoons Co^{2+}$	1.9200
$Cr^{2+} + 2 e \rightleftharpoons Cr$	-0.9130
$Cr^{3+} + e \rightleftharpoons Cr^{2+}$	-0.4070
$Cr^{3+} + 3 e \rightleftharpoons Cr$	-0.7440
$Cr_2O_7^{2-} + 14 H^+ + 6 e \rightleftharpoons 2 Cr^{3+} + 7 H_2O$	1.3600
$Fe^{2+} + 2 e \rightleftharpoons Fe$	-0.4470
$Fe^{3+} + 3 e \rightleftharpoons Fe$	-0.0370
$Fe^{3+} + e \rightleftharpoons Fe^{2+}$	0.7710
$2 HFeO_4^- + 8 H^+ + 6 e \rightleftharpoons Fe_2O_3 + 5 H_2O$	2.0900
$Mn^{2+} + 2 e \rightleftharpoons Mn$	-1.1850
$Mn^{3+} + e \rightleftharpoons Mn^{2+}$	1.5415
$MnO_2 + 4H^+ + 2 e \rightleftharpoons Mn^{2+} + 2 H_2O$	1.224
$Ni^{2+} + 2 e \rightleftharpoons Ni$	-0.2570
$[PdCl_4]^{2-} + 2 e \rightleftharpoons Pd + 4 Cl^-$	0.5910
$[PdCl_6]^{2-} + 2 e \rightleftharpoons [PdCl_4]^{2-} + 2 Cl^-$	1.2880
$[PtCl_4]^{2-} + 2 e \rightleftharpoons Pt + 4 Cl^-$	0.7550
$[PtCl_6]^{2-} + 2 e \rightleftharpoons [PtCl_4]^{2-} + 2 Cl^-$	0.6800
$TcO_4^- + 8 H^+ + 7 e \rightleftharpoons Tc + 4 H_2O$	0.4720
$Ti^{2+} + 2 e \rightleftharpoons Ti$	-1.6280
$UO_2^{2+} + 4 H^+ + 6 e \rightleftharpoons U + 2 H_2O$	-1.4440
$Zn^{2+} + 2 e \rightleftharpoons Zn$	-0.7618

Some examples of well-studied heavy metal efflux pumps are the P-type ATPase transport protein CopA, known to be involved in copper resistance (Rensing et al., 2000) and the resistance-nodulation-cell division (RND) family proteins, CzcA and CusA, which bind and export Cu^+ and Ag^+ in *E. coli* (Kim et al., 2011). In partly silver-resistant *E. coli* bacteria, the detoxification mechanism for silver is based on the expression of the CusCFBA copper/silver efflux systems that actively export the silver ions from the cytoplasm and bind it in the periplasm (Lin et al., 2014). In some bacteria, metal ions transported by efflux pumps may be retained in the periplasm even after the efflux process, along with the metal ions sequestered by EPSs and by other metal-binding proteins (Blindauer, 2011). The ions bioaccumulated in the cytoplasm, periplasm and in the extracellular matrix can later become sites for nucleation and formation of nanoparticles (Figure 2).

2.4 Metal transformation

Some microorganisms have a remarkable ability to transform heavy metal ions in their environment and to produce MNPs. Even when sequestered, the high reactivity of transition metal ions could disrupt metabolic processes or damage DNA molecules. Various metal ions have a high binding affinity for biological macromolecules such as nucleic acids, or thiol-containing proteins (Delmar et al., 2014; Boedicker et al., 2021), and therefore, they need to be transformed into inert or less toxic substances. This is mediated by redox-active metabolic pathways in order to change solubility and toxicity, and often leads to complexation or precipitation of metals extracellularly (Silver, 1996; Bruins et al., 2000; Hood and Skaar, 2012). Alternatively, biomethylation is a metabolic process in which methyl groups are transferred to the toxic metal ions or metalloids to create less toxic, sometimes volatile compounds. Hg, Sn, As, Se, Te, Au, Tl, and Pb have been reported as methyl group acceptors in primary and secondary metabolic processes (Kosolapov et al., 2004). The resulting products are more toxic than the inorganic compounds in many cases, so it is debatable whether methylation is, in fact, a detoxification mechanism. However, it is important to note that the volatility has an important effect on reducing the concentration of the metals in the surrounding environment. Extended descriptions of the general pathways for biomethylation can be found elsewhere (Ridley et al., 1977a; Ridley et al., 1977b; Fatoki, 1997).

Some bacteria can decrease the mobility of metal ions through enzymatically promoted redox reactions that reduce the metals irreversibly, leading to the assembly into metal clusters. An illustration of the general process of reduction of the metal ions to neutral ions by redox proteins intra- and extracellularly can be found in Figure 2. The electron-accepting potential of different metal ions known to be reduced by bacteria are shown in Table 1. The reduction potential is expressed as the E_0 value, ranging from very negative E_0 values for compounds that are easily oxidized, to large positive E_0 values for compounds that readily accept electrons (are easily reduced). “Precious” metals such as Au, Pd or Ag have cations species with very positive potentials and are frequently reduced into nanoparticles by bacteria.

The cornerstone of every living organism is energy conservation where chemical or light energy is ultimately converted into adenosine triphosphate (ATP). ATP production is facilitated by substrate-level phosphorylation, oxidative phosphorylation, or photophosphorylation. In order to achieve this, electrons need to be transferred in an oxidation-reduction coupled reaction. This electron movement within the cell is facilitated by electron carriers, such as nicotinamide adenine dinucleotide (NAD^+ /NADH), which promotes a diversity of reduction-oxidation reactions as they allow a variety of electron partners to interact with each other (Muller, 2003; Herrmann et al., 2008; Schuchmann and Müller, 2012). It is these metabolic reactions and electron carriers that are diverted and used for metal ion reduction.

On an extracellular level, bacterial growth is heavily influenced by the oxidation-reduction (redox) potential of the environment, and in turn, bacteria can modify the redox potential of their environment. Surprisingly, this ability is highly species-specific and can be exploited to identify different species by using redox

electrodes (Reichart et al., 2007). A change in redox potential indicates the availability of electron acceptors and donors. Since bacteria can inhabit every niche that can support life, their diversity is also manifested in the type of electron acceptors that they can utilize intracellularly. Under aerobic respiration conditions, oxygen is the final electron acceptor while under anaerobic respiration conditions, a variety of electron acceptors can be utilized, such as nitrate (NO^3), trimethylamine oxide/dimethyl sulfoxide (TMAO/DMSO), carbon dioxide (CO_2) or organic electron acceptors such as fumarate, depending on the bacterial species studied (Kröger et al., 1992; Vincent et al., 2021). Metal-based respiration is characterized by the utilization of manganic manganese (Mn^{4+}) or ferric iron (Fe^{3+}) as electron acceptors. Bacteria can reduce these metal compounds through mechanisms that involve redox-active proteins like reductases, cytochromes, and metallothioneins (Bloch et al., 2021).

Sulfate- and metal-reducing bacteria are frequently employed for the synthesis of metal nanoparticles, as these organisms are rich in membrane redox-active proteins and therefore easily enzymatically reduce different metal ions. These ‘reducing’ microorganisms can use the metal cations as terminal electron acceptors while performing anaerobic respiration, reducing Fe^{3+} to Fe^{2+} and Mn^{4+} to Mn^{2+} for energy conservation (Lloyd, 2003). These proteins however, are not necessarily highly specific and multiple enzymes are capable of reducing several redox-active metals ions (Barton and Fauque, 2009). The interaction of some bacteria with non-essential, toxic metal ions such as Au^{3+} , Ag^+ , Pd^{2+} and Pt^{2+} also upregulates the expression of multiple redox-active enzymes located on the cell walls, in periplasmic space and intracellular contents, such as hydrogenases and NADH reductases, which can reduce ions to insoluble complexes that are subsequently transformed into MNPs (Omajali et al., 2015; Chen et al., 2019). One example is nitrate reductase known to be involved in the bioreduction of the bound Ag^+ to Ag^0 in *Bacillus licheniformis* as defense from heavy metals exposure (Kalimuthu et al., 2008; Rajora et al., 2016). As suggested by their negative reduction potential (Table 1), the NAD(P)H-dependent reduction of ions such as Cd^{2+} , Zn^{2+} , Co^{2+} or Ni^{2+} to metallic form may not be energetically favored, so the reduction of these ions is uncommon in bacteria and the particular cases of reduction must involve different mechanisms (Nies, 1992). In *Shewanella* strains, EPS-induced reduction and indirect electron transfer using electron shuttles such as flavins, L-cysteine, and quinones are possible alternative pathways that have been thoroughly described elsewhere (Yang et al., 2023). Metal NPs reduced and precipitated in the extracellular and intracellular space may possess different characteristics than their chemically produced counterparts. The biomolecules associated with them create a biological cap that stops nanoparticle growth, minimizes cytotoxicity, and may affect their chemical and physical properties (Bulgarini et al., 2021). The reduced metal particles accumulate without much effect on the cell population. Therefore, the formation of MNPs can be regarded as a by-product of microbial defense mechanisms, of bacterial metabolism, or as a biomineralization process intended to control, immobilize, or decrease the heavy metal bioavailability.

3 Bacterial synthesis of nanoparticles

During the microbial reduction of metals into MNPs, cations are transformed into ions with a lower valence. A special case is the precious metals, including Pd, Pt, Au, and Ag, that are easily reduced into elementary forms (Zhan et al., 2012). The challenge of producing nanoparticles using bacteria, is identifying the exact chemical components and mechanisms involved in nanoparticle formation. The pathways may result in nanoparticles formed only extracellularly, intracellularly, or both, and there is a debate about which method is the most efficient for production of NPs in industrial processes. The intracellular nanoparticles formed in living cells are attached to the biological material, making their purification difficult; however, capping of the nanoparticles provides better control of their size, generating more homogeneous populations of biocompatible nanoparticles with interesting novel physical and chemical properties. In contrast, nanoparticles produced externally are preferred in many cases due to their faster production, facile recovery, and simple purification. These extracellular nanoparticles can be produced using bacterial cell-free supernatants, cell lysate supernatants, and some living bacterial strains. In this section, examples of relevant metal-based nanoparticles produced by bacteria are described.

3.1 Bacterial metal nanoparticles in nature

Even though naturally occurring nanoparticles are widely found in living organisms, the intracellular accumulation of solid metals is usually not a favorable condition for the cells and can lead to cell death. A complete metal particle detoxification would require energy and elaborated mechanisms of particle excretion (Griffin et al., 2017). This is probably the reason why only few bacterial species produce metal-based nanoparticles as part of their normal metabolic processes. The most remarkable example are magnetotactic bacteria, an extraordinary group of Gram-negative organisms that rely on biosynthetic iron-based crystals to orient and migrate along the geomagnetic field lines in a behavior known as “magnetotaxis” (Yan et al., 2012). The highly specialized organelles made of nanometer-sized metal crystals wrapped in a membrane are called magnetosomes. They are composed of magnetic iron oxide magnetite (Fe_3O_4) or iron sulfide greigite (Fe_3S_4) of different shapes and sizes depending on the exact bacterial species. The magnetosomes are frequently aligned in chains across the motility axis of the cell. This imparts the bacteria with a permanent magnetic dipole moment, causing them to align passively in a parallel orientation with external magnetic fields (Monteil and Lefevre, 2020). The cells swim along the geomagnetic field lines of the Earth to the oxic-anoxic interface of the aquatic habitat where are the most favorable conditions for growth (Le Nagard et al., 2018).

Despite the abundance of magnetotactic bacteria in the environment, only a few strains have been isolated into pure culture due to their particular growth requirements. Strains from the proteobacterial genus *Magnetospirillum* are the most common isolates. However, recent publications report up to 16 different lineages that include *Proteobacteria*, *Nitrospirota*, and *Omnitrophota* (Gareev et al., 2021; Goswami et al., 2022). The

strains *Magnetospirillum gryphiswaldense* MSR-1 [first isolated in 1991 by Schleifer *et al.* (Schleifer *et al.*, 1991)], *Magnetospirillum magnetotacticum* strain MS-1 and *Magnetospirillum magneticum* AMB-1, are currently the most studied bacteria for the understanding of magnetosome formation and its complex genetic regulation (Nudelman and Zarivach, 2014). In *M. gryphiswaldense* MSR-1, the magnetosome island (MAI) comprises most of the genes that control the magnetosome synthesis. These genes encode all the essential processes in the major steps of the organelle formation and determine the morphology and chemical composition of the particles (Uzun *et al.*, 2020; Dziuba *et al.*, 2021). In the past, different models of magnetosome biomineralization have been proposed (Schuler, 2002; Yan *et al.*, 2012; Nudelman and Zarivach, 2014). Currently, four major steps are considered necessary to achieve the biomineralization. The first step is i) the cytoplasmic membrane invagination into vesicles, followed by ii) the arrangement of specific magnetosome proteins into the organelle membrane. Then, iii) the internalization and accumulation of iron into the vesicles by energy-dependent transport proteins takes place. Here, the cell rapidly chemically transforms the Fe ions and combines them into metal crystals. Specific proteins guide this process in order to avoid the toxic effect of intracellular Fe. Finally, iv) the magnetosomes are assembled into a linear chain along cytoskeletal filaments (Dziuba *et al.*, 2021).

The bacteria tightly controls the size and morphology of the magnetosomes. Magnetosome crystals typically fall in a size distribution of about 30–120 nm. However, some species can form particles up to 250 nm in length (Yan *et al.*, 2012). The spirillum-shaped bacterium *M. magneticum* AMB-1, originally collected from fresh water sediments of a natural spring in Tokyo, presents magnetite magnetosomes with an average diameter of 50 nm, aligned in chains of around 15 particles per cell (Matsunaga *et al.*, 1991). In contrast, the *M. gryphiswaldense* MSR-1 bacteria were found to produce chains of up to 60 homogeneous magnetosomes with particle sizes of around 42 nm (Schuler, 2002). Both strains, like other bacteria from the *Magnetospirillum* genus, produce cubo-octahedral crystalline magnetosomes. In general, three different morphologies of magnetosomes can be found in nature: i) cubic or cubo-octahedral, ii) elongated hexa- or octahedral and iii) even more elongated crystals with large, anisotropic faces, showing tooth, arrowhead, or bullet shapes (Cypriano *et al.*, 2022). These crystal structures are consistently replicated in the magnetosomes of bacteria of the same strain and have a direct influence on the final magnetic behavior of the particles.

The magnetosomes, due to their narrow size distribution, low aggregation, and strong ferromagnetism, have many potential technical applications. The low toxicity of bacterial magnetosomes in comparison with synthetic magnetic nanoparticles makes them especially attractive for biomedical applications. Cytotoxicity of bacterial magnetosomes varies depending on various factors, including cell type, incubation time, and concentration. While many types of magnetite nanoparticles [such as Superparamagnetic iron oxide nanoparticles (SPION)] are considered cytotoxic at exposure levels above 70–100 µg/ml (Alphandéry, 2014; Singh *et al.*, 2010; Toropova *et al.*, 2017), a study by Alphandéry *et al.* in

MDA-MB-231 cells suggested low cytotoxicity due to magnetosome exposure at concentrations below 1,000 µg/ml which can be further improved by removing bacterial endotoxins and using biocoatings (Alphandéry *et al.*, 2011; Gareev *et al.*, 2021). In a recent study, Gwisai *et al.* evaluated the use of the ferromagnetic properties of AMB-1 bacterial magnetosomes for targeted cancer therapy. Thanks to their susceptibility to external magnetic fields, magnetotactic bacterial cells were magnetically manipulated and studied as a vehicle for tumor infiltration and drug delivery (Gwisai *et al.*, 2022). In a similar approach, Xing *et al.* successfully demonstrated the colonization and ablation of tumors in mice by means of *in vivo* magnetically manipulated *M. magneticum* AMB-1 bacteria, showing their enormous potential for an efficient cancer treatment (Xing *et al.*, 2021). Other potential application of magnetosomes include their use as magnetic resonance contrast agents. *In vivo* experiments were conducted on mice to examine how magnetosomes were distributed and eliminated after injection as a contrast agent in magnetic resonance imaging (MRI). The researchers concluded that their use in MRI was adequate in terms of spatial resolution and sensitivity (Nan *et al.*, 2021).

Microorganisms play an important role in the process of biomineralization and metal geochemistry. The metals transformation into nanoparticles is also a natural process observed in some astounding microorganisms known as dissimilatory metal-reducing bacteria. In anoxic environments with abundant metal species such as Fe³⁺, Mn^{3+/4+}, U⁶⁺, Cr⁶⁺, Co³⁺ and Tc⁷⁺, these metal cations are reduced into nanoparticles by the bacteria (Lovley, 1993; Shi *et al.*, 2016). All these elements have in common that they are good electron acceptors due to their high reduction potential. Then, during anaerobic respiration, the bacteria can replace oxygen as the terminal electron acceptor with the available cations. Fe³⁺ is the most abundant possible electron acceptor in anoxic environments. Due to its comparatively high reactivity with oxygen, elemental Fe is not frequently found in nature, but instead, is commonly found in the form of iron oxides. In metal- and sulfur-reducing microorganisms like, *Geobacter sulfurreducens*, *Geobacter metallireducens* GS15 and *Shewanella oneidensis* MRI, specialized membrane proteins are suggested to be involved in the Fe³⁺ reduction. Their outer membranes are rich in c-type cytochromes that transfer electrons coupled to the oxidation of lactate and other carbon sources to soluble Fe³⁺ oxides resulting in iron oxide NPs (Lovley *et al.*, 1993; Mehta *et al.*, 2005; Shi *et al.*, 2012). Many Fe-based NPs naturally synthesized by bacteria consist of diverse compositions of iron oxides. The metal-based anaerobic mechanism of respiration is considered part of the natural cycle of precipitation of many heavy metals into anoxic sediments (Lovley, 1993). Multiple processes of bioremediation of heavy metals from the environment and contaminated water streams have been engineered based on the reducing ability of these bacteria (Iravani and Varma, 2020). Other transition metals such as gold, silver, and copper have high positive reduction potentials and are exchanged with iron. Bacteria readily precipitate them during remediation, which can then be applied to the biogenic production of these metal nanoparticles.

TABLE 2 Bacteria-mediated metal-based nanoparticles reported in the literature.

Metal	Name of organism	NP	Size	Morphology	Localization	References
Au	<i>Bifidobacterium lactis</i>	Au	5–40 nm	Hexagonal	Intracellular	Chen et al. (2021)
	<i>Bacillus cereus</i>	Au	20–50 nm	Spherical/Hexagonal/Octagonal	Extracellular	Pourali et al. (2017)
	<i>Bacillus Licheniformis</i>	Au	60–146 nm	Spherical	Intracellular	Tikariha et al. (2017)
	<i>Caldicellulosiruptor changbaiensis</i> CBS-Z	Au	1–20 nm	----	Membrane	Bing et al. (2018)
	<i>Escherichia coli</i>	Au	6–60 nm	Spherical	Extracellular	Chen et al. (2021)
	<i>Lactobacillus casei</i>	Au	7–56 nm	----	Membrane	Kikuchi et al. (2016)
	<i>Marinobacter pelagius</i> RS11	Au	2–10 nm	Spherical/Triangular	----	Sharma et al. (2012)
	<i>Paracoccus haeundaensis</i> BC74171	Au	15–35 nm	Spherical	Extracellular	Patil et al. (2019)
	<i>Pseudomonas stutzeri</i> KDP_M2	Au	10–20 nm	Spherical	----	Desai et al. (2021)
	<i>Sporosarcina koreensis</i> DC4	Au	92 nm	Spherical	Extracellular	Singh et al. (2016)
	<i>Vibrio alginolyticus</i>	Au	100–150 nm	Anisotropic	----	Shunmugam et al. (2021)
Ag	<i>Aeromonas</i> THG-FG1.2	Ag	8–16 nm	Spherical	Supernatant	Singh et al. (2017)
	<i>Bacillus brevis</i>	Ag	22–60 nm	Spherical	Supernatant	Saravanan et al. (2018)
	<i>Bacillus cereus</i>	Ag	5–7 nm	Spherical	----	Ibrahim et al. (2021)
	<i>Bacillus clausii</i>	Ag	30–80 nm	Spherical	Supernatant	Mukherjee et al. (2018)
	<i>Bacillus Pumilus</i> ROM6	Ag	20–70 nm	Spherical	Supernatant	Esmail et al. (2022)
	<i>Escherichia coli</i> 116AR	Ag	5–70 nm	----	Membrane	Lin et al. (2014)
	<i>Escherichia coli</i> Top 10	Ag	2–40 nm	----	Supernatant	Baltazar-Encarnación et al. (2019)
	<i>Lactobacillus Acidophilus</i>	Ag	10–20 nm	Spherical	Supernatant	Abishad et al. (2022)
	<i>Lactobacillus brevis</i>	Ag	30–100 nm	Spherical/Triangular/Hexagonal	Supernatant	Riaz Rajoka et al. (2020)
	<i>Paenarthrobacter nicotinovorans</i> MAHUQ-43	Ag	13–27 nm	Spherical	Supernatant	Huq and Akter (2021)
	<i>Pseudomonas aeruginosa</i>	Ag	25 nm	Spherical	Supernatant	Quinteros et al. (2019)
	<i>Pseudomonas putida</i> MVP2	Ag	6–16 nm	Spherical	Membrane/Supernatant	Gopinath et al. (2017)
	<i>Pseudomonas stutzeri</i>	Ag	22–46 nm	Spherical	Extracellular	Bachii et al. (2021)
	<i>Pseudomonas stutzeri</i>	Ag	10–50 nm	Anisotropic	----	Desai et al. (2020)
<i>Sporosarcina koreensis</i> DC4	Ag	102 nm	Spherical	Extracellular	Singh et al. (2016)	
<i>Stenotrophomonas maltophilia</i>	Ag	93 nm	Cuboidal	Supernatant	Oves et al. (2013)	
Pt	<i>Escherichia coli</i> MC4100	Pt	2.3–4.5 nm	Spherical	----	Attard et al. (2012)
	<i>Pseudomonas kunmingensis</i> ADR19	Pt	3.95 nm	Spherical	Supernatant	Eramabadi et al. (2020)
	<i>Psychrobacter faecalis</i> FZC6	Pt	2.49 nm	Spherical	Supernatant	Eramabadi et al. (2020)
	<i>Vibrio fischeri</i> NRRL B-11177	Pt	3.84 nm	Spherical	Supernatant	Eramabadi et al. (2020)
	<i>Jeotgalicoccus coquinae</i> ZC15	Pt	5.74 nm	Spherical	Supernatant	Eramabadi et al. (2020)
	<i>Sporosarcina psychrophila</i> KC19	Pt	4.24 nm	Spherical	Supernatant	Eramabadi et al. (2020)
	<i>Kocuria rosea</i> MN23	Pt	5.85 nm	Spherical	Supernatant	Eramabadi et al. (2020)
	<i>Pseudomonas putida</i> KT244	Pt	8.06 nm	Spherical	Supernatant	Eramabadi et al. (2020)

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TABLE 2 (Continued) Bacteria-mediated metal-based nanoparticles reported in the literature.

Metal	Name of organism	NP	Size	Morphology	Localization	References
	<i>Acinetobacter calcoaceticus</i>	Pt	2–3.5 nm	Cuboidal	Intracellular/ Membrane	Gaidhani et al. (2014)
Pd	<i>Bacillus benzeovorans</i>	Pd	1.7–5.8 nm	Anisotropic	Intracellular	Omajali et al. (2015)
	<i>Bacillus megaterium</i> Y-4	Pd	10–40 nm	Spherical	Intra/Extracellular	Chen et al. (2019)
	<i>Bacillus wiedmannii</i> MSM	Pd	10–36 nm	----	Membrane	Chen et al. (2018)
	<i>Citrobacter</i> sp.	Pd	11.3–15.6 nm	----	Membrane	Matsena et al. (2020)
	<i>Citrobacter</i> sp.	Pd	17.6–25.8 nm	Anisotropic	Membrane	Matsena and Chirwa (2021)
	<i>Cupriavidus metallidurans</i>	Pd	20–40 nm	Dendrite-Shaped	Intracellular	Tan et al. (2020)
	<i>Desulfovibrio desulfuricans</i>	Pd	3–13 nm	----	Intra/Extracellular	Mikheenko et al. (2022)
	<i>Desulfovibrio desulfuricans</i>	Pd	1.1–6.9 nm	Cubo-octahedron	Intracellular	Omajali et al. (2015)
	<i>Escherichia coli</i> BL21	Pd	2–3 nm	Spherical	Intracellular	Bachar et al. (2020)
	<i>Escherichia coli</i> MC4100	Pd	1–30 nm	Anisotropic	Intracellular/ Membrane	Gomez-Bolivar et al. (2019b)
	<i>Shewanella loihica</i> PV-4	Pd	4–10 nm	Spherical	Intra/Extracellular	Wang et al. (2018)
	<i>Shewanella oneidensis</i> MR-1	Pd	2–12 nm	Spherical	Extracellular	Zhang et al. (2022a)
<i>Shewanella oneidensis</i> MR-1	Pd	2–25 nm	----	Supernatant	Zhang et al. (2022b)	
Fe	<i>Bacillus cereus</i>	Fe ₃ O ₄	18–29 nm	Spherical	Supernatant	Fatemi et al. (2018)
	<i>Bacillus subtilis</i>	Fe ₃ O ₄	60–80 nm	Spherical	Supernatant	Khan et al. (2020)
	<i>Escherichia coli</i>	Fe ₃ O ₄ / Fe ₂ O ₃	18 nm	Spherical	Intra/Extracellular	Crespo et al. (2017)
	<i>Proteus vulgaris</i>	----	20–30 nm	Spherical	Supernatant	Majeed et al. (2021)
	<i>Pseudomonas aeruginosa</i>	Fe ₃ O ₄ / Fe ₂ O ₃	----	----	Extracellular	Crespo et al. (2017)
	<i>Pseudomonas putida</i>	Fe	1–4 nm	Spherical	Intra/Extracellular	Zaki et al. (2021)
Co	<i>Bacillus pasteurii</i>	Co ₃ O ₄	10–31 nm	Anisotropic	----	Hsu et al. (2018)
	<i>Bacillus subtilis</i>	Co ₃ O ₄	31.2 nm	Anisotropic	----	Mubraiz et al. (2021)
	<i>Bacillus subtilis</i>	Co ₃ O ₄	2–5 nm	----	Membrane	Shim et al. (2011)
	<i>Bacillus thuringiensis</i>	Co	84.81 nm	Spherical	----	Marimuthu et al. (2013)
	<i>Marinobacter hydrocarbonoclasticus</i>	Co	8–22 nm	Spherical	Intracellular	Zaki et al. (2021)
	<i>Microbacterium</i> sp. MRS-1	Co ₃ O ₄	10–100 nm	Spherical/pentagonal	Intra/Extracellular	Sundararaju et al. (2020)
	<i>Micrococcus lylae</i>	Co ₃ O ₄	2–10 nm	----	Membrane	Shim et al. (2013)
	<i>Proteus mirabilis</i> 10B	Co ₃ O ₄	22.1 nm	Quasi-spherical	Intracellular	Eltarahony et al. (2018)
Ni	<i>Bacillus subtilis</i>	Ni ₃ (PO ₄) ₂	40–90 nm	Anisotropic	----	Yu and Jiang (2019)
	<i>Microbacterium</i> sp. MRS-1	NiO	100–500 nm	Quasi-spherical	Extracellular	Sathyavathi et al. (2014)
	<i>Pseudomonas alcaliphila</i>	Ni	----	Anisotropic	Intra/Extracellular	Zhan et al. (2012)
Zn	<i>Alkalibacillus</i> sp. W7	ZnO	1–30 nm	Hexagonal/Quasi-spherical	Supernatant	Al-Kordy et al. (2021)
	<i>Cyanobacterium Nostoc</i> sp. EA03	ZnO	50–80 nm	Star shape	Supernatant	Ebadi et al. (2019)
	<i>Bacillus</i> sp PTCC 1538	ZnO	99 nm	Nano-rods	----	Mahdi et al. (2020)
	<i>Halomonas elongata</i> IBRC-M 10214	ZnO	18.11 nm	Anisotropic	Supernatant	Taran et al. (2017)
	<i>Lactococcus lactis</i> NCDO1281	ZnO	55 nm	Spherical	----	Mahdi et al. (2020)

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TABLE 2 (Continued) Bacteria-mediated metal-based nanoparticles reported in the literature.

Metal	Name of organism	NP	Size	Morphology	Localization	References
	<i>Pseudomonas geniculata</i>	Zn	4–13 nm	Spherical	Intracellular/ Membrane	Zaki et al. (2021)
	<i>Shewanella oneidensis</i> MR-1	ZnS	5.1 nm	Spherical	Extracellular/ Membrane	Xiao et al. (2015)
Cu	<i>Enterococcus thailandicus</i>	Cu	1–4 nm	Spherical	Intracellular	Zaki et al. (2021)
	<i>Escherichia</i> sp. SINT7	Cu	22.33–39.00 nm	Spherical	Extracellular	Noman et al. (2020)
	<i>Pseudomonas fluorescens</i> MAL2	Cu	20–80 nm	Spherical/hexagonal	----	El-Saadony et al. (2020)
Ti	<i>Halomonas elongata</i> IBRC-M 10214	TiO ₂	104.63 nm	Spherical	Supernatant	Taran et al. (2017)
Cr	<i>Alishewanella</i> sp. WH16-1	Cr ₂ O ₃	100–200 nm	Spherical	Intracellular	Xia et al. (2018)
	<i>Bacillus cereus</i>	Cr ₂ O ₃	8–60 nm	Anisotropic/Spherical	Extracellular/ Membrane	Dong et al. (2013)
	<i>Bacillus subtilis</i>	Cr ₂ O ₃	4–50 nm	Spherical	----	Kanakalakshmi et al. (2017)
Cd	<i>Bacillus badius</i>	CdS	20–80 nm	----	Supernatant	Sharma et al. (2021)
	<i>Pedobacter</i> sp. UYP1	CdS	2.8–4.9 nm	Anisotropic	Extracellular	Carrasco et al. (2021)
	<i>Raoultella</i> sp. X13	CdS	5–8 nm	----	----	Xu et al. (2021)

3.2 Biosynthetic nanoparticles

Bio-inspired NPs of different metals have been successfully synthesized using a large variety of bacterial strains. Under optimal conditions in temperature, pH and redox state, some bacterial species can reduce metal ions and form nanoparticles. Among the metals successfully recovered by bacteria in form of nanoparticles are iron, manganese, chromium, cobalt, palladium, gold, silver, arsenic, selenium, uranium, and polonium (Boedicker et al., 2021). Their resulting size-distribution, morphology and functional properties are highly dependent on the protocols used for the biosynthesis as well as on the type of bacteria and metal involved. In Table 2, details of recent, published protocols for metal nanoparticles fabrication using different bacterial strains are listed.

3.2.1 Gold nanoparticles

Metallic gold (Au) can be used in a wide range of applications due to its high stability, oxidation resistance, and biocompatibility. In nanoparticle form, gold displays an improved potential for chemical catalysis and has antimicrobial effects. Despite these antibacterial properties, some microorganisms have been successfully used to synthesize Au NPs. One of the first bacterial species studied for the reduction of Au was *Bacillus subtilis*. In their work, Beveridge and Murray exposed bacterial cells to solutions of Au³⁺ chloride at room temperature and observed the formation of Au NPs of octahedral morphology with sizes of approximately 5–25 nm (Beveridge and Murray, 1980; Iravani, 2014). Since then, many other species and strains have been examined for their capacity to synthesize Au NPs of diverse morphologies and dimensions. *Pseudomonas stutzeri* cells produce Au NPs in the size range of 10–20 nm with a spherical morphology when incubated at 80°C in a medium with chloroauric acid (HAuCl₄) as the precursor (Desai et al., 2021). *Escherichia coli* also biosynthesizes spherical Au NPs found primarily in the extracellular matrix with dimensions

that vary with the pH of the medium from 6 to 60 nm in size. In similar conditions, Au NPs of sizes between 5 and 40 nm can be prepared with *Bifidobacterium lactis* bacteria, but with hexagonal morphologies and mostly intracellularly (Chen et al., 2021). Thus far, however, the complex mechanisms of Au NPs formation by bacteria are still not completely understood. For *Lactobacillus casei* bacteria, it was found that high cell numbers and high concentrations of Au salt solutions inhibit the particle formation. The same study suggested a direct participation of unsaturated fatty acids from di- and tri-glycosyldiacylglycerol glycolipids in the membrane in the formation of Au NPs (Kikuchi et al., 2016).

3.2.2 Silver nanoparticles

The production of Ag NPs is of special interest for their uses in the biotechnology industry. Drug delivery, diagnostics, cancer treatment and antibacterial agents are some of their most known applications (Jain et al., 2021). Several bacterial species have been exploited in the biogenic synthesis of intracellular and extracellular Ag NPs, including species from the *Pseudomonas* (Rajora et al., 2016; Quinteros et al., 2019), *Lactobacillus* (Riaz Rajoka et al., 2020; Abishad et al., 2022) and *Bacillus* (Mukherjee et al., 2018; Saravanan et al., 2018; Ibrahim et al., 2021; Esmail et al., 2022) genus. An example is *P. stutzeri* AG259, which was originally isolated from a silver mine and can bioaccumulate and synthesize silver crystalline nanoparticles when cultured in presence of high concentrations of silver salt (AgNO₃). These Ag and Ag₂S NPs are usually found in the bacteria plasma membrane and display triangular or hexagonal morphologies with a wide range of sizes from 35 to 200 nm (Klaus et al., 1999). Synthesis of Ag NPs with cell-free supernatants of *Stenotrophomonas maltophilia* bacteria results in cuboidal NPs of the average size of 93 nm (Oves et al., 2013), while *Pseudomonas aeruginosa* extracts can be used to synthesize spherical nanoparticles of 25 nm in size (Quinteros et al., 2019).

3.2.3 Platinum nanoparticles

Metals from the Platinum group of elements are notorious for their outstanding catalytic properties, in particular when used in nanoparticle form. However, limited studies have been conducted with bacteriogenic Pt nanoparticles, and their applications are rarely explored (Bloch et al., 2021). Zero-valent Pt NPs produced by the acidophilic Fe³⁺-Reducing *Acidocella aromatica* PFBC and *Acidiphilium cryptum* SJH bacterial strains were tested in a Cr⁶⁺ reduction experiment for their catalytic activity. The experiment demonstrated comparable catalytic efficiency to a commercially purchased Pt/C catalyst (Matsumoto et al., 2021). Yet, the potential applications of Pt NPs also include their use in diagnostics (Dash et al., 2021), anticancer treatments (Baskaran et al., 2017), and as antibacterial agents (Hosny et al., 2022).

Live bacterial cells and bacterial lysate supernatants have been studied for Pt NP production. Typical synthesis of intracellular Pt NPs is performed under anaerobic conditions and starts with the incubation of bacteria such as *E. coli* or *Plectonema boryanum* in aqueous solutions of H₂PtCl₆ or Na₂PtCl₄ (Lengke et al., 2006; Attard et al., 2012; Gaidhani et al., 2014). The cells are then loaded with the metal ions and in some cases sodium formate solutions are added as an external electron donor for accelerating the metal reduction. For the extracellular biosynthesis of nanoparticles, the cells are ultrasonicated and centrifuged. Then only the cell lysate supernatant is incubated with the Pt precursor solutions. Most of the Pt nanoparticles crystalize in spherical morphologies. *Pseudomonas kunmingensis* ADR19, *Psychrobacter faecalis* FZC6 and *Pseudomonas putida* KT244 synthesize spherical Pt NPs of the average sizes of 3.95, 2.49 and 8.06 nm (Eramabadi et al., 2020). Other species, such as *Acinetobacter calcoaceticus*, synthesize small cuboidal Pt NPs of 2–3.5 nm in size (Gaidhani et al., 2014).

3.2.4 Palladium nanoparticles

Palladium is a precious metal with outstanding catalytic properties. Currently it is extensively used in car converters and is crucial in a large variety of industrial-scale chemical reactions; in particular, it is an indispensable tool for modern organic synthesis (Chernyshev and Ananikov, 2022). In nanoparticle form, palladium is utilized for hydrogenation and as a carbon-carbon bond forming catalyst in Heck reactions and in Suzuki-Miyaura coupling. The synthesis of Pd NPs by bacteria has progressed rapidly, and a wide range of bacterial species and strains have been studied for the efficient production of nanoparticles. A recent study by Mikheenko et al. describes the formation of Pd NPs by sulfate-reducing bacteria, *Desulfovibrio desulfuricans*, and their application for the Heck reaction and hydrogenation. The cells were grown in anaerobic conditions, and a Na₂PdCl₄ solution in HNO₃ has been used with H₂ gas as supporting electron donor. The examination of the samples showed Pd NPs on the cell surface and in the different membrane layers with sizes in the range of 3–13 nm (Mikheenko et al., 2022). Some additional examples include the metal-reducing bacterium *Shewanella oneidensis* MR-1, which can synthesize extracellular 2–12 nm Pd NPs (Zhang et al., 2022a), the metal-resistant species *Cupriavidus metallidurans* (Tan et al., 2020), and the sulfate-reducing bacterium, *Desulfovibrio fructosivorans* (Mikheenko et al., 2008). Other strains studied for their capacity for Pd NP synthesis, which are not specialized in metal reduction for detoxification include *E. coli* (Bachar et al., 2020), *Bacillus*

megaterium (Chen et al., 2019), and *Bacillus benzeovorans* (Omajali et al., 2015).

3.2.5 Iron-based nanoparticles

Iron is an indispensable element for all living organisms, known mainly as a co-factor in important biological redox reactions. The use of iron in nanoparticle form has attracted considerable interest in applications as contrast agents, as a drug carrier, and in cancer treatment (Samuel et al., 2021). It should be noted that not just the reduced metal but also some iron oxides possess remarkable magnetic properties that are attractive in countless applications, making the development of new methods for the synthesis of Fe nanoparticles an attractive field of research. Bio-production of iron-based nanoparticles is frequently described as a clean, simple, and economic way to obtain Fe NPs. Organisms such as bacteria can utilize various Fe sources to fulfill their nutritional requirements and have elaborate mechanisms to regulate the uptake of Fe ions. Some bacteria, including metal-reducing and magnetotactic bacteria (see above), also have the ability to reduce Fe ions and form crystals naturally.

For Fe-based NP biosynthesis, different sources of iron can be used, such as FeSO₄, FeCl₃, FeCl₂, and iron citrate. The NPs produced by *E. coli* living cells can be found intracellularly and extracellularly, depending on the iron precursor used, the pH and the metal concentration (Crespo et al., 2017). *E. coli* and *P. aeruginosa* cell extracts facilitate the synthesis of spherical magnetic Fe₃O₄ NPs when incubated on 1 mM FeSO₄ at pH 6.5 for 48 h and 37°C (Crespo et al., 2017). Fe₃O₄ NPs were also produced in cell-free *Enterococcus faecalis* supernatants incubated with FeCl₃ and FeCl₂ solutions. In this case, the reported nanoparticles were cubical, hexagonal, and irregular in shape of between 15 and 20 nm in size (Samuel et al., 2021). *Bacillus cereus* cell-free supernatant can also be used to reduce Fe into spherical magnetic Fe₃O₄ NPs in the size range of 18–29 nm (Fatemi et al., 2018).

3.2.6 Cobalt-based nanoparticles

Cobalt is a transition metal with interesting magnetic, catalytic, optical, and electrical properties. Cobalt oxide nanoparticles are considered promising in technologies for energy storage (Shim et al., 2011; Hsu et al., 2018), catalysis (Jang et al., 2015), and as antimicrobial agents (Hafeez et al., 2020; Mubraiz et al., 2021). The synthesis of pure Co NPs by microorganisms can be challenging due to the extreme toxicity of high concentrations of Co ions. Similar to Fe, Co is highly reactive in zero-valent state, and when in contact with aqueous solutions, it rapidly oxidizes. Therefore, the NPs produced by bacteria are typically composed of more stable, oxidized forms of cobalt such as Co₃O₄.

In *G. sulfurreducens*, the upregulation of c-cytochrome OmcC in Co-rich environments is an indication of Co competition with Fe for binding to the cytochromes, that ultimately promotes the reduction of Co²⁺ to Co⁰ and its precipitation on the cell surface (Dulay et al., 2020). In other methods, Co₃O₄ NPs of 10–31 nm size are produced by chemical alteration in the media when the urealytic *Bacillus pasteurii* hydrolyzes urea in the presence of high concentrations of Co(NO₃)₂ (Hsu et al., 2018). *Brevibacterium casei* bacteria produce quasi-spherical 6-nm Co₃O₄ NPs when incubated in aqueous solution of cobalt acetate (Kumar et al., 2008). Other strains

TABLE 3 Bacteria-mediated bimetallic metal-based nanoparticles reported in the literature.

Name of organism	NPs	Size	Morphology	Localization	References
<i>Bacillus benzeovorans</i>	Pd-Ru	1–8 nm	Core-shell	Membrane	Omajali et al. (2019)
<i>Cupriavidus necator</i>	Pd-Au	10–50 nm	Spherical	Membrane	Hosseinkhani et al. (2012)
<i>Deinococcus radiodurans</i>	Au-Ag	60–400 nm	Spherical	Supernatant	Weng et al. (2020)
	Au-Ag	----	Spherical	Supernatant	Li et al. (2018)
<i>Escherichia coli</i>	Au-Pd	16 nm	Spherical	Intracellular/Membrane	Deplanche et al. (2012)
	Pd-Ru	1–3 nm	Core-shell	Intracellular/Membrane	Gomez-Bolivar et al. (2019a)
<i>Lactobacillus</i>	Au-Ag	100–500 nm	Irregular	Membrane	Nair and Pradeep (2002)
<i>Paenibacillus polymyxa</i>	FeO-MnO	11–54 nm	Spherical	Supernatant	de França Bettencourt et al. (2020)
<i>Shewanella oneidensis</i>	Pd-Fe ₃ O ₄	5.5 nm	----	----	Tuo et al. (2015)
	Au-Fe ₃ O ₄	15.4 nm	----	----	Tuo et al. (2015)
	PdAu-Fe ₃ O ₄	8.3 nm	----	----	Tuo et al. (2015)
	Pd-Pt	3–40 nm	Spherical	Intracellular/Extracellular	Xu et al. (2019)
	Pd-Au	1–50 nm		Intracellular/Extracellular	De Corte et al. (2011)
	Pd-Ag	5–60 nm	Core-shell	Membrane	Kimber et al. (2021)
	Pd-Au	4–15 nm	Core-shell	Extracellular	Kimber et al. (2021)
<i>Shewanella putrefaciens</i>	Pd-Pt	4–60 nm	Flower-shaped	Membrane	Tuo et al. (2017)
<i>Spirulina platensis</i>	Au-Ag	17–25 nm	Core-Shell	Supernatant	Govindaraju et al. (2008)

studied for Co NP synthesis include *Micrococcus lylae*, *Bacillus subtilis*, *E. coli*, and *Haloarcula vallismortis* (Jang et al., 2015).

3.2.7 Nickel-based nanoparticles

In microorganisms, there are highly specific and efficient systems for the transport and regulation of nickel in the cell to avoid its accumulation and toxicity in the cytoplasm (Navarro et al., 1993). Taking into account that at high concentrations Ni is extremely toxic to bacteria, the interaction between Ni and the cells has to be carefully controlled. In addition, due to its low redox potential the reduction of Ni ions by bacteria is not energetically favorable for NP formation under standard growth conditions (Zhan et al., 2012). However, a recent study with metal-reducing bacteria *Pseudomonas alcaliphila* described the successful reduction of Ni²⁺ by incubation at 28°C under aerobic conditions in a solution with 2 mM NiCl₂ and sodium citrate as an electron donor. The formed Ni NPs were found intracellularly and in the bacterial periplasm, with irregular shapes (Zhan et al., 2012). Another example is the synthesis of NiO NPs by *Microbacterium sp.* MRS-1, as a result of the bioremediation of nickel electroplating industrial wastewater. The synthesized Ni NPs had spherical, flower-like structures and displayed particle sizes in the range of 100–500 nm (Sathyavathi et al., 2014).

3.2.8 Other elements, alloys, and bimetallic nanoparticles

Many other types of metal-based nanoparticles have been produced successfully using bacteria. These include

nanoparticles composed of elements such as Zn, Cr, Cd, Ti, Cu, and different mixtures of metals. For example, antibacterial nanoparticles made of TiO₂ and ZnO can be bio-synthesized with bacteria. The Gram-negative bacterium *Halomonas elongata* can be used to produce spherical TiO₂ NPs and anisotropic ZnO NPs by incubating the cells with various concentrations of TiO(OH)₂ and ZnCl₂ solutions at different temperatures. The synthesized TiO₂ and ZnO NPs were on average of 104.63 ± 27.75 and 18.11 ± 8.93 nm in size, respectively (Taran et al., 2017). Other examples are the nanoparticles produced by the metal-reducing bacterium *Shewanella oneidensis* MR-1, known for its ability to live in heavy-metals polluted environments and studied for the synthesis of NPs of a wide range of metal ions, including ZnS (Taran et al., 2017), Pd (Zhang et al., 2022a; Zhang et al., 2022b), Cr (Wang et al., 2013) and U (Burgos et al., 2008). Synthesis of Te NPs has also been reported using a methanogenic microbial consortium in 270 ml continuous reactors as an alternative of Te recovery in wastewater treatments (Ramos-Ruiz et al., 2017).

Although microbial-mediated monometallic nanoparticles have been extensively studied, there is limited research on the production of bimetallic nanoparticles by bacteria. The synergistic effect of metal combinations can result in superior or novel catalytic, electronic, and optical properties. Therefore, bimetallic nanoparticles often exhibit improved performance that could be interesting for different applications (Xu et al., 2019). Exposing bacteria to high concentrations of various mixes of heavy metal ions can result in the formation of nanoparticles made of combinations of

these elements. Bimetallic nanoparticles can have structures such as core-shell, alloys, crown jewel, cluster-in-cluster, hollow, and porous NPs (Sasireka and Lalitha, 2021) and it is not surprising that the synthesis methodology has a direct effect on the final architecture of the formed bimetallic NP. An example is the synthesis of spherical bimetallic Pd-Pt NPs by *S. oneidensis* MR-1 prepared by incubation of the cell's biomass in a Pd²⁺ and Pt⁴⁺ mixed solution. Research showed that the synthesized polycrystalline Pd-Pt NPs possessed an improved catalytic performance in comparison with pure Pd or Pt NPs (Xu et al., 2019). Extracellular biosynthesis of bimetallic FeO-MnO NPs can be performed using *Paenibacillus polymyxa*. In this case, cell-free extracts were incubated with solutions of FeCl₃ and MnSO₄ at 45°C in the dark for 5 h and the formed spherical nanoparticles had sizes in the range of 11.28–543.59 nm. These particles are suitable as micronutrient additives to fertilizers for crop production (de França Bettencourt et al., 2020). For core-shell Pd-Ru bimetallic NP production, Gomez-Bolivar et al. incubated *E. coli* bacteria in a Pd²⁺ solution for an initial reduction of Pd under H₂ on the cell surface. The biomass with Pd⁰ was then resuspended in Ru³⁺ solution for Pd-Ru NPs formation. Pd-Ru NPs synthesized mainly at the cell surface, although small MNPs were also present intracellularly. (Gomez-Bolivar et al., 2019a). Table 3 summarizes examples of bimetallic nanoparticles produced by different bacteria.

4 Discussion—challenges for potential industrial-scale synthesis

There seems to be an enormous potential for a cost-effective and environmentally friendly synthesis of metal nanoparticles by bacteria. Yet, some special considerations must be assessed before the implementation of these approaches on a large scale and for commercial applications. The most common disadvantages of nanoparticle synthesis using microorganisms is the polydispersity of the particles, low yield and agglomeration (Narayanan and Sakthivel, 2010). Many bacterial strains that enable high yields of NPs are extremophilic organisms that require harsh environmental conditions in terms of temperature, radiation, pH and medium composition (metal concentration, oxygen, salinity, etc.) in order to thrive (Atalah et al., 2022). The complicated culture conditions that are necessary for their isolation and cultivation, and the fact that small modifications of the environment can immediately result in the disruption of the metabolic routes that promote the metal ion reduction, make them challenging to use in large-scale processes. An example is the effect of dissolved oxygen concentration (DO) on the yield of magnetosomes produced by magnetotactic bacteria. It was suggested that *M. gryphiswaldense* MSR-1 bacteria form magnetosomes as a response to a low DO that is detrimental for their growth. Thus, only a strict control of the DO during production would guarantee higher yields of magnetosomes (Sun et al., 2008). This illustrates that optimized conditions for bacterial growth and nanoparticle formation must be determined in detail before any large-scale synthesis is considered, and that it is crucial to evaluate how controllable these parameters are on larger scales. Usually, large-scale cultivation requires further refinement of nutrients control and other culture conditions (Liu et al., 2010). In addition, the cost of specific culture media for microbial growth,

instrumentation and facilities needs to be considered in potential commercial productions (Capuzzo, 2021).

By tuning the metal concentration and cell density, it is possible to obtain well-defined nanoparticles with narrow size distribution and homogeneous morphology using bacteria (Bing et al., 2018; Yu et al., 2020). The development of efficient mechanisms to supervise and adjust these parameters, in combination with choosing the ideal bacterial species and strains, would be important for an effective large-scale synthesis. Microbial MNP synthesis can occur intracellularly or extracellularly depending on the reduction mechanism used by the selected organism. Most studies favor the extracellular, cell lysate or cell-free production, as the resulting nanoparticles require less complex downstream processing. Intracellular synthesis tends to require a further purification processes to release nanoparticles from the cytosol, and ultrasound treatment to reduce agglomeration (Marooufpour et al., 2019). In addition, the biosynthesized NPs frequently use biological material as nucleation sites and scaffolding. Therefore, many of them feature biocappings that may have desired or undesired effects on the nanoparticle properties (Schröfel et al., 2014). Some of the capping agents ensure the production of small homogeneous nanoparticles by preventing the agglomeration and by decreasing their toxicity (Yahyaei et al., 2016). However, a removal process for these biocoatings from the nanoparticles is sometimes necessary depending on the targeted application. Excess proteins, ligands and impurities hinder the catalytic performance of MNPs like Ag NPs, and protocols such as dialysis, filtration, and sucrose density centrifugation have been introduced as purification methods (Khositanon et al., 2020; Ahmad et al., 2021). A study by Khositanon et al., reported the removal of up to 73.3% of ligands by continuous-flow solvent extraction in a production of Ag NPs coated with surfactants (Khositanon et al., 2020). Yet, most of the methods to clean the bio-nanoparticles have proven to be time consuming, laborious, or not cost-effective, which may prevent the profitable use of the particles for their intended purposes.

Because of these technical hurdles, only few examples have been reported for the successful, large-scale production of NPs, showing that further research is necessary to develop sustainable production processes (Gahlawat and Choudhury, 2019). Successful examples include the productions of ZnS NPs by the thermophilic bacterium *Thermoanaerobacter* sp. X513 in 100-L and 900-L fermenters (Moon et al., 2016), and CdS NPs in cultures from 10 ml up to 24 L of volume (Moon et al., 2013). Magnetic, Fe-based NPs were synthesized by *Thermoanaerobacter* sp. TOR-39 in 35 L reactors (Moon et al., 2010).

The key parameters that have a significant effect on NP yield are time of incubation, biomass concentration, and type of precursor, aside from the choice of bacterial species. In principle, these parameters are relatively easy to control, and along with further understanding of the bacterial redox activity and the mechanism of metal transport would greatly benefit the development of strains that naturally have a high tolerance for heavy metals and remarkably produce large populations of nanoparticles. Then, the insights gained in numerous studies give hope that industrial-scale protocols can be implemented for commercial applications in the future (Narayanan and Sakthivel, 2010).

Author contributions

AC and DL contributed to conception of the manuscript. AC wrote the first draft and AS wrote sections of the manuscript. DL, AS, and PM conducted manuscript editing and proofreading. All authors contributed to the article and approved the submitted version.

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