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Review

Heavy Metals Influence on the Bacterial Community of Soils: A Review

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Abstract: The increasing rate of natural resource use leads to an increase in the anthropogenic load on the soil. As the result of industrial, metallurgical and mining activities, excessive amounts of heavy metals (HMs) enter the soil. In addition, they can be introduced with waste and drainage water from various enterprises. Accumulating in the soil, HMs can negatively affect the soil bacterial community, which is one of the main factors of its "health". Molecular genetic methods based on shotgun sequencing or metabarcoding of standard DNA sequences (for example, the 16S rRNA gene for bacteria) are the modern ways to assess the bacterial diversity of soils. This review presents the results of modern studies on the effect of HMs on the soil bacterial communities, using metagenomic methods. Based on the analysis of publications over the past two decades, a generally negative effect of pollutants on the taxonomic composition and diversity of bacterial communities has been shown. The influence of factors modulating the toxicity of metals and metalloids was noted: the amount and composition of salts, soil pH, ecosystem type, rhizosphere presence and other soil properties. In this paper, promising directions of research are outlined.

Keywords: pollution; soil; bacteria; archaea; metals; metalloids; biodiversity

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1. Introduction

Soil is an essential component of terrestrial ecosystems. It provides a wide range of functions, such as food production, climate and water regulation, energy provision and is the habitat for various life forms [1]. Soil bacterial communities play a critical role in nutrient cycling, soil fertility and carbon sequestration, all which are of great importance for soil ecological functions [2]. Species diversity of soil bacterial communities is considered a key attribute associated with soil resistance and resilience [3]. According to modern concepts, high biodiversity prevents deterioration of ecological functions, since a larger number of species provides a higher probability that an ecosystem will retain its functions if some of the species are eliminated or suppressed by stressful effects. The soil bacterial population probably has the highest level of bacterial diversity of all environments. It is estimated that each gram of soil contains approximately 10 billion bacteria and thousands of different phyla of bacteria [4]. The composition and diversity of soil bacterial communities can be influenced by various environmental factors.

Soil has the ability to hold various pollutants such as heavy metals (HMs), pesticides or hydrocarbons and their derivatives [5]. Anthropogenic activities, such as mining and metallurgical industries, are the main source of heavy metal contamination of soils. Heavy metals can migrate to the soil of agricultural land from mining and smelting plants [6]. In addition, excessive use of pesticides and fertilizers can also contribute to the high levels of HMs in agricultural land [7]. Soil pH and moisture can also affect the mobility and spread of metal contaminants [8]. Due to natural processes, such as the wind, rain and erosion, soil particles containing HMs can travel more than 20 km from their point of origin, affecting soils and water systems indirectly associated with the original site [9].

One of the most important characteristics of soil bacterial communities is their biodiversity. Biodiversity of bacteriocenosis is determined by its richness, i.e., the number

of operational taxonomic units (OTUs) in a community, and its diversity, i.e., the uniformity of representation and distribution of OTUs. As a rule, the Chao index is used as a quantitative measure of bacterial community richness, and the Shannon index is used as a diversity measure. Studying soil bacterial community biodiversity is an important way to assess soil well-being. Currently, molecular biology methods are widely used to assess the structure and diversity of bacterial communities. Both partial analysis and analysis of the whole community are possible. Partial community analysis involves strategies based on polymerase chain reaction (PCR), where total DNA or RNA samples extracted directly from soil are used as a template. PCR product analysis can be performed by clone library, DNA microarray, genetic fingerprinting, or a combination of these methods. Analysis of the entire community is carried out by studying the 16S rRNA gene sequence, as well as complete bacterial genome sequencing, metagenomics, metatranscriptomics, proteomics and metaproteomics [10,11]. The advent of next generation sequencing (NGS) has revolutionized our understanding of bacterial communities in a variety of environments.

Metagenomics involves the isolation of genomic DNA directly from the environment, without the need to pre-culture organisms in a laboratory. Thus, genomic analysis is applied to the entire bacterial community, bypassing the need to isolate and culture individual parts of the bacterial population to classify microorganisms into communities [12]. Currently, two main approaches are used: metabarcoding and shotgun sequencing of complete metagenomic DNA. Metabarcoding is the sequencing of marker gene amplicons; 16S rRNA genes are usually sequenced to study the taxonomic structure of prokaryotic communities. Metabarcoding does not make it possible to assess the effect of HM contamination on functional changes and bacterial community metabolism, however, it provides a fairly clear community structure. In addition, amplicon sequencing data is much easier to analyze. Shotgun sequencing, on the contrary, provides complete genetic information about the bacterial community, allowing reconstruction of metabolic pathways and biogeochemical cycles of elements. However, a large amount of data from shotgun sequencing is more difficult to analyze, and obtaining a taxonomic structure with the same resolution requires a large depth of sequencing, which significantly increases the cost of analysis and further increases the amount of data, making the analysis difficult. Thus, metagenomics is an essential tool for studying soil bacterial communities and provides an excellent way to assess bacteriocenosis structure. High-throughput sequencing based on 16S rRNA is currently a common tool for in-depth study of soil bacterial community composition and abundance [2,13].

Thus, the purpose of this review is to analyze current publications devoted to the problem of studying the impact of HMs entering soil as the result of anthropogenic activities on prokaryotic soil communities.

2. The Influence of Heavy Metals on the Bacterial Communities of Soils

In recent years, soil pollution with HMs has attracted worldwide attention due to their high toxicity, non-biodegradability and long-term accumulative behavior [14]. HMs not only alter soil fertility, but also disrupt the bacterial community and lead to biodiversity loss [15] (Table 1).

Table 1. Effect of heavy metals on the soil bacterial community.

No.	Object	Location	Soil Type	Pollutant	Taxonomic Composition Changes	Impact on Diversity	Notes	References
Agricultural soils								
1	Soils from corn fields	Shandong Province, North China	Solonchaks, Luvisols, Cambisols, Regosols	Cr, Zn, Pb, Ni, Cu, As, Cd, Hg	Prevalence of *Actinobacteria* and *Proteobacteria*	Reduced diversity in the most HM polluted area	Has influenced bacterial diversity the most	[7]
2	Soil from an agricultural greenhouse	Vila do Conde, Northern Portugal	Sandy soil	Cu, Zn in the form of salts SO_4^{2-} or NO^{3-}	Prevalence of the phyla *Proteobacteria*, *Actinobacteria* and *Firmicutes* Increase in the abundance of *Chloroflexi*, *Planctomycetes*, *Patescibacteria* and *Latescibacteria* in the presence of NO_3^- compared to SO_4^{2-} Decrease in *Bacteroidetes* and *Proteobacteria* in the presence of NO_3^- compared to SO_4^{2-}	Decreased diversity	SO_4^{2-} reduced the richness and diversity of bacteria more strongly	[16]
3	Rice field soils	X District, Eastern China	No data	Cu, Zn, Cd, Pb, Ni, Cr	Heavy pollution: increase in *Proteobacteria*, decrease in *Verrucomicrobia*, *Firmicutes* and *Chloroflexi*	Increased diversity with high, medium and no pollution Reduced diversity with low pollution		[17]
4	Rice field soils	Zhejiang Province, China	Loamy clay soil	Cd, Cu, Zn	Prevalence of the *Proteobacteria*, *Actinobacteria*, *Acidobacteria* and *Chloroflexi* phyla In a field experiment, there was a decrease in *Actinobacteria*, with an increase in HM content In the laboratory, an increase in the number of *Actinobacteria*, *Acidobacteria* and a decrease in *Proteobacteria*	Not investigated		[18]

Table 1. *Cont.*

No.	Object	Location	Soil Type	Pollutant	Taxonomic Composition Changes	Impact on Diversity	Notes	References
Agricultural soils								
5	Agricultural soils	Dabaoshan mining area in northern Guangdong Province, China	No data	Cu, Pb, Zn, Cd	Prevalence of *Acidobacteria*, *Proteobacteria* and *Chloroflexi*	No data	Acid mine drainage irrigation enriched the bacterial phylum *Acidobacteria* and the archaeal phylum *Crenarchaeota*	[6]
6	Rice field soils from mercury mining sites	Guizhou, Hunan and Shanxi Provinces, China	No data	Hg	Dominant mercury-methylating microbes were members of the phyla *Proteobacteria*, *Euryarchaeota*, *Chloroflexi* and two unnamed groups	Decreased diversity		[19]
7	Rice field soils	Wanshan, Southwest China	Red soil (Alfisol)	Hg	Prevalence of the *Proteobacteria*, *Firmicutes*, *Actinobacteria*, *Chloroflexi*, *Bacteroidetes*, *Planctomycetes*, *Acidobacteria*, *Gemmatimonadetes*, *Verrucomicrobia* and *Saccharibacteria* phyla An increase in the content of *Gemmatimonadetes* and *Proteobacteria*, with an increase in the concentration of water-soluble Hg	Decreased diversity	The addition of humic acids and fulvic acids increased the level of water-soluble Hg, enhancing its toxic effect on the soil bacterial community	[20]
8	Field soils	Raron, Switzerland	No data	Hg	Emergence of Hg-resistant bacteria of the *Proteobacteria*, *Verrucomicrobia*, *Planctomycetes*, *Actinobacteria* and *Bacteroidetes* phyla	Increased diversity with prolonged exposure to Hg (>10 years) No short-term Hg effect (30 days)		[21]
9	Agricultural soils	Sichuan Province, China	No data	Cd	Prevalence of the *Proteobacteria*, *Acidobacteria* and *Chloroflexi* phyla	Decreased diversity		[22]

Table 1. *Cont.*

No.	Object	Location	Soil Type	Pollutant	Taxonomic Composition Changes	Impact on Diversity	Notes	References
10	Cornfield soil microcosm	Yangling, Shaanxi Province, Northwest China	Sandy loam soil	Cd	The abundance levels of the genera *Massilia*, *Lysobacter*, *Pseudoduganella* and *Bacillus* first increased and then decreased, and the abundance of the genera *Gaiella*, *Perlucidibaca*, *Sphingomonas*, *Nocardioides* and *Aeromicrobium* first decreased and then increased	Decrease in alpha diversity and its increase within 90 days (end of experiment)		[23]
11	Agricultural soils	Mianyang (China)	No data	Cd	Prevalence of the *Proteobacteria*, *Chloroflexi*, *Actinobacteria*, *Acidobacteria*, *Nitrospirae*, *Gemmatimonadetes* and *Verrucomicrobia* phyla	Cd had no effect on diversity		[24]
12	Soils of rice fields near the Sb mine	Dushan County, southwest China	No data	Sb, As	Prevalence of the *Proteobacteria*, *Acidobacteria*, *Actinobacteria*, *Chloroflexi*, *Bacteroidetes*, *Verrucomicrobia*, *Planctomycetes*, *Gemmatimonadetes*, *Nitrospirae* and *Firmicutes* phyla	Diversity did not decrease	Fe (III) can affect bacterial communities, reducing the bioavailability of Sb and As	[25]
13	Agricultural and mining soils	Guanajuato State, México	Vertisols	As	Prevalence of *Proteobacteria*, *Acidobacteria* and *Actinobacteria* The most abundant were representatives of the genus *Bradyrhizobium* and non-cultivated organisms of the family *Rhodospirillaceae*	No data	More bacteria resistant to As were shown in mining soils than in agricultural soils	[26]

Table 1. *Cont.*

No.	Object	Location	Soil Type	Pollutant	Taxonomic Composition Changes	Impact on Diversity	Notes	References
Industrial soils								
14	Soils near an existing Sb processing plant and a nearby landfill	South Korea	No data	Sb, As, Cu, Zn and Pb	Prevalence of the phyla *Proteobacteria*, *Acidobacteria*, *Chloroflexi* and *Actinobacteria*	Reduced diversity in the samples with extreme Sb content (compared to soils with high and low Sb content)	Bacterial community composition was influenced by Pb	[27]
15	Topsoil from the site of large-scale mining operations	Picher, Ottawa County, Oklahoma, USA	No data	Pb, Cd, Zn and Mg	Bacterial abundance negatively correlated with Pb, Cd, Zn, and Mg Pb and Zn correlated with significant increases in the phyla *Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, *Chloroflexi*, *Planctomycetes*, *Proteobacteria* and *Verrucomicrobia*	Decreased diversity		[9]
16	Acidic and neutral soils of the Xikuangshan mine	Hunan Province, China	No data	Sb, As, Pb, Cu, Cr, Zn and Cd	Prevalence of the *Acidobacteria*, *Proteobacteria*, *Chloroflexi* and *Actinobacteria* phyla	Decreased diversity	Cr (VI) reduced species diversity most strongly	[28]
17	Soils near a vanadium smelter	Panzhihua City, China	No data	V	Prevalence of the *Actinobacteria*, *Proteobacteria*, *Chloroflexi*, *Acidobacteria* and *Firmicutes* phyla	Decreased diversity		[5]
18	Soils near a vanadium smelter	Panzhihua City, China	No data	V	The original contaminated soils were dominated by *Bacteroidetes* and *Proteobacteria*, *Actinobacteria* and *Firmicutes* After 240 days with vanadate, *Proteobacteria*, *Acidobacteria* and *Actinobacteria*, prevailed in all samples	Decreased diversity		[29]
19	Uranium tailing soil	Southern China	No data	U	Prevalence of *Actinobacteria*, *Proteobacteria*, *Planctomycetes*, *Acidobacteria* and *Firmicutes*	Decreased α-diversity	*Robiginitalea*, *Microlunatus* and *Alicyclobacillus* were the dominant genera in radioactive soil	[30]

Table 1. *Cont.*

No.	Object	Location	Soil Type	Pollutant	Taxonomic Composition Changes	Impact on Diversity	Notes	References
20	Soils from Hg mining areas	West Hunan Province and East Guizhou Province, southwest China	No data	Hg	Total Hg was positively related to the relative abundance of *Firmicutes* and *Bacteroidetes*, methylmercury concentration was negatively correlated with the relative abundance of *Nitrospirae*	Hg pollution was negatively related to bacterial abundance, but positively related to the diversity of bacteria		[31]
21	Soil from a gold mining area	Northwest of Beijing, China	No data	As	Prevalence of *Actinobacteria*, *Proteobacteria*, *Acidobacteria* and *Chloroflexi*	Shannon index increased in moderate- and high-As soils	*Actinobacteria*, *Proteobacteria*, *Acidobacteria*, and *Chloroflexi* were the dominant phyla of As metabolism gene host bacteria	[32]
22	Contaminated industrial effluent soil	Sipcot lake area, Ranipet, Vellore district, Tamilnadu, India	No data	Cr, Fe	Relative abundance of *Lactobacillaceae* (24%), *Desulfobulbaceae* (13%), *Staphylococcaceae* (10%), *Enterococcaceae* (6%), *Desulfovibrionales* (5%), *Carnobacteriaceae* (5%), *Desulfobacteraceae* (4%), *Enterobacteriaceae* (4%), *Acetobacteraceae* (3%) and *Geobacteraceae* (3%)	No data	Reduction of Cr(VI) to Cr(III) by FeS particles, generated by the biospheric bacteria, was elucidated	[33]
23	Contaminated industrial effluent soil	Sipcot lake area, Ranipet, Vellore district, Tamilnadu, India	No data	Cr, Fe	Prevalence of *Proteobacteria*, *Firmicutes* and *Bacteroidetes* Relative abundance of classes (%): *Acidobacteria* (48.47), *Deltaproteobacteria* (9.70), *Alphaproteobacteria* (6.80), *Gammaproteobacteria* (5.70), *Clostridia* (3.10), *Epsilonproteobacteria* (2.60), *Bacilli* (2.50), *Actinobacteria* (1.40) and *Flavobacteria* (1.20).	No data		[34]

Table 1. *Cont.*

No.	Object	Location	Soil Type	Pollutant	Taxonomic Composition Changes	Impact on Diversity	Notes	References
Rhizosphere soils								
24	Rhizosphere soil of *Robinia pseudoacacia*, collected from two sites surrounding a Pb–Zn smelter	Southeast Mianxian County, Shaanxi Province, China	Yellow-brown soil	Cd	Decreased *Gemmatimonadetes*, *Bacteroidetes*, *Cyanobacteria*, *Planctomycetes*, *Armatimonadetes* and *Elusimicrobia* Increased *Acidobacteria*, *Chloroflexi*, *Nitrospirae*, *Verrucomicrobia* and *WS3*	Decreased α-diversity	Rhizobia inoculation	[35]
25	Rhizosphere soil of *Alyssum murale*	Northern Pindus Mountains, Greece	Ultramafic soils	Ni, Mn, Mg, Fe	Prevalence of *Chloroflexi* (63.5% ± 11.9), *Actinobacteria* (15.8% ± 7.3), *Proteobacteria* (8.2% ± 4.3), *TM7* (4.7% ± 3.0), *Bacteroidetes* (2.9% ± 1.5), *Gemmatimonadetes* (1.1% ± 0.8) and *Acidobacteria* (1.2% ± 0.6)	Nickel drives the bacterial community diversity	Rhizosphere bacterial community of Ni-hyperaccumulator plants	[36]
26	Rhizosphere soils of *Odontarrhena chalcidica*, *O. smolikana*, *O. rigida* and *Noccaea ochroleuca*	Librazhd and Pogradec districts, Eastern Albania	Ultramafic (i.e., serpentine) soils	Ni, Fe, Mg	Prevalence of *Proteobacteria* (31.7% ± 4.9) > *Acidobacteria* (19.2% ± 4.2) > *Actinobacteria* (16.0% ± 3.4) > *Gemmatimonadetes* (10.0% ± 3.4) > *Chloroflexi*. (7.8% ± 2.1) > *Bacteroidetes* (7.4% ± 4.0) > *Nitrospirae* (2.4% ± 2.5)	Cation exchange capacity was the most important factor influencing the bacterial community diversity and structure	Rhizosphere bacterial community of Ni-hyperaccumulator plants	[37]
Other soils								
27	Soils of different parts of the North China Plain	Shandong, Hebei, Henan, Liaoning provinces, Beijing City, China	No data	Cd	Prevalence of the *Proteobacteria*, *Actinobacteria*, *Firmicutes* and *Chloroflexi* phyla Increase in the abundance of *Proteobacteria*, *Gemmatimonadetes* and *Bacteroidetes*, with an increase in the bioavailability of Cd	Decreased diversity	Addition of salt leads to transfer of Cd into smaller soil aggregates and an increase in its bioavailability	[38]
28	Abandoned farmland soils	Sichuan Province, China	Sandy loam	Pb, Cd and Zn	Prevalence of the *Bacteroidetes*, *Acidobacteria*, *Chloroflexi*, *Proteobacteria* and *Actinobacteria* phyla	Increasing diversity with long-term exposure	The structure of the bacterial community was most strongly influenced by acid-soluble Pb	[15]

Table 1. *Cont.*

No.	Object	Location	Soil Type	Pollutant	Taxonomic Composition Changes	Impact on Diversity	Notes	References
29	Commercial soils Lufa 2.2 and 2.4	LUFA Speyer, Germany	No data	Nanoscale zero-valent Fe	Prevalence of *Proteobacteria*, *Verrucomicrobia*, *Firmicutes* and *Actinobacteria* Increase in the number of *Verrucomicrobia* Decrease in the number of *Actinobacteria* and *Bacilli*	No data		[39]
30	Commercial soil Lufa 2.3	LUFA Speyer, Germany	No data	Pb, Zn and Cd	Decrease in the number of *Proteobacteria*, *Actinobacteria*, *Verrucomicrobia* and *Bacteroidetes* phyla Increase in the number of *Firmicutes*	No data		[14]
31	Mangrove sediments	Mangalavanam and Puthuvypin, Central Kerala, India	Sediments	Cd, Zn	Prevalence of *Proteobacteria*, *Bacteroidetes*, *Firmicutes*, *Acidobacteria* and *Actinobacteria*	No data	Prevalence of cobalt, zinc and cadmium resistance in metaresistome	[40]
32	Soils from deciduous and coniferous forests, hydromorphic soils in the area of the secondary-lead plant	North of France (Ardennes)	Luvic cambisols, hydromorphic gleysol	Pb	Prevalence of *Proteobacteria*, *Actinobacteria*, *Verrucomicrobia*, *Chloroflexi*, *Planctomycetes*, *Bacteroidetes* and *Gemmatimonadetes* Increase in *Proteobacteria* and *Chlamydiae* and decrease in *Verrucomicrobia* numbers with increasing Pb contamination	No data		[41]

The stress caused by HM pollution can change the characteristics of bacterial communities [42]. The diversity and abundance of sensitive soil bacteria can decrease, while resistant bacteria can easily adapt and increase in abundance, thereby forming a specific structure of the bacterial community [24]. HM contamination constantly affects bacterial biomass and activity [43].

The most common toxic metals and metalloids are mercury (Hg), lead (Pb), cadmium (Cd), copper (Cu), chromium (Cr), manganese (Mn), zinc (Zn) and arsenic (As, metalloid). Among them, Zn, Mn and Cu perform the function of microelements in plants, while biological functions have not been shown for Hg, Pb, Cd, Cr and As [7]. General influence trends of metal and metalloid pollution on bacterial and archaeal soil communities are shown in Figure 1.

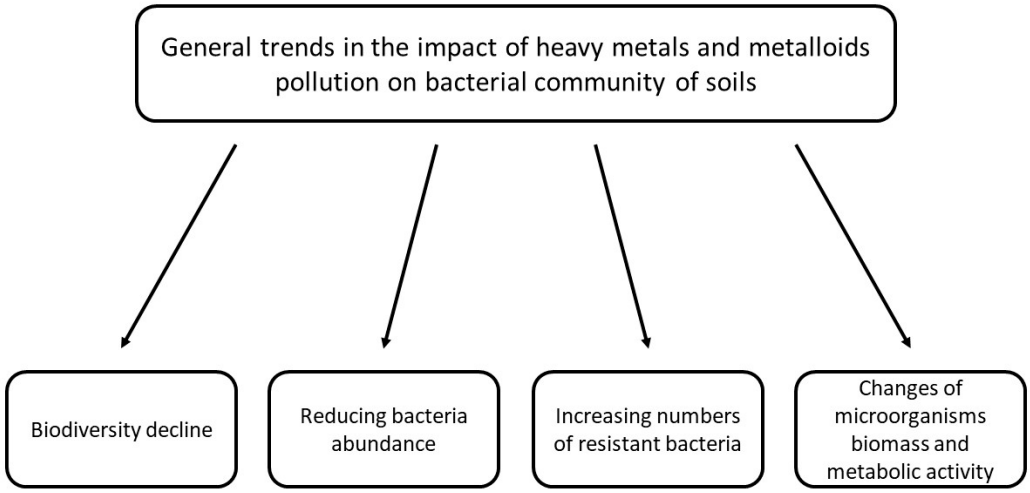

Figure 1. General trends in the impact of heavy metal and metalloid pollution on bacterial soil communities.

3. The Role of Bioavailability and Mobility of Heavy Metals

HMs exist in various forms, such as free metal ions, interchangeable metal ions, soluble metal complexes, and metals bound in other compounds. These forms lead to different levels of bioavailability and, accordingly, different effects on bacterial communities. For example, the influence of copper and zinc salts (sulfates or nitrates) on variations in the structure of the bacterial community was shown [16]. The relative abundance of the phyla *Chloroflexi*, *Planctomycetes*, *Patescibacteria* and *Latescibacteria* was higher in the soil with nitrate salts than in the soil enriched with sulfates, while the abundance of *Bacteroidetes* and *Proteobacteria* phyla was lower. In soils with additions of both metals, the relative abundance of the phyla *Proteobacteria*, *Actinobacteria* and *Firmicutes* was significantly higher than that of the control. It was noted that the soil samples with an addition of HMs had lower values of richness (richness (number of ASVs (amplicon sequence variants)) and Chao index) and diversity (Fischer index) compared to the control samples without metals. Sulfate had a stronger effect on reduction of these indicators than nitrate. Thus, HM salt anions modulate the biological effects of HM ions.

HM mobility depends on various factors, including soil properties, climatic conditions, plant characteristics and agricultural practices. Cui et al. [7] found that the bacterial diversity was significantly influenced by soil pH and the presence of As, Cr and Ni. Soil samples from corn fields of the Shandong Province in Northern China were studied. The content of HMs in the soils here turned out to be increased compared to other places due to mining and heavy industries. Actinobacteria and proteobacteria accounted for more than 50% of the total bacterial richness. The authors believe that as a result of selective

pressure, phylotypes with a tolerance to HMs were selected, while sensitive ones became less frequent.

It has been shown that experimental soil treatment with nanoscale zero-valent iron leads to an increase in the relative abundance of the *Verrucomicrobia* phylum and a decrease in the percentage of the *Bacilli*, and especially *Actinobacteria* phyla. The bioavailability and toxicity of nanosized iron were significantly affected by soil pH and the content of organic matter in it. At a low pH, the dissolution of iron nanoparticles is accelerated, high pH prevents its dissolution, and soil organic material reduces its toxicity and is able to neutralize ROS resulting from Fenton-like processes [39].

The interaction between soil pH, and HMs and metalloids (Cd, Pb, Cu, Cr, Zn, Sb and As) was also described by Ma et al. [28] in the example of acidic and neutral contaminated soils of the Sb mine (Lengshuijiang, China). Bacteriocenosis reacted differently to HMs in acidic and neutral soils. Zn and Pb concentrations showed a stronger correlation with the bacterial community structure than other HMs in acidic soils. However, the main factors influencing the bacterial communities in neutral soils were Sb, As and Cr. At the phylum level, the most numerous phyla in the studied soils were *Acidobacteria*, *Proteobacteria*, *Chloroflexi* and *Actinobacteria*, accounting for about 89.89% of all bacteria. The most abundant phylum, *Acidobacteria*, averaged at 37.28% in acid samples and 22.92% in neutral samples. Most bacteria were positively correlated with HMs in both acidic and neutral soils. In acidic soils, *Rhodobium*, *Sphingopyxis*, *Streptomyces*, *Burkholderia*, *Mucllaginbacter*, *Phenylobacterium*, *Flavobacterium* and *Arthrobacter* were positively correlated with one or more HMs (Sb, As, Cd and Zn). In neutral soils, *Gaiella*, *Arthrobacter*, *Nitratireductor*, *Iamia*, *Chryselinea*, *Rhodobium*, *Candidatus*, *Entotheonella*, *Sphingomonas*, *Steroidobacter*, *Solirubrobacter* and GAL15 were positively correlated with several HMs (Zn, Sb, As, and Cd). In addition, *Acidothermus*, *Anaeromyxobacter*, *Acinetobacter*, *Delftia*, *Citrobacter* and *Stenotrophomonas* were highly positively correlated with Cr.

The acidity of soils contaminated with HMs has a dual effect on changes in the structure of soil bacterial communities. Changes in pH, which lead to an increase in the solubility of HMs and metalloids, amplify their toxicity and biological effects, and influence the structure of the bacterial community. On the other hand, depending on soil acidity, an ecological niche that promotes the prosperity of certain bacterial taxa, regardless of HM presence, is created. In addition to pH, the presence of other salts can affect solubility and, consequently, bioavailability of HMs. Thus, salinity stress contributed to an increase in cadmium bioavailability [38] due to the destabilization of soil aggregates and movement of Cd from large soil aggregates into smaller fractions. The authors have shown a significant role of taxa such as *Sphingomonadaceae*, *Pyrinomonadaceae*, *Nitriliruptoraceae*, *Bacillaceae*, *Halomonadaceae* and *Pseudomonadaceae* in the "fate" of cadmium. Proteobacteria were the most numerous phyla found in soils contaminated with cadmium.

In the study of bacteriocenosis of soil contaminated with Cr by wastewater from tanneries (Vellore district, Tamil Nadu, India), the relative abundance of individual bacterial taxa at the family and genus levels were shown, namely *Lactobacillaceae* (24%), *Desulfobulbaceae* (13%), *Staphylococcaceae* (10%), *Enterococcaceae* (6%), *Desulfovibrionales* (5%), *Carnobacteriaceae* (5%), *Desulfobacteraceae* (4%), *Enterobacteriaceae* (4%), *Acetobacteraceae* (3%) and *Geobacteraceae* (3%) [33]. Researchers attribute the dominance of these bacteria to their active participation in lessening chromium toxicity by reducing it from Cr (VI) to Cr (III). As a result of this reduction, the solubility of chromium decreases, and its bioavailability and toxicity fall.

In another study on the bacterial communities of the same soils [34], taxonomic profiling at the genus level revealed 177 genera of bacteria. In the studied soil, the following bacterial OTUs (%) were the most abundant: *Acidobacteria* (48.47), *Deltaproteobacteria* (9.70), *Alphaproteobacteria* (6.80), *Gammaproteobacteria* (5.70), *Clostridia* (3.10), *Epsilonproteobacteria* (2.60), *Bacilli* (2.50), *Actinobacteria* (1.40) and *Flavobacteria* (1.20). The analysis of metagenomic data revealed the dominance of the *Proteobacteria*, *Firmicutes* and *Bacteroidetes* phyla. Gamma proteobacteria play an important role in the oxidation of sulfides and lead to the biodegra-

dation of pollutants, while *Alphaproteobacteria* and *Deltaproteobacteria* show high resistance and the ability to bioremediate Cr through bioabsorption, bioleaching, biomineralization, intracellular accumulation and enzyme-catalyzed transformation in the presence of HMs. Firmicutes show resistance to environmental stressors, such as hypersalinity, low oxygen levels and the presence of pollutants in soil and water systems. Bacteroidetes are involved in the biodegradation of various organic pollutants, survive in low oxygen conditions, and also efficiently degrade resistant proteins. In general, the results of the study showed that this bacterial community plays an important role in the bioreduction and immobilization of chromium, and exhibits syntrophy during decomposition of complex leather industry waste in soil.

Park et al. [27] showed that bacteriocenosis is influenced not only by the concentration of HMs and metalloids, but also by their bioavailability, as well as combined contamination with different metals. The effect of Sb and other toxic metals (loids) (As, Cu, Zn and Pb) on soil bacteria, in the vicinity of an existing Sb processing plant and a nearby landfill in South Korea, was studied. There were clear differences in α- and β-diversity, as well as in the number of bacteria between groups with extreme Sb content and groups with low and high Sb content. Interestingly, it was not possible to find a direct correlation between the concentration of stibium in soils and changes in the bacterial community composition. This can be explained by the fact that at a high concentration in soil (up to 2%), its bioavailability was low. Pb, which was present in high total concentrations in the samples from extreme groups, was likely a significant factor influencing the bacterial community composition here.

In the paper devoted to the study of genetic material associated with As metabolism in the soils of a gold-mining area in the northwest of Beijing, China, interesting data were provided on the distribution of such genes, depending on the arsenic concentration, sampling depth, taxonomic composition of the bacterial community, soil pH, etc. [32]. The results of the study showed that arsenic recovery is an effective way of As detoxification by soil bacteria in gold mine tailings. Thus, among the studied gene clusters in samples with different contents of As and soil layers, the largest percentage (50.05–56.06%) falls on the As reduction genes (*arsABCDRT* and *acr3*). The researchers found that the *arsBCR* content increased with increasing As concentration. Interestingly, the *acr3* gene was not found in the upper soil layer (0–20 cm). The frequency of occurrence of As oxidation (*aioABERSX*) and arsenate respiration (arrAB) genes was 17.86–20.45% and 11.44–14.76%, respectively, relative to the abundance of the gene set. Moreover, the *aioE* and *arrAB* genes were the most abundant in samples with a high content of arsenic (3892–7785 mg/kg). Their content decreased in samples, with an average level of contamination at 95–479 mg/kg, and was minimal in slightly contaminated samples (13–25 mg/kg), while the *aioARS* genes had the opposite distribution pattern. The occurrence of arsenic methylation genes (*arsMPH*) was 11.29–17.99%, and was similar to the abundance of the respiration gene.

Thus, soil bacterial communities not only change their structure under the influence of HMs and metalloids, relatively enriching the taxa of bacteria that are resistant and successfully adapt to the pollution of this kind, but also actively participate in the remediation of these pollutants by changing the oxidation state catalyzed by enzymes, solubility and bioavailability, as well as absorption, leaching, mineralization and intracellular accumulation.

The results of the study of soils with different levels of As contamination showed that metallic arsenic is the most significant factor for the content of arsenic transformation genes. However, other metals (-loids), such as Pb, Cu, Zn and Cd, as well as the soil pH of abandoned gold mine tailings, also had their effects [32]. The highest biodiversity was observed in soils with high and medium levels of As contamination. In such communities, *Actinobacteria* dominated at different depths (32.6–38.9%). *Proteobacteria* were the second most common phylum (21.8–26.7%), followed by *Acidobacteria* (12.7–16.6%) and *Chloroflexi* (6.2–7.8%). The main phyla with the highest positive correlation with metals and metalloids content were *Chlorobi*, *Proteobacteria*, *Planctomycetes* and *Nitrospirae.*

Mercury can also alter the bacterial community structure, reduce diversity and is toxic to soil bacteria [19,44]. However, it should be taken into account that the form of mercury is also of great importance. Thus, Frossard et al. [45] showed that bioavailable, especially water-soluble Hg (WHg), can play a more significant role in changing the bacterial community than total Hg in contaminated soil, and cause a decrease in the bacterial community biodiversity. Soil samples from China, from areas with a 600-year history of mercury mining, were studied [31]. The content of mercury in the samples ranged from 0.27 to 52.4 mg/kg, and in most samples exceeded 0.6 mg/kg. The total number of bacteria in the samples decreased with the increase in the total mercury content, and was also negatively correlated with the content of methylmercury in the soils of rice fields. At the same time, bacterial diversity (Shannon index) positively correlated with the total content of Hg, and in rice soils it increased with the increase in the content of MeHg. It should be noted that the relative abundance of *Nitrospirae* was negatively related to the content of MeHg. The decrease in the number of *Nitrospirae* was mainly due to the relative decrease in the genus *Nitrospirales* 0319.6A21sp. This suggests that sensitive taxa can be used as environmental indicators of mercury pollution in terrestrial ecosystems.

Thus, soil acidity and the form and degree of the metal (-loid) oxidation affect its solubility, bioavailability and, as a result, its toxicity to soil bacteria, biodiversity and bacterial community structure. On the other hand, the HM selective pressure promotes the selection and accumulation of resistant taxa that can carry the genes for metal (-loid) metabolism enzymes and participate in their remediation by changing the bioavailability, solubility, oxidation state, as well as due to sorption and intracellular accumulation.

Therefore, numerous chemical soil properties discussed above, as well as biological factors and exposure duration discussed in the next section, can have a significant modulating effect on biological activity and toxicity of metals and metalloids in relation to bacterial communities. These modulating factors, considered in the analyzed publications, are presented in Figure 2.

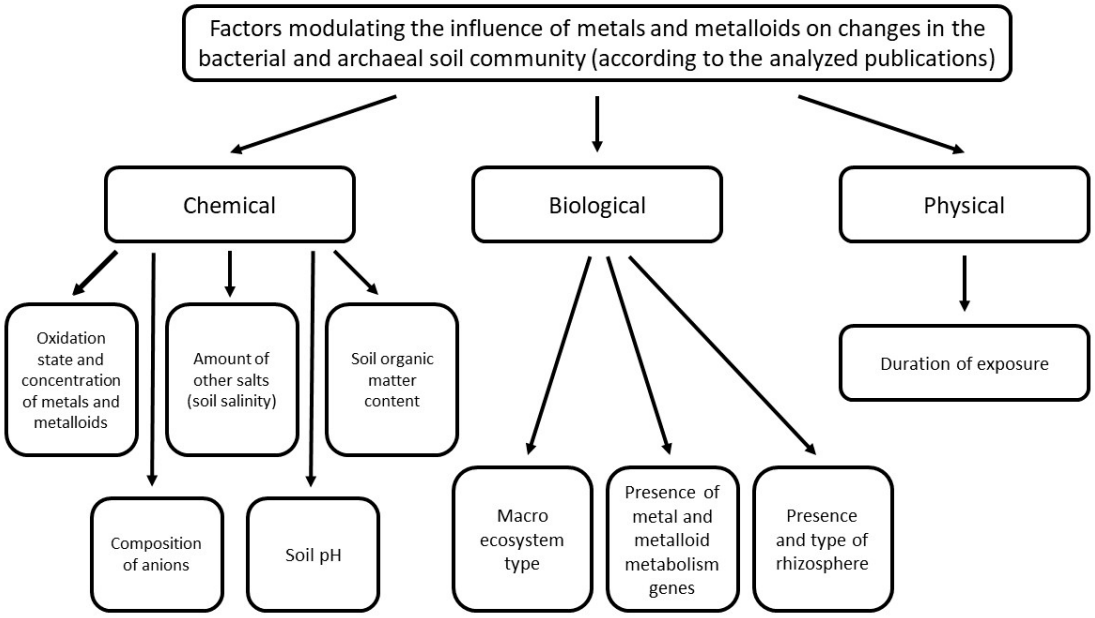

Figure 2. Factors modulating the influence of metals and metalloids on changes in the bacterial and archaeal community (according to the analyzed publications).

4. The Role of Ecosystem Type, Concentration and Duration of Exposure to Heavy Metals

The bacterial community composition is also significantly affected by the type of ecosystem and the level of pollution in it [41]. The bacterial community of soils in long-

term, lead-contaminated contrasting ecosystems (soils under deciduous and coniferous forests, as well as hydromorphic soils) was studied. The most common phyla of bacteria in these soils were *Acidobacteria*, *Actinobacteria*, *Verrucomicrobia*, *Chloroflexi*, *Planctomycetes*, *Bacteroidetes* and *Gemmatimonadetes*. In the soils of coniferous forests, a lower proportion of *Acidobacteria* and *Proteobacteria* was found compared to deciduous forests and hydromorphic soils. On the contrary, coniferous soil samples were characterized by a higher proportion of *Actinobacteria* (18%) than deciduous (12%) and hydromorphic (8%) soils. *Proteobacteria* and *Chlamydiae* were more abundant in heavily polluted samples than in moderately polluted samples in all types of ecosystems. On the contrary, the content of *Verrucomicrobia* decreased with increasing levels of lead contamination.

On the other hand, *Proteobacteria*, *Bacteroidetes*, *Firmicutes*, *Acidobacteria* and *Actinobacteria* dominated mangrove sediments (Kerala, India) contaminated with cadmium and zinc. In all samples, the majority of the reads belonged to the *Proteobacteria* phylum (53.593–75.99%), and was annotated to the classes *Gammaproteobacteria* and *Deltaproteobacteria* [40]. Genus-level analysis showed predominance of *Anaeromyxobacter*, *Geobacter*, *Pseudomonas*, Candidatus *Solibacter* and *Pelobacter* in the studied datasets. In the course of functional annotation of the metagenomic analysis data, the authors determined a significant distribution of Co/Zn/Cd resistance genes in the bacteriocenosis.

When conducting a study in soil microcosms artificially contaminated with cadmium ($CdCl_2$ in the amount of 50 mg/kg) and a mixture of phenanthrene and n-octadecane (in the amount of 1000 mg/kg), the functional stability of the bacterial community was established, which returned to its original abundance in 90 days after the start of the experiment [23]. Differences between day 0 and day 90 samples were significantly smaller in functional profiles than in taxonomic profiles, with the former changing faster than the latter. In this work, bacterial communities showed a clear pattern of succession in response to pollution, the alpha diversity of the soil first decreased and then recovered. For OTU taxonomic profiles, with an average relative abundance of >0.005%, two clusters were clearly identified in the experiment. The first cluster included 48 OTUs, the population levels of which first increased and then decreased. OTUs in cluster 1 mainly belonged to the genera *Massilia*, *Lysobacter*, *Pseudoduganella* and *Bacillus*, indicating their potential for hydrocarbon degradation and metal tolerance. The second cluster included 884 OTUs, which first decreased in number and then recovered to their original level. It was dominated by the genera *Gaiella*, *Perlucidibaca*, *Sphingomonas*, *Nocardioides* and *Aeromicrobium*. This can probably be explained by the fact that bacteria included in cluster 2 were inhibited by HM toxicity at the early stage of contamination, but later they could adapt to this stress condition due to a high growth rate and evolutionary adaptation. By the end of the incubation period (90 days), the bacterial community composition of the experimental soils was also significantly affected by the species of leguminous plants which the microcosms were sown with.

In another work, a decrease in the richness and an increase in the diversity of bacteria (Chao and Shannon indices, respectively) were shown with the increase in the HM concentration [15]. When studying the combined effect of HM fractions on bacterial communities in soils contaminated with Pb, Cd and Zn, it was found that long-term exposure to HMs on bacteria changed the richness, diversity and structure of their communities. Here, acid-soluble Pb was also the main factor influencing the bacterial community structure. The predominant phyla of bacteria in chronically contaminated soils were *Bacteroidetes*, *Acidobacteria*, *Chloroflexi*, *Proteobacteria* and *Actinobacteria*, which accounted for more than 85% of the total soil bacteria. Taxa (*Marmoricola*, *Nocardioides* and *Gibberella*) sensitive to HMs were found, which were proposed to be used as bioindicators of soil pollution by these metals.

Molecular methods were used to study the impact of HM pollution on the structure of the bacterial community in the soil of Picher, an abandoned mining town in Oklahoma, USA [9]. The number of bacteria negatively correlated with the concentrations of Pb, Cd, Zn and Mg. No correlations were found between the diversity indices of the entire

community with the concentrations of four metals important for the study area (Al, Pb, Zn and Cd). However, for seven phyla (*Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, *Chloroflexi*, *Planctomycetes*, *Proteobacteria* and *Verrucomicrobia*), individual correlations were found between HM concentration and bacterial abundance for at least one of the four metals selected for analysis (Al, Cd, Pb and Zn).

The negative impact of HMs (Cd, Cu, Zn) on bacterial biomass was also described in Song et al. [18] when studying the soil of rice fields in China. Bacterial biomass decreased with increasing concentration of HMs in soil, in both long-term and short-term experiments. Copper had the strongest effect on bacterial biomass and bacterial community compared to Zn and Cd. A synergistic effect of HMs was found, and the synergistic effect between Cu and Cd was greater than Cu and Zn.

The structure of the soil bacterial community in six rice fields contaminated with antimony, and arsenic was most strongly influenced by the content of nitrates, As, Sb and Fe (III) [25]. *Bradyrhizobium*, *Bryobacter*, Candidatus *Solibacter*, *Geobacter*, *Gemmatimonas*, *Halingium* and *Sphingomonas* were identified as the main phyla of the studied soils. These taxa strongly correlated with As and Sb impurity fractions and are likely to be able to metabolize As and Sb. As and Sb showed stronger effects on soil bacterial diversity compared to soil properties. The authors believe that the main microbiome identified in this study may have been shaped by exposure to Sb and As contamination.

In the study of agricultural soils and mine soils with a high arsenic content from the state of Guanajuato, Mexico [26], the dominance of *Proteobacteria*, *Acidobacteria* and *Actinobacteria* was noted in the composition of bacterial communities. The *Proteobacteria* phylum was the most abundant, accounting for 39.6% in agricultural soils and 36.4% in mining soils. *Acidobacteria* were the second most abundant at 11.6% and 24.2%, while *Actinobacteria* accounted for 19.0% and 14.2% in agricultural and mining bacterial communities, respectively. In this study, the widespread distribution of the *Bradyrhizobium* genus bacteria and uncultivated organisms of the *Rhodospirillaceae* family was also noted. Bacterial isolates capable of reducing As were isolated from mine soils, containing 39 mg/kg of As (versus 15 mg/kg of As in agricultural soils). All of them were identified as representatives of the genera *Bacillus* and *Williamsia*. Such microorganisms are the adaptation of the bacterial community to the high content of arsenic and can affect its bioavailability, mobility and content in soils.

Agricultural soils in the Hengshi River Basin, in the Dabaoshan Mining District (Guangdong, China), are heavily polluted by acid mine drainage (AMD) irrigation. The result of such irrigation was a decrease to values of 4.3–5.5 in soil pH. In the control plot, soil pH was 6.5. In addition, under the influence of AMD, the content of SO_4^{2-} and HMs (Cu (43.56–249.89 mg/kg), Pb (43.79–144.50 mg/kg), Zn (70.33–293.06 mg/kg) and Cd (0.34–2.91 mg/kg)) increased significantly [6]. The result of the study of these soil microbiomes found that they are dominated by *Acidobacteria*, *Proteobacteria* and *Chloroflexi*, which accounted for >70% of all identified sequences. The most abundant phylum was *Acidobacteria*, which accounted for 29% to 38% of the soil bacteria. The control plot was dominated by *Chloroflexi* (29%) and *Proteobacteria* (24%), while *Acidobacteria* made up a smaller proportion of the total bacterial community than in the contaminated plots. Among archaea, the *Crenarchaeota* (62–86%), *Euryarchaeota* (8.9–31%) and *Parvachaeota* (3.8–6.5%) phyla predominated the contaminated areas. The same three phyla also dominated the reference plot, accounting for 48% (*Euryarchaeota*), 34% (*Crenarchaeota*) and 19% (*Parvachaeota*), respectively. At the levels of phylum and class, the bacterial taxa *Acidobacteria*, *Deltaproteobacteria* and *Ktedonobacteria*, as well as the archaeal phylum *Crenarchaeota*, dominated the soils contaminated with AMD. At a lower taxonomic level, the heavily polluted sites were dominated by *Koribacteraceae*, *Acidobacteriales* and *Solibacteriales*, while the control site was dominated by *Methanosarcinales*, *Methanocella* and *Nitrososphaerales*. HMs such as Cu, Pb and Zn were positively correlated with *Acidobacteria* and *Crenarchaeota* and, conversely, negatively correlated with *Proteobacteria* and *Euryarchaeota*, while Cd was highly correlated with *Methanoregula*. Predominance of *Acidobacteria* in contaminated sites suggests that chronic irrigation of rice

soils with acid mine drainage may form a specific ecological niche favored by acidophilus bacteria. For archaea, irrigation of soils with AMD results in a change in dominance from *Euryarchaeota* to *Crenarchaeota*.

In the work of Fajardo et al. [14], it was shown that stress in bacteria exposed to HMs in contaminated soil causes a shift in the composition of the bacterial community, and different groups of bacteria react differently to pollution. We studied the impact of high concentrations of HMs (Pb, Zn and Cd) on the soil bacterial community for 160 days. The HM mixture caused selective pressure on the soil microbiome, and the bacterial composition of the samples changed dramatically as the exposure time increased. The number of representatives of the phyla *Proteobacteria*, *Actinobacteria*, *Verrucomicrobia* and *Bacteroidetes* clearly decreased after incubation with HMs (thus, they were the most sensitive taxa). *Firmicutes* turned out to be the most HM-resistant phylum, as its relative number in the bacterial community structure increased after incubation with HMs.

The opposite trend was found by Lin et al. [17]. In the heavily contaminated soils of rice fields on the east coast of China, the abundance of *Proteobacteria* was significantly higher than in other soil samples, while the relative abundance of *Verrucomicrobia*, *Firmicutes* and *Chloroflexi* was significantly lower than in clean soils. Bacterial phyla *Proteobacteria*, *Acidobacteria* and *Bacteroidetes* showed a greater resistance to HM contamination in areas with high, medium and low HM contamination, respectively. The alpha diversity of bacteria in soils with high, medium and no HM contamination was higher than in soils with a low level of HM contamination.

The inhibitory effect of vanadium on the richness and diversity of bacterial communities in soils contaminated with it has been shown [5]. Long-term (240 days) exposure of different soil samples to vanadium led to the fact that initially different bacterial communities became similar to each other and consisted of *Proteobacteria*, *Acidobacteria* and *Actinobacteria*, with the predominance of bacteria that can bear or reduce the toxicity of vanadium [29].

High concentrations of cadmium also negatively affect the richness and diversity of soil bacteria [22]. However, cases have been described when, at different levels of cadmium contamination, the diversity of bacterial composition did not undergo significant changes [24]. The authors believe that the Cd dose in the study areas was still not high enough to suppress bacterial activity, and the Chao index (alpha diversity) was positively correlated with total and bioavailable soil cadmium.

In the work of [21], there was no short-term (30 days) effect of mercury pollution on the structure and activity of the bacterial community. However, long-term (years-long) mercury pollution had a significant impact on the structure and diversity of bacterial communities. Interestingly, the abundance of bacteria and the Shannon diversity index were increased in areas with high and medium pollution compared to areas with low pollution. It was shown that bacteriocenosis adapted to long-term high Hg content in the soil. The bioavailability of mercury can increase when organic additives (humic and fulvic acids) are introduced into the soil, which leads to a decrease in bacterial diversity in the treated soils [20]. An increase in Hg content was positively associated with the relative abundance of *Firmicutes* and *Bacteroidetes*, *Chitinophagaceae*, *Ferruginibacter*, *Sphingobacteriaceae*, *Pedobacter* and *Clostridium* sensu stricto 1 [31]. *Firmicutes* and *Bacteroidetes* are fast growing opportunistic phyla that can benefit from environmental disturbance by occupying niches normally occupied by other bacterial taxa. Taxa such as *Proteobacteria*, *Bacteroidetes* and *Actinobacteria*, which can carry the *Hg merA* resistance gene also tended to increase in number with an increase in the total content of Hg and $[CH_3Hg]^+$ in soils. According to the authors, absence of the mercury pollution effect on the number of bacteria in short-term experiments may be due to the fact that the dead bacteria DNA was also extracted from the soil, and the abundance of bacteria was evaluated using quantitative PCR, hiding the adverse effects of mercury.

The metagenome of uranium tailings soils in the south of China was studied [30]. Uranium concentrations in contaminated samples exceeded 40 mg/kg, which is almost 10 times the concentration in uncontaminated samples. Comparison of the bacterial community

structures at the level of phyla showed that at different depths (0–15, 15–30, and 30–45 cm, respectively), they were similar. Regardless of the depth, the five dominant bacterial groups were *Actinobacteria* (14.4–60.7%), *Proteobacteria* (29.9–49.6%), *Planctomycetes*, *Acidobacteria* and *Firmicutes* [30]. At the genus level, the proportion of several genera (*Robiginitalea*, *Microlunatus*, *Alicyclobacillus* and *Azorhizobium*) in radioactive soil was significantly higher than in uncontaminated soil, indicating that these bacteria are better adapted to the environment contaminated with uranium than others. The results of the study showed that alpha diversity in uranium-contaminated soil was much lower than in uranium-free soil, and, accordingly, there were fewer phyla of bacteria in the radioactive soil. At the same time, beta diversity increased with increasing sampling depth, and, accordingly, the difference in species composition between contaminated and uncontaminated soil increased with increasing soil depth. Most of the dominant genera in this study, such as *Azorhizobium* (α-proteobacteria), *Chelativorans* (α-proteobacteria), *Variovorax* (β-proteobacteria), *Delftia* (β-proteobacteria) and *Citrobacter* (γ-proteobacteria) belong to *Proteobacteria*. The results of this study showed that proteobacteria are the most adaptable phylum in the environment, and it can be used to remediate a uranium-contaminated environment.

Based upon the data above, *Proteobacteria*, *Acidobacteria* and *Actinobacteria* dominate polluted soils in all types of ecosystems; *Bacteroidetes*, *Firmicutes* and *Chloroflexi* also make up a significant proportion of the bacterial community. Thus, contamination with metals (-loids) has no less strong influence on bacterial community formation than other environmental conditions. The dominance of these taxa is likely associated with resistance and the ability to adapt to HMs.

As a rule, high HM content in soil reduces the alpha diversity of bacterial communities [6,15,30]. However, cases were noted when HM contamination increased [17,21] or did not change [24] the level of species richness (Chao index) of the bacterial community. This may be due to moderate concentrations of HMs, which stimulate the growth of resistant bacteria without significant suppression of species sensitive to HM contamination. In addition, for some HMs, a more even distribution of taxa (Shannon diversity index) was noted in areas with medium or high levels of pollution [21].

The effect of HM contamination on the soil bacteriocenosis is significantly time dependent. Thus, at short-term exposure to mercury for 30 days, no changes in the structure of the bacterial community were noted [21]. In soil microcosms polluted with hydrocarbons and cadmium, during a 90-day experiment, the succession of the bacterial community was noted, during which first a drop and then a restoration of the number of bacteria sensitive to pollutants was observed [23]. Resistant species displayed reversed dynamics and the community has largely recovered, at least functionally. Despite the dominance of these types of bacteria in naturally contaminated soils, the abundance of *Proteobacteria*, *Actinobacteria*, *Verrucomicrobia* and *Bacteroidetes* decreased when exposed to HMs for 160 days [14]. That is, representatives of these phyla of bacteria need a sufficiently long period of adaptation to HMs in order to dominate in bacterial community. Interestingly, the impact of vanadium on different bacterial communities of various soils for 240 days led to similarity of bacteriocenoses and dominance of the already mentioned *Proteobacteria*, *Acidobacteria* and *Actinobacteria* [5]. Unlike short-term exposure, long-term exposure to HMs (particularly mercury) changes the structure of soil bacterial community [21]. It is likely that the results of short-term studies of the HM effects on the soil bacterial communities structure are influenced by the methods used. Since extracellular bacterial DNA can persist in the soil for a long time, metagenomic DNA PCR can distort the results of short-term experiments [31].

5. Effects of Heavy Metals on Rhizosphere Bacterial and Archaeal Community

When studying the genetic diversity of bacterial communities in the rhizosphere of Ni hyperaccumulator plants (*Odontarrhena chalcidica*, *O. smolikana*, *O. rigida*, and *Noccaea ochroleuca*) in Albania, 14 phyla of bacteria were identified. The main phyla (>1% of the total number of sequences) were in the following order: *Proteobacteria* (31.7% ± 4.9) > *Acidobacteria* (19.2% ± 4.2) > *Actinobacteria* (16.0% ± 3.4) > *Gemmatimonadetes* (10.0% ± 3.4) > *Chloroflexi* (7.8% ± 2.1)

> *Bacteroidetes* (7.4% ± 4.0) > *Nitrospirae* (2.4% ± 2.5) [37]. *Proteobacteria* showed a negative correlation with magnesium and nickel content, *Acidobacteria* had a positive correlation with Ni, *Gemmatimonadetes* displayed a negative correlation with Fe, Ca, N, C and C organic concentrations, *Chloroflexi* correlated positively with Mg, and *Bacteroidetes* showed a negative correlation with Mg and Pb in the soil. In the rhizosphere of nickel hyperaccumulators, *Proteobacteria* were the dominant phylum. *Acidobacteria* and *Actinobacteria* also made up a significant part of rhizosphere bacterial communities. At the same time, it is known that *Proteobacteria* and *Actinobacteria* prefer soils rich in organic carbon, which is typical for the rhizosphere. *Acidobacteria* are likely to receive protection from elevated pH values in the rhizosphere, as pH is the most prominent among the environmental factors that correlate with their abundance in soils.

It was quite unexpected that the *Chloroflexi* phylum reached an average relative abundance of only 7.8%, since this phylum, which is typical of chemically extreme soils, was found to be dominant in nickel mine dump samples [36,46]. Recently, it was also found to be the most dominant phylum in the rhizosphere of the hyperaccumulator plant *O. chalcidica* growing on the ultrabasic soils of continental Greece [36].

The influence of cadmium pollution level was also studied by planting *Robinia pseudoacacia*, along with inoculation with rhizobia on the composition of the soil bacterial community [35]. The level of pollution has been established to be the factor most strongly affecting the structure of the bacterial community. The two levels of contamination (4.52 ± 0.24 and 20.52 ± 0.73 mg/kg Cd) comparison showed that the proportion of *Gemmatimonadetes*, *Bacteroidetes*, *Cyanobacteria*, *Planctomycetes*, *Armatimonadetes* and *Elusimicrobia* was significantly lower in heavily contaminated soil. On the contrary, the share of *Acidobacteria*, *Chloroflexi*, *Nitrospirae*, *Verrucomicrobia* and *WS3* in heavily polluted soil increased. The second most impacting factor for the bacterial community was *Robinia pseudoacacia* planting. The mean alpha diversity was lower in the rhizosphere than in the non-rhizosphere soil. The proportion of *Proteobacteria* and *Bacteroidetes* was significantly higher in rhizosphere samples compared to soils outside the rhizosphere at both pollution levels, while the proportion of *Acidobacteria*, *Gemmatimonadetes*, *Chloroflexi*, *Nitrospirae*, *WS3*, *Armatimonadetes* and *Elusimicrobia* was clearly lower in the rhizosphere. On the contrary, inoculation with symbiotic rhizobia had little effect on the structure of the bacterial community. The relative abundance of genera such as *Mesorhizobium*, *Lentzea*, *Nocardioides*, *Streptomyces*, *Variovorax*, and *Rhodococcus* increased in the inoculated rhizosphere compared to the non-inoculated control. The results of the study showed that soil conditions exerted greater selection pressure on bacteria in the soil groundmass and *R. pseudoacacia* rhizosphere than plants did, and that bacterial diversity in both the rhizosphere and soil samples decreased with increasing levels of contamination.

The structure of the rhizospheric bacterial community of *Elsholtzia haichowensis*, a well-known indicator of elevated copper content, widespread in China on copper-contaminated soils, was studied [47]. Samples of rhizosphere soils were taken from contaminated areas with various degrees of Cu contamination near copper mines and in a non-metallic area. At contaminated sites, Cu concentrations in soil ranged from 502 to 2760 mg/kg, while Zn concentrations ranged from 127 to 2100 mg/kg. The highest indices of alpha diversity were found in the *E. haichowensi* rhizosphere or bulk soils of the non-metallic region, while the lowest indices were found in the most polluted non-rhizospheric soils. In all soils, the alpha diversity indices of archaea were significantly lower than those of bacteria. Bacterial OTUs belonged to 49 phyla, with the following dominating with more than 1%: *Proteobacteria* (33.84%), *Acidobacteria* (22.89%), *Bacteroidetes* (9.10%), *Actinobacteria* (7.71%), *Chloroflexi* (7.65%), *Gemmatimonadetes* (4.58%%), *Cyanobacteria* (3.67%) and TM7 (1.62%). OTUs of archae belonged to three phyla, with *Crenarchaeota* accounting for 94.26%, followed by *Parvarchaeota* (3.11%) and *Euryarchaeota* (2.50%). In this study it was found that environmental factors, according to the degree of influence on the structure of the microbiocenosis, can be arranged in the following order: soil pH > heavy metals > nitrogen

> soil texture. HMs, primarily Cu and Zn, but also Cr, Ni and Cd, account for most of the variation in all domains, indicating their strong influence on the entire bacterial community.

The dominant genus of the ammonia-oxidizing archaea positively correlated with total Cu was Candidatus *Nitrososphaera gargensis* (4.88–99.54%), possessing a Cu-translocating ATPase and a putative Cu transport system (CopC-CopD) that contribute to its resistance to Cu [48,49]. The bacterial genera *Bradyrhizobium* and *Flavisolibacter* dominated metal-bearing soils, accounting for 0.21–4.99% and 0.07–16.88% of the bacterial profile, respectively; their abundance positively correlated with the content of HMs. In this study, it was found that rhizosphere had a higher number of bacteria than non-rhizosphere soils. This may be due to root exudates, which are secreted by host plants and can stimulate bacterial growth, activity and turnover [50,51].

The presence of HMs in the rhizosphere of *E. haichowensis* as the dominant plant in the studied metal-bearing areas (Tonglushan and Fengjiashan, China) can be considered a key factor in influencing the rhizosphere bacterial community. The authors showed that *E. haichowensis* can reduce the availability of HMs, and thus reduce their toxicity to rhizospheric bacteria.

The abovementioned works show that *Proteobacteria* dominate the rhizosphere bacterial communities of soils contaminated with HMs. *Acidobacteria*, *Actinobacteria*, *Bacteroidetes* and *Chloroflexi* also have a significant abundance in them. The rhizosphere had a higher bacterial abundance and biodiversity than non-rhizosphere soils. At an increase in the level of soil contamination, the number of representatives of *Acidobacteria*, *Chloroflexi* and *Nitrospirae* usually increased.

General effects of metals on rhizosphere soil bacterial community, considered in the abovementioned publications, are presented in Figure 3.

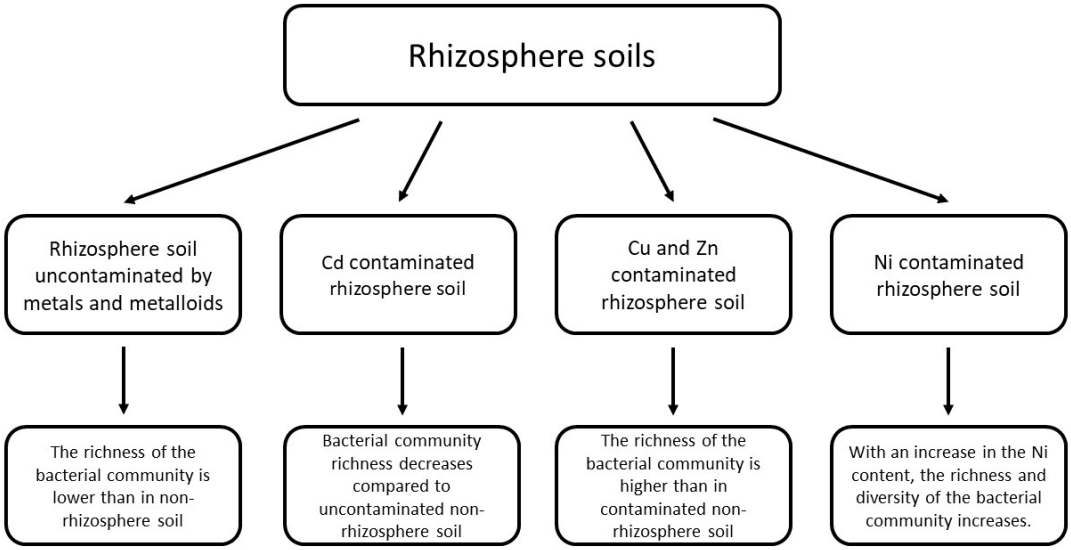

Figure 3. General effects of metals on rhizosphere soil bacterial community (according to the analyzed publications).

6. Prospects for the Development of Research

Studies have shown that bacterial taxa are very closely related to each other and form a single ecological network consisting of ecological clusters [52,53]. These clusters probably maintain soil fertility, provide nutrient cycling, and perform other fairly sustainable ecological functions [54–56]. The stability of bacterial ecological clusters is probably due to the fact that the bacteria that make up the clusters often have specific ecological niches and are metabolically related to each other. For example, it has been established that taxa in some ecological clusters have a close relationship with the soil pH level, the soil moisture degree, the type of macro-ecosystem, as well as the spectrum and availability of organic and inorganic substrates [52]. These results suggest that the metagenomic assessment

of soil bacterial communities can identify sensitive taxa, which can be used as potential environmental indicators of pollution with various HMs and the disturbance of soil ecosystem functions. The selection and detailed study of sensitive indicator taxa and clusters could lead to introduction of rapid and efficient metagenomic methods for diagnosing ecological health, sustainability and productivity, and qualitative, and possibly quantitative, soil contamination.

Another very promising line of research in our opinion is related to rhizosphere bioremediation of HM pollution. Unlike organic pollutants, HMs are not degraded, but are extracted or stabilized by plants [57,58]. Rhizospheric bacteria affect HM transformation by changing the soil pH, releasing chelating substances, and changing the redox potential [59]. They are also able to increase plant productivity by secreting plant hormones and improving nutrient availability [60].

In this context, plants capable of HM hyperaccumulation are of particular interest. The Ni hyperaccumulators discussed above can serve as an example. This Ni-hyperaccumulative flora can be a candidate for use in bioextraction and phytomining [61–63]. As it is known, bacteria can change the degree of oxidation, mobility, and also accumulate HMs. However, HMs, at least those that do not form volatile compounds, cannot be removed from the soil only due to bacterial activity, and plants must participate in HM bioremediation processes. Therefore, for the development of sustainable, environmentally friendly, and cost-effective biotechnologies for HM removal from contaminated soils, it is extremely important to search for and study HM-hyperaccumulator plants, as well as to ensure the efficient operation of their rhizosphere. When using effective hyperaccumulators, not only is HM phytoextraction from soil possible, but, in the case of precious metals, their phytomining is also feasible.

7. Conclusions

Soil contamination with HMs is a significant problem for the modern world and especially for agriculture, which largely depends on the "health" of soil. The study of soil bacterial communities is currently widely used to assess the degree of human activity negative impact. However, according to the results of the studies carried out, it is difficult to unambiguously determine how pollutants affect the taxonomic composition and diversity of soil bacteria. This may be due to the fact that soil is an extremely heterogeneous habitat, in which many factors are combined: pH, texture, organic matter content, moisture, temperature, vegetation cover, etc. In addition, the design of the experiment also plays a significant role, as the difference in results between long-term field and short-term laboratory tests is shown.

A number of studies have shown the possibility of soil bacteriocenosis adaptation to long-term (years-long) impacts of pollutants, while an acute, relatively short-term impact negatively affects the richness and diversity of soil bacteria. For example, long-term exposure to HMs can lead to tolerance emergence in the bacterial community, because sensitive bacteria die out, and tolerant taxa survive under stressful conditions. Thus, soil bacteria can adapt to long-term heavy metal pollution by changing the taxonomic composition and structure of the bacterial community, while maintaining the functional diversity and ecological roles of the microbiome. On the other hand, at low concentrations, HMs (Zn, Cu, Cd, Hg) can even increase the number and diversity of bacteria. To a large extent, the toxicity of a pollutant depends on the dose, as in the case of Fe, Ni, Cd, for which a weak correlation with bacterial diversity was found, for example.

The resistance of soil bacterial communities can possibly be explained by functional redundancy, i.e., by the fact that the functions of the species that are sensitive to pollution can be replaced by the functions of the species that are resistant to pollution, which were already present in the soil in small quantities. Bacteria are also able to survive a wide range of environmental changes through gene changes, resulting in increased resistance to pollutants. Thus, soil bacterial communities are complex, finely regulated systems,

sensitive to pollution, and at the same time possessing an amazing potential for adaptation and restoration of structure and function, even in the most adverse conditions.

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