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Interactions between Hg and soil microbes: microbial diversity and mechanisms, with an emphasis on fungal processes

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Abstract

Mercury (Hg) is a highly toxic metal with no known biological function, and it can be highly bioavailable in terrestrial ecosystems. Although fungi are important contributors to a number of soil processes including plant nutrient uptake and decomposition, little is known about the effect of Hg on fungi. Fungi accumulate the largest amount of Hg and are the organisms capable of the highest bioaccumulation of Hg. While referring to detailed mechanisms in bacteria, this mini-review emphasizes the progress made recently on this topic and represent the first step towards a better understanding of the mechanisms underlying Hg tolerance and accumulation in fungal species and hence on the role of fungi within the Hg cycle at Hg contaminated sites.

Key points:

- The fungal communities are more resilient than bacterial communities to Hg exposure
- The exposure to Hg is a threat to microbial soil functions involved in both C and nutrient cycles
- Fungal (hyper)accumulation of Hg may be important for the Hg cycle in terrestrial environments
- Understanding Hg tolerance and accumulation by fungi may lead to new remediation biotechnologies

Keywords: mercury (Hg) - soil - fungi - chronic/acute exposure - environment - communities

Introduction

History of Hg contamination

Long before modern science, the trace element (TE) mercury (Hg) was found to be a very special metal because of its particularities. Indeed, Hg found in cinnabar ore (HgS) has specific chromatic properties and can be used as a pigment to apply brilliant red colour (vermilion). The first traces of HgS use by humans were discovered during the Neolithic Age (ca. 4000–3000 BCE) as a preservative for human bones. Moreover, Chinese, Egyptian, Hindu, Roman or Greece civilizations used vermilion on skeletons, sculptures, ceremonial cups, buildings or paintings (Parsons and Percival 2015). Furthermore, Hg is liquid at ambient temperature, making it a special metal that Aristotle (384-322 BCE) referred to as “fluid silver” and “quicksilver” (Wisniak 2008). Hg has one of the lowest boiling points of all metals, 357°C at atmospheric pressure (Mukherjee et al. 2004); in addition, many other properties have been attached to Hg. For example, Hg was also used for religious ceremonies or as an ingredient in traditional medicines (Pal et al. 2014).

Hg is rare; it is the 16th rarest element on Earth and is classified as one of the quantitatively most important pollutant groups of TE. Methyl-Hg (MeHg) poisoning due to seafood consumption was observed in Minamata Bay, where major environmental pollution was revealed in 1956. Studies on Minamata disease indicated impairment in intracellular calcium homeostasis, alteration of glutamate homeostasis and oxidative stress as important events in MeHg-induced neurotoxicity (Farina et al. 2012). The neurotoxic effects of MeHg is of concern for human health even at low concentrations (Lebel et al. 1996). In 1956, the Minamata Bay seafood displayed high levels of Hg (5.61 to 35.7 ppm), while high levels of Hg (max. 705 ppm) were also detected in the hair of patients, their family and the inhabitants of the Shiranui Sea coastline (Harada 1995). Studies on the fate of Hg in the environment have revealed that aquatic ecosystems are particularly sensitive to MeHg exposure due to rapid

biomagnification through the food webs of top aquatic predators, such as large fish or birds (Campbell et al. 2008). MeHg is also incorporated into bird eggs during their formation (Provencher et al. 2014) and can cross the mammalian placenta. The human population is primarily exposed to MeHg by seafood consumption (Li et al. 2014), but other studies have indicated rice consumption as a possible source of Hg contamination (Meng et al. 2014).

Hg is a pollutant that affects all groups of organisms and ecosystems, including microbial communities, fishes, plants, birds and humans. Therefore, investigations of the Hg cycles and transfers within the biosphere have been widely studied to determine the fate of the Hg emitted into aquatic (Lavoie et al. 2013) and terrestrial (Mahbub et al. 2017) environments to estimate and prevent the future development of Hg contamination. Nonetheless, the microbial processes involved in the cycle and the changes in microbial communities are still unclear. This review aims to expose the current understanding of Hg changes in microbial communities as well as Hg biotransformation and biomagnification in microorganisms, with a special emphasis on fungal organisms as known Hg bioaccumulators.

The fate of Hg released from natural and anthropogenic sources

Worldwide monitoring of Hg showed that this element has a ubiquitous distribution worldwide, occurring in all classes of igneous rocks, suggesting it was released in the atmosphere by volcanic activities in the early phase of Earth. The background level of Hg in all soils is approximately 5 µg/kg DM (Von Burg 1995; Canil et al. 2015), but with significant local variations. Large Hg deposits have been found in China, Kyrgyzstan, Mexico, Peru and Russia. According to Merchant Research and Consulting Ltd , 85% of the world production came from China in 2016. Hg ores generally contain approximately one percent of Hg (1000 mg/kg), although the strata mined in Spain typically contain up to 9000 mg/kg (Wang et al. 2012). Hg is also found in fossil fuels such as coal, gas and oil in nonnegligible amounts. For example, a study carried out in the USA showed that among the 900 million tons of coal burnt

in 1999, there was 75 tons of Hg (Pavlish et al. 2003). The mining activity and fossil fuel consumption released Hg, which was contained as a trace element (TE) in geological stock (HgS), into the air, water and sediment. Hg is also released when used in products or in industrial and chemical processes such as small-scale gold mining in China or Brazil, silver and lead mining, silver amalgamation for dental applications or chlor-alkali industrial processes. The global Hg consumption in 2005 was estimated to be approximately 3798 tons, and experts have determined that since the industrial revolution, the overall global Hg deposition in the environment has increased by a factor of 3 ± 1 (Lindberg et al. 2007). The trends of global anthropogenic emissions shown a decrease in Europe and North America between 1990 and 2010 because of industrial efforts to decrease Hg emission, and worldwide emissions mostly came from East and Southeast Asia (Pacyna et al. 2010). Hg is also released in the environment from forest during potential wildfires (Zhou et al. 2016). The ratio between anthropogenic and natural source emissions was estimated in 2008, and anthropogenic sources accounted for 2320 tons of worldwide emitted Hg, mostly due to fossil fuel consumption (35%), while natural sources of Hg accounted for 5207 tons of Hg with a dominance of volatilization from the oceans (52%) (Pirrone et al. 2010).

Environmental Hg mostly exists in the gaseous elemental form (Hg^0), as inorganic divalent $\text{Hg}(\text{II})$, and as organo-Hg compounds, such as monomethyl Hg (MeHg) (Hsu-Kim et al. 2013). Due to its chemical properties, Hg volatilization occurs at low temperature and pH (optimal at 30°C and at pH 2), and Hg is easily transferred into the atmosphere (Takeuchi et al. 2001). Atmospheric Hg is dominated by the extremely volatile form Hg^0 (generally $> 95\%$ of total airborne Hg), whereas only minor amounts of other species (mainly particulate-phase Hg ($\text{Hg}(\text{p})$) have been detected (Stratton and Lindberg 1995). Hg^0 can be oxidized into mercuric ion Hg^{2+} in the Earth's atmosphere by photochemical reactions, and then it may precipitate by

rainfall and dry deposition (Bacci et al. 1994; Paige Wright et al. 2016). The oxidized Hg finally falls on terrestrial surfaces (60%) and into aquatic systems (40%) (Mahbub et al. 2017).

In the soil, an important factor is the complexation of Hg by dissolved organic matter (OM), whose increased with increasing pH (Yin et al. 1996). Since the OM-bound Hg is less available, bioavailability of Hg in soil increases with low dissolved OM. Without any dissolved OM, a soil adsorbed more Hg(II) (or released less) under alkaline conditions than under acidic conditions (Yin et al. 1996). A relevant indicator of the adsorption capacities of a soil is the organic carbon content (strong correlation $R^2 = 0.92$) (Yin et al. 1997). The processes of adsorption and desorption of Hg(II) in soils with larger organic matter content than 11.0 g C kg⁻¹ show an S-type isotherm and not a L-type isotherm or C-type isotherm, suggesting that the interaction between OM and Hg affects adsorption rate. Together, these results revealed that the dissolved OM content of the soil is the major factor that restricts Hg diffusion.

Impact of Hg on soil fungi

A disturbance in the soil can imply i) the adaptation of the indigenous microorganisms, or ii) a change in the composition of the microbial community and a change or a conservation of the microbial-associated functions. Understanding the effects of Hg on soil fungal communities has progressed by the use of several approaches that are detailed below. It is important to consider whether the selected experimental designs reflect acute or chronic effects of Hg on the soil fungal community. Field experiments with long-term Hg exposure can be considered chronic Hg exposure, whereas experiments with artificial soil contamination in controlled conditions are considered acute Hg exposure (Frossard et al. 2018).

Common approaches for the study of Hg toxicity towards fungi consist of measuring the growth rate of fungal strains on Hg-enriched synthetic growth media. The Hg chemical form most commonly used is HgCl₂ (Table 1). Under axenic conditions, Hg fully inhibited the growth of 9 species of wood-rotting fungi at concentrations ranging between 10 and 100 µM of HgCl₂

(Baldrian et al. 2000). The growth of 21 fungi isolated from soil was inhibited in a range from 10 to 100 μM of HgCl_2 , (Sanglimsuwan et al., 1993). Under controlled conditions, soil colonization by the white-rot fungus *Pleurotus* was strongly inhibited by 100 mg Hg/kg (Baldrian et al. 2000). A negative effect of Hg was reported for 6 species of ectomycorrhizal (ECM) fungi, with a decrease in radial growth rate and biomass production in the presence of Hg (Crane et al. 2010). Corroborating those results, in a recent study we measured the Hg tolerance of 103 ECM and endophytic fungal isolates collected from TE- and Hg-polluted sites and 2 isolates from an unpolluted site by growing them on Hg-amended medium to determine their *in vitro* tolerance, which was measured by growth inhibition. For most fungi, the minimum inhibitory concentration (MIC) fell within the 10 to 200 μM Hg (HgCl_2) range, testifying the high Hg toxicity for fungi under *in vitro* conditions (unpublished data). Three ectomycorrhizal and three endophytic isolates were further chosen to determine their response to Hg in more details, by measuring radial growth, biomass and Hg uptake (Fig. 1). These data highlight the wide range of Hg tolerance between fungal species. Literature converges toward a high Hg toxicity for the fungi under *in vitro* conditions compared to other TE. Indeed, when compared with Cd, Co, Cr, Cu, Mn, and Pb, Hg was the most toxic element tested (Baldrian et al. 2000). In *Ganoderma lucidum*, the toxicity of TE on fungal growth in pure culture was classified in the following order: $\text{Hg} > \text{Cd} > \text{Cu} > \text{U} > \text{Pb} > \text{Mn} = \text{Zn}$ (Tham et al. 1999).

Hg toxicity was also assessed under natural conditions. In a field experiment, Jean-Philippe et al. (2011) investigated the effects of Hg on ECM fungi along a long-term Hg-contaminated gradient with up to 758 mg total Hg (THg)/kg in soil. Surprisingly, even though the maximal Hg concentration was relatively high in comparison with the Hg-enriched plate approach, they found no significant correlation between Hg and ECM fungal abundance. The lack of a negative impact of Hg on soil fungal abundance was confirmed by Hg acute exposure experiments (Frossard et al. 2017; 2018, Tardy et al. 2014) as well as Hg chronic exposure

experiments (Müller et al. 2001; Frossard et al. 2018). Additionally, Frossard et al. (2018), in a field experiment, showed that the fungal growth rate was not affected by a high Hg soil concentration. Taken together, these results contradict the Hg toxicity assays conducted *in vitro* conditions (Baldrian et al., 2000; Crane et al., 2010; Sanglimsuwan et al., 1993). A possible explanation is that Hg generally presents a low biodisponibility in soil compared with the high Hg availability for *in vitro* toxicity assays. The ability to maintain a typical fungal abundance in Hg-contaminated soils could also be explained by the selection of Hg-resistant fungi potentially leading to a decrease in potential Hg-sensitive fungal taxa.

DNA-based experiments highlighted significant changes in the genetic structure of the soil fungal community in response to Hg contamination (Frossard et al., 2017; 2018; Tardy et al., 2014). Tardy et al. (2014), using automated ribosomal intergenic spacer analysis (ARISA), explored the responses of the fungal community to Hg stress with a spike of 20 mg HgCl₂/kg soil. After only one day of exposure, they found a change in the genetic structure of the fungal communities. In the study by Frossard et al. (2017), assessed the structure of the fungal communities of 7 soils enriched with Hg, following a gradient of HgCl₂ (0.32, 3.2 and 32 mg/kg dry soil). Changes in the fungal community structure were observed at 32 mg/kg, while a lower Hg concentration had a limited impact (Frossard et al. 2017). Frossard et al. (2018) showed a substantial change in fungal community genetic structure along three sites presenting various Hg contamination levels (0.25, 3.02 and 36.10 mg THg/kg soil). In contrast, in the same study, the authors artificially contaminated soil microcosms with Hg and observed no change in the fungal community structure. The lack of change of the fungal community composition following Hg exposure was also supported by Rieder and Frey (2013). They demonstrated that the structure of the soil fungal community was not significantly affected (5 profiles on 66-90) by a spike in MeHg ranging from 5 µg/kg or by a gradient ranging from 5 and 90 µg/kg MeHg. To explain the lack of consistency concerning the impact of Hg on the genetic structure of the

soil fungal community, Frey and Rieder (2013) suggested that Hg stress may be dependent on the soil properties and proposed a critical limit (environmental impacts) concentration for soluble Hg of 4 µg Hg/kg dry soil.

The assessment of the soil fungal diversity was generally conducted in parallel with the characterization of the genetic structure of the communities. At a Hg-contaminated chlor-alkali tailings dump with Hg concentrations ranging from 2.92 to 9.08 mg/kg soil, Durand et al. (2017) observed a negative correlation between the soil fungal diversity and soil Hg concentration. A decrease in fungal diversity was also measured in response to Hg addition in forest soil microcosms (Frossard et al. 2017). In contrast, Hg addition in pasture soil microcosms did not impact fungal diversity (Frossard et al. 2018). Surprisingly, in a field experiment, the soil fungal diversity increased with the soil Hg concentration (Frossard et al. 2018). Nevertheless, the factors explaining this phenomenon have not been yet clearly identified and could be due to the (1) the preadaptation of the soil fungal communities to Hg, (2) a change in fungal communities towards Hg-resistant taxa or (3) a lack of Hg toxicity due to low Hg bioavailability in soils.

Impact of Hg on soil bacteria

In this section, we analyse the impact of Hg on i) bacterial communities based on viable heterotrophic bacteria (VHB) counting and molecular biomass quantification and ii) bacterial community structure and diversity.

One of the most widely used techniques to study the effect of Hg exposure on bacterial communities relies on the assessment of viable heterotrophic bacteria (VHB) and the number of Hg-resistant (HgR) bacteria (Table 1). The percentage of HgR bacteria is usually evaluated by plating soil solutions on media enriched with HgCl₂. In the literature, the effect of the number of VHB in response to acute Hg exposure remains contrasted. A study on the structure of bacterial communities after various types of perturbation showed that the addition of 100 mg HgCl₂/kg leads to a decrease in the number of VHB (Bressan et al. 2008). However,

unexpectedly, for other soil types, such as pasture, cultivated, forest and industrial, Hg spiking generally did not affect the VHB percentage (Drønen et al. 1998; Harris-Hellal et al. 2009; Müller, 2001; Ranjard et al. 1997; 2000). Additionally, a decrease in the number of VHB after Hg exposure has also been described in many studies (Holtze et al. 2006; Ruggiero et al. 2011). More surprisingly, an increase in soil VHB could be measured in response to Hg exposure (Rasmussen and Sørensen, 2001; Van Faassen, 1973). In the case of acute Hg exposure of non-initially contaminated soils, an enrichment of HgR bacteria was often described (Drønen et al. 1998; Holtze et al. 2006; Müller et al. 2001; Ranjard et al. 1997, 2000; Rasmussen and Sørensen, 2001; Ruggiero et al. 2011; Van Faassen, 1973). The HgR bacterial enrichment could explain the stable number of VHB before and after acute exposure by comparison with control soils. If the percentage of HgR bacteria generally increased after Hg exposure, a decrease in the percentage of HgR bacteria was also observed only a few days after Hg spiking (Drønen et al. 1998). This phenomenon could be explained by volatilization or adsorption of Hg in soil, which could reduce the bioavailability of Hg, therefore decreasing the Hg selective pressure. Bacterial Hg resistance has been mainly attributed to the *mer* operon system and mostly the *merA* gene (Barkay et al. 2003). The consistent trend of an increase in HgR bacteria in response to Hg contamination is strongly supported by the increase in the abundance of the *merA* gene across various soil types for both acute and chronic Hg exposure (Frossard et al. 2017; 2018). While the increase of HgR bacteria in response to Hg seems to be a consistent trend, the VHB response presents contrasted patterns.

Molecular biomass quantification of bacteria using a quantitative PCR approach after Hg exposure presented the same trend as VHB counting, with a decrease (Frossard et al. 2017; Liu et al. 2018), no change (Frossard et al. 2018; Tardy et al. 2014) or an increase (Liu et al. 2014) in the bacterial abundances. Liu et al. (2014) followed the bacterial molecular biomass with 16S qPCR along a long-term Hg gradient and showed no correlation with THg.

Conversely, bacterial molecular biomass was remarkably positively correlated with MeHg under chronic Hg exposure (Liu et al. 2014), although MeHg is known to be one of the most toxic forms of Hg, especially for bacteria. However, MeHg can be very toxic to other soil ecological guilds, such as fungi or protozoa, which potentially interact with bacteria. This positive effect of MeHg on bacterial molecular biomass could be an indirect effect of changes in interactions between ecological guilds in soil, in favour of bacteria; for example, in changing the prey-predator dynamics between bacteria and protozoa (Holtze et al. 2003). Direct quantification of bacterial biomass parallels the results obtained by VHB counting, thus indicating that bacterial abundance can not be used as a predictable trend showing the response of soil bacteria to Hg contamination.

Bressan and collaborators (2008) followed the evolution of the soil bacterial community structure after various minor perturbations (CuCl_2 , 50 mg/kg DM; herbicide atrazine, 1.5 mg/kg DM; or heat shock, 35°C for 48 h) and a more severe perturbation with 100 HgCl_2 /kg dry soil. They found that HgCl_2 addition resulted in a severe perturbation of the bacterial community structure. Besides, the study showed that Hg spikes have less important impact on the bacterial community structure on soils previously exposed to perturbations. As this effect was observed for the three minor perturbations, the authors hypothesized that a generic response occurred at the community level and that no metal tolerance selection was particularly involved at a community level. Few studies have attempted to compare bacterial communities under chronic Hg exposure in the environment.

A study on Hg-enriched perturbed soil of a chlor-alkali tailings dump revealed a clear dominance of the genus *Pseudomonas* of Gammaproteobacteria (Zappelini et al., 2015). A second study at the same chlor-alkali site revealed that bacteria from the *Chloroflexi* phylum dominated the soil community (Durand et al. 2018). Other studies showed significant changes in the genetic structure of the soil bacterial community after acute Hg exposure (Frossard et al. 2017; Harris-Hellal et al. 2009; Mahbub et al. 2016a and b; Ranjard et al. 2000; Tardy et al. 2014). In contrast, chronic Hg exposure

seemed to not impact the genetic structure of the bacterial community (Frossard et al. 2018). These results may indicate that bacterial communities are more sensitive to acute Hg exposure than chronic Hg exposure. A low concentration of soil Hg (between 4.4 and 11.1 mgTHg/kg DM) leads to a statistically significant decrease in the bacterial diversity of 20% (Mahbub et al. 2016b). The decrease in bacterial diversity was correlated with the Hg concentration in neutral and alkaline low organic carbon-containing soil but not in rich organic carbon-containing acidic soil, which contains less water-soluble Hg. In addition, the water-soluble Hg obtained with deionized water extraction (Mahbub et al. 2016a) led to a change in the bacterial diversity at lower concentrations ranging from 3.8 to 22.8 $\mu\text{g Hg}^{2+}/\text{L}$ and could be an informative index for the bioavailability of Hg in soils. These negative impacts of Hg on soil bacterial diversity were observed in other studies, mostly with acute exposure (Frossard et al. 2017; Liu et al. 2018; Müller et al. 2001; Ruggiero et al. 2011). Surprisingly, chronic Hg exposure appeared to lead to an increase in bacterial diversity (Frossard et al. 2017; Liu et al. 2014; 2018). As for the bacterial community genetic structure, the impact of Hg on soil bacterial diversity seems to be linked with the Hg exposure type.

Impact of Hg on soil microbial functions

Microbes play a crucial role in soil C (carbon) and nutrient cycles, directly contributing to soil C stocks as well as plant productivity (van der Heijden et al. 2008). By impacting the microbial communities, Hg may alter the associated microbial functions. Baldrian et al. (2000) demonstrated in pure culture that Hg negatively impacts the production of two fungal enzymes (laccase and manganese peroxidase) involved in organic matter degradation. These *in vitro* results are supported by other studies demonstrating a decrease in C mineralization and heterotrophic respiration in response to Hg exposure (Bringmark et al. 1998; Landa et al. 1978; Harris-Hellal et al. 2009; Tardy et al. 2014). All these studies concerned acute Hg exposure, and chronic Hg exposure seemed to not affect microbial respiration (Frossard et al. 2018; Holtze et al. 2003; Müller et al. 2002). Casucci et al. (2003) showed that Hg decreased the activity of two enzymes implicated in phosphorus and sulfur cycles in soil. Hg also negatively impacted

the soil nitrogen mineralization rate and nitrification rate (Van Faassen 1973, Liu et al., 2010). To determine the effect of Hg on ammonia-oxidizing bacteria (AOB), real-time PCR assays of the *amoA* genes were used (Liu et al. 2009). The AOB community was dominated by *Nitrosopira*-like sequences, and this result appeared to be a consistent trend; the *Nitrosopira*-like sequences decreased as the concentration of Hg increased. Moreover, Hg led to a major disturbance that had a negative impact on ammonium oxidizers and nitrifiers (Mahbub et al., 2016b). Taken together, these results suggest that Hg could be a threat to microbial soil functions involved in both C and nutrient cycles.

Microbial mechanisms related to Hg exposure, what about fungi?

Microorganisms are present in all types of environments and are essential for the life of higher-level organisms (Nair and Padmavathy 2014). Therefore, ubiquitous organisms have been exposed to all types of pollutants, and selective pressures from a metal-containing environment have led to the development of resistance systems for virtually all toxic metals in bacteria (Bruins et al. 2000) or fungi (Bellion et al. 2006). Autonomous cells have developed a wide variety of mechanisms to maintain homeostasis in a highly concentrated metal environment; for example, extracellular chelation by excreted ligands, cell-wall binding, enhanced efflux, intracellular chelation or subcellular compartmentation. The effects of the inorganic form of Hg on many cellular processes (dehydrogenase activity, urease production, nitrification, ATP production, total microbial population, total nitrogen fixers, microbial biomass carbon, alkaline phosphatase, methane oxidation and respiration) have been previously reviewed (Mahbub et al. 2017).

Microbial resistance mechanisms to Hg are not fully understood, although some mechanisms have been proposed: (i) cell wall binding of Hg limits Hg uptake (Kinoshita et al. 2013), (ii) production of thiols (such as glutathione) to chelate Hg in sulfhydryl groups (SH) limit the bioavailability of Hg (Wu and Wang 2014), (iii) similarly production of selenium-rich

proteins may chelate Hg (Kavčič et al. 2019) and (iv) biovolatilization systems involving mercuric reduction and methylation (Urík et al. 2014; Lu et al. 2016). After a brief update on bacterial mechanisms, this review will focus on fungal mechanisms.

Lessons learned from research on bacteria

Research on Hg and bacteria has produced three times more publications than on Hg and fungi (Fig. 2). The Hg resistance biovolatilization systems of bacteria have attracted many researchers. The most studied example of biovolatilization in the environment takes place during the polar spring in the arctic region. The process is known as atmospheric Hg depletion events. Within a year, Hg(II) wet and dry deposition occurs, and in the summer, after the snow and ice have melted, water carries Hg(II) into lakes where it could be re-emitted by Hg-resistant bacteria or volatilized to Hg⁰ as a resistance system (Steffen et al. 2008; Lescord et al. 2015). The best understood biochemical mechanism of Hg bacterial biovolatilization involves the reduction of Hg(II) to volatile Hg(0) by inducible mercuric ion reductase coded by the *mer* operon (Dash and Das 2012). The *mer* operon contains genes that encode the functional proteins for regulation (*merR*), transport (*merT*, *merP* and/or *merC*, *merF*) and reduction (*merA*) (Nascimento and Chartone-Souza 2003). The additional *merB* gene (coding for organomercurial lyase) is required to confer resistance to many organomercurials, such as methylHg and phenylHg, by hydrolysing the R-Hg bond before the reduction of Hg²⁺. In general, additional *merB* genes are found downstream of the *merA* gene in the *mer* operon (Osborn et al. 1997). The *merA* gene has been mostly detected in subsurface (Oregaard and Sørensen 2007) and water (Moller et al. 2014) environments. The importance of microbial processes for Hg volatilization in comparison to abiotic transformation in the Hg global cycle has been questioned. In aquatic systems, experiments have shown that the biotic-light-dependent transformation of ionic Hg (Hg²⁺) in Hg⁰ accounted for an average of 30% of the total natural transformation, while photochemistry contributed to 30% and low-light production

accounted for 40% (Kuss et al. 2015). The experimental conditions used allowed phytoplankton genera to carry out photosynthesis, but not the high-light adapted cyanobacteria. These results suggested that the cyanobacterial genera *Synechococcus* and *Aphanizomenon* were the main transformers of ionic Hg (Hg^{2+}) into Hg^0 .

Studies are also exploring other bacterial adaptation mechanisms to Hg exposure through chemical transformation. Indeed, microbial Hg methylation transforms inorganic Hg into the highly volatile and bioaccumulated neurotoxin methylHg with a rapid transfer into the food web. Moreover, a balance exists between anaerobic methylation and demethylation of inorganic Hg by microorganisms, influencing net MeHg production in anoxic water and sediments (Lu et al. 2016), hence the interest in methylation and demethylation in microorganisms is growing. In soils, the best-known contributors to methylation were found to be sulfate-reducing bacteria (SRB) (Holloway et al. 2009), while iron-reducing bacteria (IRB) coexisting with SRB were involved in the methylation process in the freshwater environment (Yu et al. 2012). Although some bacterial taxa are known to be capable of methylation and demethylation under anaerobic conditions (Pak and Bartha 1998), the lack of a genetic marker for microbial MeHg production has prevented non-culture-dependent studies of the distribution of Hg-methylating organisms in nature. By directly measuring MeHg production in several bacterial and archaeal strains encoding *hgcAB*, it was confirmed that a specific gene cluster (*hgcAB*) (Parks 2013) was linked to Hg methylation (Gilmour et al. 2013). Since then, many species have been defined as MeHg producers, including sulfate and iron-reducing bacteria but also methanogens, syntrophic, and acetogenic bacteria, or fermentative *Firmicutes* (Gilmour et al. 2013; Figueiredo et al. 2016; Lu et al. 2016). Recently, Lu et al. (2016) isolated the strain *G. bemidjiensis* Bem, which has the capacity to mediate the three main mechanisms related to Hg: Hg(II) reduction, Hg(0) oxidation, and MeHg production/degradation under anoxic conditions.

Are fungi terrestrial Hg hyperaccumulators?

A long history of the ecological survey of Hg concentrations in edible and nonedible mushrooms revealed that many fungi bioaccumulate large amounts of Hg in the environment (Supplemental Table S1), and some fungi could be considered hyperaccumulators of Hg referring to the metal hyperaccumulation defined for plants. In figure 3, we compared the maximum Hg concentration and maximum Hg bioconcentration factor (BCF) of microfungi. The BCF is defined as the ratio between the THg concentration in fungi and the THg concentration in soil. The BCFs of *Boletus pinophilus* or *Boletus aereus* were found to be 491 and 425, respectively (Melgar et al. 2009) (Fig. 3). *Boletus edulis* from the Indira mine region in Slovenia showed 69.0 ± 14.8 mg/kg DM (in cap, mature) and in young cap was 103 ± 7.60 mg/kg DM (Kavčič et al. 2019). The Hg uptake capacity by fungi of the *Boletaceae* family is even more obvious in control environment. For example, Hg concentrations in *Boletus* species from background (unpolluted) areas can reach 9.9 ± 2.7 mg/kg DM with a bioconcentration factor (BCF) of 250 considering the low concentration of Hg in the soil of the Borecka Forest in Poland (0.005 to 0.096 mg/kg DM) (Falandysz et al. 2002). High Hg BCF values were also found for the *Agaricus* genus; for example, a value of 365 was reached for *Agaricus macrosporus* (Fig. 3). Other genera, such as *Lepista*, *Lycoperdon* and *Macrolepiota*, showed Hg accumulation from their environment (Fig. 3).

Consequently, some fungal species have been proposed to be bioindicators for Hg pollution, including *Agaricus arvensis*, *Agaricus campestris*, *Agaricus edulis*, *Agaricus haemorrhoidarius*, *Agaricus xanthodermus*, *Amanita rubescens*, *Amanita strobiliformis*, *Coprinus comatus*, *Lycoperdon perlatum*, *Marasmius oreades* and *Mycena pura* (Mejstrik and Lepsova 1993; Wondratschek and Röder 1993). We could suggest that several Boletaceae, such as *Boletus edulis*, *Boletus pinophilus* and *Boletus aereus*, could be added to the list. Obviously, the THg content in the soil should influence the BCF of Hg in fungi. A recent study proposed

to survey the BCF of 15 saprotrophic and wood-rotting fungal strains grown in semi-natural medium enriched with an Hg gradient from 0 to 20 ppm to measure the translocation rate. The results showed that the BCF decreased with the increase in Hg in the substrate, whereas the THg in the biomass rose with the Hg content in the substrate (Gabriel et al. 2016).

Fungi accumulate significant amounts of Hg, particularly at sites enriched in Hg (such as the mercuriferous belt), but also accumulate significant amounts of Hg at unpolluted sites. It is a peculiarity of macromycetes to accumulate Hg in a soil with a low Hg content that contrast with vascular plants, essentially accumulating Hg from Hg-enriched soils (Falandysz and Borovička 2013). In the terrestrial environment, fungi are the best bioaccumulating organisms for Hg, and the total Hg distribution in the vegetal cover of a forest area showed variations of accumulation among the various components of the ecosystem as follows: peas, rosehips < tree leaves (early summer) < leaves (flowering plant) < apple blossoms < berries < twigs < shrub leaves < sedge < needles (average) < ferns < aquatic vegetation < grasses < bark < liverwort < mosses < tree fungi < lichens < saprophytic fungi < ectomycorrhizal fungi (Nasr and Arp 2016).

Several factors have been studied for a better understanding of Hg bioaccumulation in fungi. The Hg content of higher fungi appeared to be species-dependent and varied as a function of the fungal tissues; globally, the cap contained more Hg than the stalk. The Hg concentration is also affected by the developmental stage of the fruiting bodies, which decrease during senescence in some fungi (emergence > maturity > senescence) (Nasr et al. 2012). This was for instance confirmed in the work of Kavčič et al. (2019) that measured 103 ± 7.60 mg THg /kg DM in younger caps of *B. edulis* and 92.6 ± 18.4 mg THg /kg DM in fruiting bodies of *Scutiger pes-caprae* both from Slovenia, while they only measured 69.0 ± 14.8 mg THg /kg DM in mature caps of *B. edulis* and 41.9 ± 2.25 mg THg /kg DM in fruiting bodies of *S. pes-caprae*. In those fungi the hymenium contained more than 50% of the accumulated Hg. Nonetheless some macromycetes species may not follow this trend (Falandysz et al. 2020a). The

morphology of the hymenium and/or the mode of development of the hymenium could be a key aspect of the accumulation of Hg in macromycetes fruiting bodies.

The total Hg content in fungi is positively correlated with the Hg bioavailability in myceliated soil and substrate type (wood, forest soil and mineral soil) (Nasr and Arp 2011). It was previously highlighted that metal bioaccumulation in fungi is primarily influenced by species differences and not by soil factors (Leyval et al. 1997); however, environmental variables such as pH, temperature, and geological properties affect Hg uptake by organisms (Boening 2000). Moreover, it was shown that the THg content in fungi was negatively correlated with the total sulfur concentration in myceliated soil and positively correlated with the total sulfur content in fungi (Nasr and Arp 2016). These results implied that Hg bound to organic matter mitigates Hg accumulation in fungi. Nevertheless, readers should keep in mind that Hg deposition after atmospheric transit can also be a source of fungal contamination, at least under certain climates. Indeed, Hg accumulation was found in fungi isolated from Gongga Mountain in China. The absence of industrial activities, urbanization and Hg ore deposits in this area suggested deposition as the major source of elevated Hg observed; for instance, 3,285 mg THg /kg DM was measured in the cap of *Gymnopus erythropus*. Gongga Mountain has its own microclimate, a ‘circumpolar’ climate, and hence is sensitive to contamination by persistent pollutants that are trapped by cold temperature and wet precipitation (Falandysz et al. 2014). Moreover, determination of the bioaccumulation factor (BAF), defined as the ratio between THg concentration in the fruiting body of the fungi and the bioavailable Hg concentration in the soil, could be a better indicator for Hg uptake by fungi but requires bioavailable Hg to be determined. In conclusion, results from the literature suggest that fungal species may be the main factor influencing the accumulation of Hg in fungal tissues, and some fungal species behave like Hg sponges in the terrestrial environment. Despite the potential threat of edible mushrooms hyperaccumulating Hg, even in soils with low Hg concentrations,

the specific mechanisms leading to Hg accumulation and resistance of fungi remain fairly undiscovered. Nonetheless, understanding the fungal mechanisms of uptake and transformations of Hg is arousing growing interest in the scientific community (Falandysz 2019a, 2019b, 2020b).

Hg tolerance mechanisms in fungi

The fungi had high Hg bioaccumulation factors despite low Hg concentrations or low bioavailability in the soil, which raises the question of how fungal cells manage to cope with Hg toxicity. Fungi show resistance to Hg at ranges far superior to those measured for bacteria (Rajapaksha et al. 2004). In the fungal kingdom, it has been assumed that the accumulation and transport of Hg could depend on the production of proteins rich in cysteine and their sulfhydryl (SH) groups. These proteins, also named thiols (Stijve and Besson 1976), are produced in ECM fungi and include metallothioneins and glutathione chelators (Khullar and Reddy 2016). It has been suggested that there is a strong correlation between the amount of SH groups in fungal proteins and Hg content in fungi (*Agaricus*), while almost no correlation for other TE was found (Kojo and Lodenius 1989). Induction of metallothioneins by HgCl₂ has not been demonstrated for fungi but exists in rats (Piotrowski et al. 1974). A recent study showed that higher Hg contents in the edible mushrooms *B. edulis*, *B. aereus* and *Scutiger pes-caprae* resulted in greater Hg tetra-thiolate complexation, but also HgSe complexation (Kavčič et al. 2019). The study revealed that Hg mainly coordinated to di-thiols (43–82%), followed by di-selenols (13–35%) and tetra-thiols (12–20%). In addition to selenium-rich proteins that may limit Hg bioavailability in mushrooms, they found evidence of di-amino Hg complex with Hg(N-R)₂ or Hg complex with two N in heterocyclic amines.

The toxicity of Hg compounds is dependent on the ability to release Hg²⁺, which has a high affinity for other cellular ligands. Compounds providing two or three thiolate ligands activate organomercurials for cleavage, indicating that the number of thiolates ligated to Hg is

influenced by binding to carbon (Miller 2007). A study showed that arbuscular mycorrhizal fungi (AMF) enable the uptake of Hg-tetra-thiolate complexes in plants grown on Hg-enriched soils (50 ppm), while Hg forms di-thiolate and di-amino complexes in non-AMF plants. Moreover, this process is AMF density-dependent, showing that AMF can modify the Hg binding environment in plant roots (Kodre et al. 2017). In soils where Hg can have extremely stable bonds with the carbon of organic matter, thiolate production by fungi may greatly influence the bioavailability of Hg from organomercurial forms. Consequently, the potential toxicity of Hg in soil may be affected by fungal communities. Moreover, the Hg resistance of some fungi could depend on the ability of those organisms to modify the Hg binding environment by SH groups to immobilize Hg in a nontoxic form.

In Hg-contaminated soil, fungi could have the potential to detoxify organomercurials by volatilization. Some fungi, such as *Yarrowia* strains, have been proven to be able to convert organomercurials to Hg(II) by fungal organoHg lysis and then reduced Hg(II) to Hg⁰ (Gadd 2007; Oyetibo et al. 2015). A study proposed an experiment with several soil fungi, and Hg was measured in the fungal biomass (Urík et al. 2014). The authors concluded that bioimmobilization of Hg was negligible compared to volatilization, and they demonstrated the biovolatilization potential of *Aspergillus niger* and *Cladosporium cladosporioides*, which reached 80% of 32.7 mg HgCl₂/l. In such experiments, we proposed that a survey of Hg volatile compounds such as MeHg should be performed to exclude the bioimmobilization hypothesis. Hg methylation has been less studied in fungi than in bacteria, however some fungi may produce Hg volatile compounds such as MeHg (Vonk and Sijpesteijn 1973). A study monitored the production of MeHg in bacteria and fungi and revealed that *A. niger*, *Scopulariopsis brevicaulis* and *Saccharomyces cerevisiae* were able to produce MeHg from sublethal HgCl₂ concentrations (Vonk and Sijpesteijn 1973). MeHg was essentially found in the mycelium in contrast to bacteria, where the MeHg produced was mostly found in the media. For *A. niger*,

studies agreed on the media detoxification capacity of the fungus but not on the fate of the Hg (biosorption or volatilization). A study on the microbial consortium of periphyton showed that Hg methylation were the most involved, however inhibition of fungal and algae also reduced methylation rates. Although, sulfate reducing bacteria and methanogens are the most involved in MeHg formation (Correia et al. 2012), fungi may produced MeHg in the soil, which has been recognized as the most toxic Hg compound (Clarkson and Magos 2006).

The mechanisms involved in volatilization, bioaccumulation or bioimmobilization of Hg compounds by fungi need to be clarified. The fate of Hg in fungal cells has been poorly studied in the past when compared to other TE. A study evaluated the factors affecting the biosorption of methylHg and Hg(II) by *S. cerevisiae* (Madrid et al. 1995). The results showed that MeHg bound easily to the yeast cell at a wide range of pH values and temperatures compared to Hg(II), which was less effectively bound to the cells. The slow Hg(II) uptake followed Michaelis-Menten kinetics for 24 h, implying saturation of binding sites or transport. The explanation proposed here for the rapid binding of MeHg was that *S. cerevisiae* was able to rapidly reduce CH_3Hg^+ to other more volatile Hg species, such as Hg(I) or Hg^0 . In addition, among various ions, chloride ions at high concentrations strongly increased the binding of Hg(II). When the concentration of metals is higher in the extracellular compartment than in the cell, metals can accumulate inside the cell through diffusion or through other transport channels. To decipher the blurred mechanisms of metal uptake by *S. cerevisiae*, researchers have compared the biosorption capacity of *S. cerevisiae* in different forms, such as living cells, dead cells, inactivated cells, and free cells, and they revealed that the vacuole was involved in detoxifying Zn, Mn, Co, and Ni but not Cu or Cd (Wang and Chen 2006). In the literature, information on the uptake or subcellular compartmentation of Hg in fungal cells is scarce. However, recent work found a putative transport system for Hg (HgCl_2) in *S. cerevisiae* and

explored subcellular compartmentation in the higher fungus *Podospora anserina* (Durand et al. unpublished data).

We proposed a schematic representation of cellular mechanisms potentially involved in Hg tolerance in ectomycorrhizal fungi (Fig. 4). Mechanisms that may be involved in the tolerance of fungi to excess metals like mercury in their environments include a reduction of metal uptake into the cytosol by extracellular chelation through extruded ligands ❶ (e.g. hydrogen sulfide (H₂S) gas which co-precipitates Hg (Amin and Latif, 2011)) and binding to cell wall components ❷ (e.g. carboxyl groups of cell walls such as chitin and chitosan, and hydrophobins (Karunasagar et al., 2003; Puglisi et al., 2012)). Hg uptake could occur through specific transporters for the acquisition of essential metals that have not yet been described ❸. Intracellular chelation of Hg in the cytosol by a range of ligands ❹ (glutathione, metallothioneins and phytochelatins (Bolchi et al., 2011; Khullar and Reddy, 2016)), and increased efflux from the cytosol to the exterior of the cell ❺ (by methylations and by volatilization (Gadd, 2007; Oyetibo et al., 2015; Urik et al., 2014)) or into sequestering compartments ❻ (storage in vacuoles by i.e., the ycf1 transporter (Gueldry et al., 2003)) are also key mechanisms that confer metal tolerance. The free-radical scavenging capacity provided by the activity of catalase (Kojo and Lodenius, 1989) or the binding of Hg to Se and SH groups (Baldrian, 2003; Collin-Hansen et al., 2007; Kavčič et al., 2019) comprise another line of defence against the toxic effects of mercury ❽.

Molecular methods could reveal new insights into cell mechanisms induced by Hg stress. Transcriptomic approaches were carried out on *Elodea nuttallii* (aquatic plant) exposed to various acute Hg exposure, and the upregulated genes were determined (Regier et al. 2013). The downregulated genes were related to ‘homeostasis of metal ions’, ‘heavy metal ion transport’ and, more surprisingly, genes related to detoxification, although not related to metallic detoxification. Another significant work used the suppression subtractive hybridization

(SSH) technique to identify the differentially expressed genes in the strikingly Hg-resistant fungus *Trichoderma harzianum* IMI 393899 grown in the presence of HgCl₂ or Cd (Puglisi et al. 2012). All 8 genes identified as upregulated after HgCl₂ exposure were also upregulated by Hg₂Cl₂, and among them, hydrophobin was predicted as having a possible role in the tolerance mechanism. Hydrophobins are a group of small cysteine-rich proteins only expressed by filamentous fungi and have the ability to dissolve hydrophobic molecules in aqueous media. Hydrophobins could be involved in the retention of Hg at the cell surface, leading to improved Hg resistance. Similarly, Müller et al. (2007) suggested that hydrophobin plays a role in Zn resistance in *Suillus luteus*, whereas other studies showed that this taxon could accumulate Hg from the environment (Minagawa et al. 1980; Falandysz et al. 2001; Saba et al. 2016). We suggest that such molecular approaches may unravel fungal mechanisms involved in acute or chronic exposure to Hg.

Conclusions

Environmental contamination by Hg is a serious problem worldwide, and an understanding of its transfer in the biosphere is needed. Microorganisms such as bacteria and fungi are believed to have many interactions with Hg; however, little is known about their impact on the cycle of Hg accumulation in the biosphere. Concerning fungi, even fewer data are available in the scientific literature compared to bacteria. Fungi accumulate the largest amount of Hg in forest ecosystem and are the organisms capable of the highest bioaccumulation of Hg. Their role in soil organic matter recycling seems to be correlated with their role in the Hg cycle. Indeed, fungi not only are exposed to the toxic effects of Hg but also may have a central role in the biomagnification and biovolatilization of Hg in terrestrial ecosystems. Moreover, breakthroughs related to Hg-contaminated soil remediation could be possible with an improved understanding of fungal resistance and of the fungal capacity of bioaccumulation/biotransformation of Hg compounds at the cell level.

Author contributions

MC and AD conceived the content of the review. AD, FM and JF investigate the literature on the topic. AD and FM wrote the manuscript. MC supervised the final arrangement of the manuscript. All authors discussed the content of the review and approved the final manuscript.

Compliance with Ethical Statement

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Legends to figures

Figure 1. The effects of HgCl₂ on the radial growth of 6 selected fungal isolates. *P. involutus* He01, *P. involutus* Pi01, *P. tinctorius* Pt01, *Leptodontidium* sp. M10, *Helotiales* Pr01 and *Cadophora* sp. Pr29 were incubated on malt agar medium supplemented with 0 to 100 µM HgCl₂ for various periods of time. Means and standard deviations of at least five replicates are presented. Values designated by the same letters were not significantly different ($p < 0.05$) according to the Kruskal-Wallis test.

Figure 2. Peer reviewed publications on mercury in the bacterial or fungal kingdom and referenced in Google Scholar since 2000.

Figure 3. Comparison between the maximum Hg concentration and maximum Hg bioconcentration factor (BCF) of macromycetes genera reported in the literature. Smallest values are represented in detail on the right.

Figure 4. Schematic representation of the cellular mechanisms potentially involved in Hg tolerance in fungi. Extrahyphal immobilization of Hg occurs through the formation of secondary minerals by excreted ligands (1) and biosorption to cell wall constituents such as chitin and chitosan (2). Hg uptake could occur, for example, through specific transporters for the acquisition of other essential metals that have not yet been described (3). Hg transformation, such as reactions involving organometals (for example, methylations) and redox reactions (5), frequently result in metal volatilization (4). Intracellular Hg immobilization involves complexation by cytoplasmic phytochelatins (PC) (7) or glutathione (GSH). Hg–glutathione complexes can be further transferred to the vacuolar compartment by the ycf1 transporter, for example (6).

Figure 1

Strain	He01	Pi01	Pt01	Me01	Pr01	Pr29
Days of exposition	42	12	42	21	35	20
EC ₅₀ (μM HgCl ₂)	95.5	9.3	85.8	96.3	75.1	24.7
MIC (μM HgCl ₂)	>100	25	100	>100	100	50

Figure 2

Figure 3

Figure 4

Table 1. Overview of tolerance of microbial communities towards Hg. The main effects are provided for the listed microbial communities, together with Hg concentrations in soils and references.

Reference	Community type	Type of study	Soil type	Initial contamination	Hg form	Exposure type	[Hg]	Effect	Feature	Method
Akerblom et al. 2010	total	controlled conditions	forest : mor layer	yes/no	HgCl ₂	acute	2.010 mg/kg	-	heterotrophic respiration for the F layer	respirometry
							0.54 to 1.93 mg/kg	o	heterotrophic respiration for L and H layer	
							0.88 to 1.29 mg/kg	-	heterotrophic respiration for the milled L-layer	
Baldrian et al. 2000	fungi	axenic culture	na	na	HgCl ₂	na	13.6 mg/l to 136 mg/l	-	growth of 9 wood-rotting basidiomycetes	na
Baldrian et al. 2000	fungi	controlled conditions	cultivated, acidic cambizol	no	HgCl ₂	chronic	50 to 100 mg/kg	-	soil colonization rate by the fungi	visual observation
								-	laccase and manganese peroxidase maximal activity	enzymatic assay
								o/+	no or positive effect of degradation of PAH by the fungi	Liquid chromatography
Bressan et al. 2008	bacteria	controlled conditions	pristine calcareous silty-clay soil	no	HgCl ₂	acute	100 mg/kg	change	bacterial community structure	ARISA
Bringmark et al. 1998	total	controlled conditions	forest soil	no	HgCl ₂	acute	5 mg/kg	-	respiration rate	respirometry
Campos et al. 2018	total	field experiment	mining soil	yes	total	chronic	4068 mg/kg	o	dehydrogenase activity	enzymatic assay
Casucci et al. 2003	total	controlled conditions	Typic Ustocreps, Haplustol Fluventic, Mollic Psammaquent	no	HgCl ₂	acute	0.136 to 2.72 mg/kg	-	microbial biomass C, alkaline phosphatase activity, arylsulfatase activity , o-DPO	fumigation , enzymatic assay
								-/+	FDA hydrolysis increase or decrease in function of the type of soil	
Crane et al. 2010	fungi	axenic culture	na	na	HgCl ₂	na	1.36 mg/l to 10.88 mg/l	-	growth rate, increase lag phase of 6 ectomycorrhizal fungi	na
Crane et al. 2012	fungi	controlled conditions	forest podzol	no	HgCl ₂	acute	88 mg/kg	-	ectomycorrhizal colonization, richness and diversity of root tips	morphological identification and counting

Drønen et al. 1998	bacteria	controlled conditions	cultivated soil	no	HgCl ₂	acute	25 mg/kg	o	number of VHB	plate counting
								-/+	rapid increasing of HgR bacteria follow by a decrease	
								-	diversity	colony morphology

Durand et al. 2017	fungi	field experiment	forest soil, chlor-alkali tailing dump	yes	Total	chronic	2.92 to 9.08 mg/kg	-	fungal diversity and richness	ITS1 rRNA gene metabarcoding
Frey and Rieder 2013	total and bacteria	controlled conditions	forest soil	no	HgCl ₂	acute	0.032 to 0.32 mg/kg	o	basal respiration and bacterial community structure	respirometry, T-RFLP
							3.2 to 32mg/kg	-	basal respiration	respirometry
								change	bacterial community structure	T-RFLP
Frossard et al. 2017	total, bacteria, fungi	controlled conditions	forest soils	no	HgCl ₂	acute	0 to 32 mg/kg	change	bacterial community structure	16S rRNA gene metabarcoding
								change	fungus community structure	ITS rRNA gene metabarcoding
								-	bacterial diversity	16S rRNA gene metabarcoding
								-	fungus diversity	ITS rRNA gene metabarcoding
								-	bacterial abundance	16S rRNA gene quantification qPCR
								o	fungus abundance	ITS rRNA gene quantification qPCR
Frossard et al. 2018	total, bacteria, fungi	field experiment	pasture soil	yes	Total	chronic	0.25 to 36.10 mg/kg	o	basal respiration	CO ₂ fluxes
								o	bacterial abundance	16S rRNA gene quantification qPCR
								o	fungus abundance	ITS rRNA gene quantification qPCR
								o	bacterial growth rate	Leucine incorporation method
								o	fungus growth rate	Acetate in ergosterol incorporation method

Frossard et al. 2018	total, bacteria, fungi	field experiment	pasture soil	yes	Total	chronic	0.25 to 36.10 mg/kg	+	bacterial diversity	16S rRNA gene metabarcoding
								+	fungus richness and diversity	ITS rRNA gene metabarcoding

		controlled conditions				acute		change	bacterial community structure	16S rRNA gene metabarcoding
								change	fungal community structure	ITS rRNA gene metabarcoding
								o	basal respiration	CO2 fluxes
								o	bacterial abundance	16S rRNA gene quantification qPCR
								o	fungal abundance	ITS rRNA gene quantification qPCR
								o	bacterial growth rate	Leucine incorporation method
								o	fungal growth rate	Acetate in ergosterol incorporation method
								o	bacterial diversity	16S rRNA gene metabarcoding
								o	fungal richness and diversity	ITS rRNA gene metabarcoding
								o	bacterial community structure	16S rRNA gene metabarcoding
								o	fungal community structure	ITS rRNA gene metabarcoding
Harris-Hellal et al. 2009	total and bacteria	controlled conditions	forest acrisol	no	HgCl ₂	acute	1 mg/kg	o	microbial biomass, VHB, carbon mineralization rates, genetic structure, functional diversity, HgR bacteria	DGGE, respirometry, plate counting, Biolog EcoPlate
							20 mg/kg	change	bacterial community structure	DGGE
								-	carbon mineralization rates	respirometry
								o	microbial biomass and VHB and HgR bacteria	plate counting
								-	functional diversity	Biolog EcoPlate
Holtze et al. 2003	bacteria	controlled conditions	industrial soil	no	HgCl ₂		3.5 to 15 mg/kg	-	VHB	plate counting
								+	<i>Pseudomonas</i> genus	
								o	respiration rate	respirometry
Holtze et al. 2006	bacteria	controlled conditions	industrial soil	no	HgCl ₂	acute	3.5 to 15 mg/kg	+	HgR bacteria	plate counting

Jean-Philippe et al. 2011	fungi	field experiment	forest inceptizol	yes	total mercury	chronic	0.70 to 758 mg/kg	-	ectomycorrhizal fungal abundance	morphological identification and counting
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Landa 1978	total	controlled conditions	uncultivated soil	no	HgCl ₂	acute	200 to 400 mg/kg	-	mineralization potential	respirometry
						chronic	1 to 100 mg/kg	-	mineralization potential	
Liu et al. 2010	archaea and bacteria	controlled conditions	cultivated	no	HgCl ₂	acute	4 to 30 mg/kg	-	potential nitrification rate	chlorate inhibition method
								o	amoA gene copy number among all treatment	quantitative PCR
								o	composition of ammonia-oxidizing archaea community	clones library, RFLP
								change	composition of ammonia-oxidizing bacteria community	
Liu et al. 2014	bacteria	field experiment	paddy soil	yes	total mercury	chronic	THg: 1.11 to 29.07 mg/kg, MeHg: 3.88 to 317 ng/kg	+	α-diversity at low THg and MeHg concentration	454 pyrosequencing
								o	α-diversity at high THg and MeHg concentration	
								o	no correlation between THg concentration and bacterial abundance	
								+	positiv correlation between MHg and bacterial abundance	16S quantitative PCR
								+	Gemmatimonadetes (phylum lvl), Anaerolineales, envOPS12, Hydrogenophilales and SBR1031 (genus lvl)	
								-	<i>Nitrospirae</i> (phylum lvl), Deltaproteobacteria and Gammaproteobacteria (class lvl)	
Liu et al. 2018	bacteria	field experiment	paddy soil	yes	Total and MeHg	chronic	THg 0.27 to 52.4 mg/kg	-	bacterial abundance	16S rRNA gene copy number qPCR
							MeHg 1.6 to 10 ug/kg	o	bacterial abundance	16S rRNA gene copy number qPCR
							THg 0.27 to 52.4 mg/kg	o	bacterial diversity	16S rRNA gene metabarcoding
							MeHg 1.6 to 10 ug/kg	o	bacterial diversity	16S rRNA gene metabarcoding

Liu et al. 2018	bacteria	field experiment	upland soil	yes	Total and MeHg	chronic	THg 0.27 to 52.4 mg/kg	-	bacterial abundance	16S rRNA gene copy number qPCR
			MeHg 1.6 to 10 ug/kg				o	bacterial abundance	16S rRNA gene copy number qPCR	
			THg 0.27 to 52.4 mg/kg				-	bacterial diversity	16S rRNA gene metabarcoding	
			MeHg 1.6 to 10 ug/kg				+	bacterial diversity	16S rRNA gene metabarcoding	
			paddy soil and upland soil				THg 0.27 to 52.4 mg/kg	+	Bacteroidetes and Firmicutes	16S rRNA gene metabarcoding
							THg 0.27 to 52.4 mg/kg	-	<i>Nitrospirae</i>	16S rRNA gene metabarcoding
Mahbub et al. 2016a	total	controlled conditions	acidic, neutral and alkaline soils, residential areas and forest	no	HgCl ₂	acute	0 to 300 mg/kg	-	dehydrogenase activity	enzymatic assay
								-	nitrification	Nitrite concentration
Mahbub et al. 2016b	bacteria	controlled conditions	acidic, neutral and alkaline soils, residential areas and forest	no	HgCl ₂	acute	0 to 200 mg/kg	change	bacterial community structure, more significant for WHg than THg	16S rRNA gene metabarcoding
								-	bacterial diversity	
								-	<i>Nitrospirae</i> and <i>Nitrosomonas</i> relative abundance	
Muller et al. 2001	total, bacteria, fungi	field experiment	na	yes	Total	chronic	511 mg/kg	+	HgR bacteria	plate counting
							7 to 511 mg/kg	-	microbial C and N biomass	Fumigation
								o	fungal biomass	N-acetylglucosaminidase activity
								-	diversity	DGGE, colony morphology
								o	substrate utilization	Biolog EcoPlate

Muller et al. 2001	bacteria	controlled conditions	cultivated	no	HgCl ₂	acute	2.5 to 25 mg/kg	o	number of VHB	plate counting
								+	Hg resistant bacteria	plate counting on Hg enriched medium, microtiter plate
								o	carbon utilization profil	Biolog EcoPlate
Muller 2002	total, bacteria	field experiment	na	yes	Total	chronic	511 mg/kg	-	diversity	DGGE, colony morphology
								o	substrate utilization	Biolog EcoPlate
								o	respiration rate	substrate induced respiration
Ranjard et al. 1997	bacteria	controlled conditions	permanent pasture, culture, forest	no	HgCl ₂	acute	10 mg/kg	o	number of VHB	plate counting
								+	Hg resistant bacteria and gram-negative bacteria	plate counting, gram staining
Ranjard et al. 2000	bacteria	controlled conditions	cultivated, silt-loam	no	HgCl ₂	acute	10 mg/kg	o	number of VHB and number of total bacteria in unfractionated soil	plate counting and direct microscopy
								+	Hg resistant bacteria	plate counting
								change	bacterial community structure	DNA fingerprinting
Rasmussen and Sørensen 2001	bacteria	controlled conditions	cultivated soil	no	HgCl ₂	acute	25 mg/kg	+	Hg resistant bacteria, culturable bacteria and r strategist bacteria	plate counting
								+	functional diversity	Biolog EcoPlate
								-	genetic diversity and culturable heterotrophic bacterial diversity	PCR DGGE and plating and counting
								+	genetic diversity and culturable heterotrophic bacterial diversity	
Rieder and Frey 2013	total, bacteria, fungi	controlled conditions	forest soil	no	MeHgCl ₂	acute	5 to 90 µg/kg	+	positive correlation between MeHg concentration and basal respiration	respirometry
								-	microbial biomass C	substrate-induced respiration method
								change	bacterial community structure	T-RFLP
								o	fungal community structure	
Ruggiero et al. 2011	total	field experiment	industrial soil	yes	total mercury	chronic	1.2 to 50 mg/kg	o	CD index values of VH and HgR bacteria	plate counting

								o	enzyme activities, total microbial biomass C content, daily basal respiration	enzymatic assay, 12C fumigation, respirometry
	bacteria	controlled conditions			total mercury and HgCl ₂	acute	10 mg/kg	+	HgR bacteria for soil with low HgR/VH ratios	plating/counting
								-	VHB for the majority of tested soils	
								o	HgR bacteria for soils with high HgR/VH ratios	
								-	diversity decreasing at 14 days after exposition	DGGE
								+	diversity	

Sanglimsuwan et al. 1993	fungi	axenic culture	na	na	HgCl ₂	na	13.6 mg/l to 136 mg/l	-	growth of 21 fungi	na
Tardy et al. 2014	total, bacteria, fungi	controlled conditions	cambisol	no	na	acute	20 mg/kg	o	bacterial abundance	16S rRNA gene quantification qPCR
								o	fungal abundance	18S rRNA gene quantification qPCR
								change	bacterial community structure	ARISA
								change	fungal community structure	ARISA
								-	respiration	CO2 fluxes
Tu et al. 1988	total	controlled conditions	sandy loam soil	no	HgCl ₂	acute	70 mg/kg	-	invertase activities	Prussian blue method
							140 mg/kg	-	microbial respiration	respirometry
Van Faasen 1973	total and bacteria	controlled conditions	clay soil	yes/no	HgCl ₂ , Hg(NO ₃) ₂ , phenylmercury acetate and MeHgCl ₂	acute	100 and 150 mg/kg	-	VHB number on Hg enriched plate	mercury enrichment plating and counting
					HgCl ₂ Hg(NO ₃) and Hg(NO ₃)			+	VHB number	plate counting
			sandy and clay soil		HgCl ₂ and phenylmercury acetate		100 mg/kg	-	dehydrogenase activity, carbon and nitrogen mineralization	respirometry
								+	partial restoration of the dehydrogenase activity after 10 days	respirometry