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HAL Authorization

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

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23 **Abstract**

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

32 **Key points:**

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

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

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43 **Introduction**

44 *History of Hg contamination*

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

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

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

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

82 ***The fate of Hg released from natural and anthropogenic sources***

83 Worldwide monitoring of Hg showed that this element has a ubiquitous distribution
84 worldwide, occurring in all classes of igneous rocks, suggesting it was released in the
85 atmosphere by volcanic activities in the early phase of Earth. The background level of Hg in all
86 soils is approximately 5 µg/kg DM (Von Burg 1995; Canil et al. 2015), but with significant
87 local variations. Large Hg deposits have been found in China, Kyrgyzstan, Mexico, Peru and
88 Russia. According to Merchant Research and Consulting Ltd , 85% of the world production
89 came from China in 2016. Hg ores generally contain approximately one percent of Hg (1000
90 mg/kg), although the strata mined in Spain typically contain up to 9000 mg/kg (Wang et al.
91 2012). Hg is also found in fossil fuels such as coal, gas and oil in nonnegligible amounts. For
92 example, a study carried out in the USA showed that among the 900 million tons of coal burnt

93 in 1999, there was 75 tons of Hg (Pavlish et al. 2003). The mining activity and fossil fuel
94 consumption released Hg, which was contained as a trace element (TE) in geological stock
95 (HgS), into the air, water and sediment. Hg is also released when used in products or in
96 industrial and chemical processes such as small-scale gold mining in China or Brazil, silver and
97 lead mining, silver amalgamation for dental applications or chlor-alkali industrial processes.
98 The global Hg consumption in 2005 was estimated to be approximately 3798 tons, and experts
99 have determined that since the industrial revolution, the overall global Hg deposition in the
100 environment has increased by a factor of 3 ± 1 (Lindberg et al. 2007). The trends of global
101 anthropogenic emissions shown a decrease in Europe and North America between 1990 and
102 2010 because of industrial efforts to decrease Hg emission, and worldwide emissions mostly
103 came from East and Southeast Asia (Pacyna et al. 2010). Hg is also released in the environment
104 from forest during potential wildfires (Zhou et al. 2016). The ratio between anthropogenic and
105 natural source emissions was estimated in 2008, and anthropogenic sources accounted for
106 2320 tons of worldwide emitted Hg, mostly due to fossil fuel consumption (35%), while natural
107 sources of Hg accounted for 5207 tons of Hg with a dominance of volatilization from the oceans
108 (52%) (Pirrone et al. 2010).

109 Environmental Hg mostly exists in the gaseous elemental form (Hg^0), as inorganic
110 divalent $\text{Hg}(\text{II})$, and as organo-Hg compounds, such as monomethyl Hg (MeHg) (Hsu-Kim et
111 al. 2013). Due to its chemical properties, Hg volatilization occurs at low temperature and pH
112 (optimal at 30°C and at pH 2), and Hg is easily transferred into the atmosphere (Takeuchi et al.
113 2001). Atmospheric Hg is dominated by the extremely volatile form Hg^0 (generally $> 95\%$ of
114 total airborne Hg), whereas only minor amounts of other species (mainly particulate-phase Hg
115 ($\text{Hg}(\text{p})$) have been detected (Stratton and Lindberg 1995). Hg^0 can be oxidized into mercuric
116 ion Hg^{2+} in the Earth's atmosphere by photochemical reactions, and then it may precipitate by

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

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

129 **Impact of Hg on soil fungi**

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

138 Common approaches for the study of Hg toxicity towards fungi consist of measuring
139 the growth rate of fungal strains on Hg-enriched synthetic growth media. The Hg chemical form
140 most commonly used is HgCl_2 (Table 1). Under axenic conditions, Hg fully inhibited the growth
141 of 9 species of wood-rotting fungi at concentrations ranging between 10 and 100 μM of HgCl_2

142 (Baldrian et al. 2000). The growth of 21 fungi isolated from soil was inhibited in a range from
143 10 to 100 μM of HgCl_2 , (Sanglimsuwan et al., 1993). Under controlled conditions, soil
144 colonization by the white-rot fungus *Pleurotus* was strongly inhibited by 100 mg Hg/kg
145 (Baldrian et al. 2000). A negative effect of Hg was reported for 6 species of ectomycorrhizal
146 (ECM) fungi, with a decrease in radial growth rate and biomass production in the presence of
147 Hg (Crane et al. 2010). Corroborating those results, in a recent study we measured the Hg
148 tolerance of 103 ECM and endophytic fungal isolates collected from TE- and Hg-polluted sites
149 and 2 isolates from an unpolluted site by growing them on Hg-amended medium to determine
150 their *in vitro* tolerance, which was measured by growth inhibition. For most fungi, the minimum
151 inhibitory concentration (MIC) fell within the 10 to 200 μM Hg (HgCl_2) range, testifying the
152 high Hg toxicity for fungi under *in vitro* conditions (unpublished data). Three ectomycorrhizal
153 and three endophytic isolates were further chosen to determine their response to Hg in more
154 details, by measuring radial growth, biomass and Hg uptake (Fig. 1). These data highlight the
155 wide range of Hg tolerance between fungal species. Literature converges toward a high Hg
156 toxicity for the fungi under *in vitro* conditions compared to other TE. Indeed, when compared
157 with Cd, Co, Cr, Cu, Mn, and Pb, Hg was the most toxic element tested (Baldrian et al. 2000).
158 In *Ganoderma lucidum*, the toxicity of TE on fungal growth in pure culture was classified in
159 the following order: $\text{Hg} > \text{Cd} > \text{Cu} > \text{U} > \text{Pb} > \text{Mn} = \text{Zn}$ (Tham et al. 1999).

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

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

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

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

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

206 **Impact of Hg on soil bacteria**

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

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

217 unexpectedly, for other soil types, such as pasture, cultivated, forest and industrial, Hg spiking
218 generally did not affect the VHB percentage (Drønen et al. 1998; Harris-Hellal et al. 2009;
219 Müller, 2001; Ranjard et al. 1997; 2000). Additionally, a decrease in the number of VHB after
220 Hg exposure has also been described in many studies (Holtze et al. 2006; Ruggiero et al. 2011).
221 More surprisingly, an increase in soil VHB could be measured in response to Hg exposure
222 (Rasmussen and Sørensen, 2001; Van Faassen, 1973). In the case of acute Hg exposure of non-
223 initially contaminated soils, an enrichment of HgR bacteria was often described (Drønen et al.
224 1998; Holtze et al. 2006; Müller et al. 2001; Ranjard et al. 1997, 2000; Rasmussen and
225 Sørensen, 2001; Ruggiero et al. 2011; Van Faassen, 1973). The HgR bacterial enrichment could
226 explain the stable number of VHB before and after acute exposure by comparison with control
227 soils. If the percentage of HgR bacteria generally increased after Hg exposure, a decrease in the
228 percentage of HgR bacteria was also observed only a few days after Hg spiking (Drønen et al.
229 1998). This phenomenon could be explained by volatilization or adsorption of Hg in soil, which
230 could reduce the bioavailability of Hg, therefore decreasing the Hg selective pressure. Bacterial
231 Hg resistance has been mainly attributed to the *mer* operon system and mostly the *merA* gene
232 (Barkay et al. 2003). The consistent trend of an increase in HgR bacteria in response to Hg
233 contamination is strongly supported by the increase in the abundance of the *merA* gene across
234 various soil types for both acute and chronic Hg exposure (Frossard et al. 2017; 2018). While
235 the increase of HgR bacteria in response to Hg seems to be a consistent trend, the VHB response
236 presents contrasted patterns.

237 Molecular biomass quantification of bacteria using a quantitative PCR approach after
238 Hg exposure presented the same trend as VHB counting, with a decrease (Frossard et al. 2017;
239 Liu et al. 2018), no change (Frossard et al. 2018; Tardy et al. 2014) or an increase (Liu et al.
240 2014) in the bacterial abundances. Liu et al. (2014) followed the bacterial molecular biomass
241 with 16S qPCR along a long-term Hg gradient and showed no correlation with THg.

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

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

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

268 seemed to not impact the genetic structure of the bacterial community (Frossard et al. 2018). These
269 results may indicate that bacterial communities are more sensitive to acute Hg exposure than chronic
270 Hg exposure. A low concentration of soil Hg (between 4.4 and 11.1 mgTHg/kg DM) leads to a
271 statistically significant decrease in the bacterial diversity of 20% (Mahbub et al. 2016b). The decrease
272 in bacterial diversity was correlated with the Hg concentration in neutral and alkaline low organic
273 carbon-containing soil but not in rich organic carbon-containing acidic soil, which contains less water-
274 soluble Hg. In addition, the water-soluble Hg obtained with deionized water extraction (Mahbub et al.
275 2016a) led to a change in the bacterial diversity at lower concentrations ranging from 3.8 to 22.8 μg
276 Hg^{2+}/L and could be an informative index for the bioavailability of Hg in soils. These negative impacts
277 of Hg on soil bacterial diversity were observed in other studies, mostly with acute exposure (Frossard
278 et al. 2017; Liu et al. 2018; Müller et al. 2001; Ruggiero et al. 2011). Surprisingly, chronic Hg exposure
279 appeared to lead to an increase in bacterial diversity (Frossard et al. 2017; Liu et al. 2014; 2018). As for
280 the bacterial community genetic structure, the impact of Hg on soil bacterial diversity seems to be linked
281 with the Hg exposure type.

282 **Impact of Hg on soil microbial functions**

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

294 the soil nitrogen mineralization rate and nitrification rate (Van Faassen 1973, Liu et al., 2010).
295 To determine the effect of Hg on ammonia-oxidizing bacteria (AOB), real-time PCR assays of
296 the *amoA* genes were used (Liu et al. 2009). The AOB community was dominated by
297 *Nitrosopira*-like sequences, and this result appeared to be a consistent trend; the *Nitrosopira*-
298 like sequences decreased as the concentration of Hg increased. Moreover, Hg led to a major
299 disturbance that had a negative impact on ammonium oxidizers and nitrifiers (Mahbub et al.,
300 2016b). Taken together, these results suggest that Hg could be a threat to microbial soil
301 functions involved in both C and nutrient cycles.

302 **Microbial mechanisms related to Hg exposure, what about fungi?**

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

315 Microbial resistance mechanisms to Hg are not fully understood, although some
316 mechanisms have been proposed: (i) cell wall binding of Hg limits Hg uptake (Kinoshita et al.
317 2013), (ii) production of thiols (such as glutathione) to chelate Hg in sulfhydryl groups (SH)
318 limit the bioavailability of Hg (Wu and Wang 2014), (iii) similarly production of selenium-rich

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

322 *Lessons learned from research on bacteria*

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

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

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

369 *Are fungi terrestrial Hg hyperaccumulators?*

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

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

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

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

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

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

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

444 the specific mechanisms leading to Hg accumulation and resistance of fungi remain fairly
445 undiscovered. Nonetheless, understanding the fungal mechanisms of uptake and
446 transformations of Hg is arousing growing interest in the scientific community (Falandysz
447 2019a, 2019b, 2020b).

448 *Hg tolerance mechanisms in fungi*

449 The fungi had high Hg bioaccumulation factors despite low Hg concentrations or low
450 bioavailability in the soil, which raises the question of how fungal cells manage to cope with
451 Hg toxicity. Fungi show resistance to Hg at ranges far superior to those measured for bacteria
452 (Rajapaksha et al. 2004). In the fungal kingdom, it has been assumed that the accumulation and
453 transport of Hg could depend on the production of proteins rich in cysteine and their sulfhydryl
454 (SH) groups. These proteins, also named thiols (Stijve and Besson 1976), are produced in ECM
455 fungi and include metallothioneins and glutathione chelators (Khullar and Reddy 2016). It has
456 been suggested that there is a strong correlation between the amount of SH groups in fungal
457 proteins and Hg content in fungi (*Agaricus*), while almost no correlation for other TE was found
458 (Kojo and Lodenius 1989). Induction of metallothioneins by HgCl₂ has not been demonstrated
459 for fungi but exists in rats (Piotrowski et al. 1974). A recent study showed that higher Hg
460 contents in the edible mushrooms *B. edulis*, *B. aereus* and *Scutigera pes-caprae* resulted in
461 greater Hg tetra-thiolate complexation, but also HgSe complexation (Kavčič et al. 2019). The
462 study revealed that Hg mainly coordinated to di-thiols (43–82%), followed by di-selenols (13–
463 35%) and tetra-thiols (12–20%). In addition to selenium-rich proteins that may limit Hg
464 bioavailability in mushrooms, they found evidence of di-amino Hg complex with Hg(N-R)₂ or
465 Hg complex with two N in heterocyclic amines.

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

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

479 In Hg-contaminated soil, fungi could have the potential to detoxify organomercurials by
480 volatilization. Some fungi, such as *Yarrowia* strains, have been proven to be able to convert
481 organomercurials to Hg(II) by fungal organoHg lysis and then reduced Hg(II) to Hg⁰ (Gadd
482 2007; Oyetibo et al. 2015). A study proposed an experiment with several soil fungi, and Hg was
483 measured in the fungal biomass (Urík et al. 2014). The authors concluded that
484 bioimmobilization of Hg was negligible compared to volatilization, and they demonstrated the
485 biovolatilization potential of *Aspergillus niger* and *Cladosporium cladosporioides*, which
486 reached 80% of 32.7 mg HgCl₂/l. In such experiments, we proposed that a survey of Hg volatile
487 compounds such as MeHg should be performed to exclude the bioimmobilization hypothesis.
488 Hg methylation has been less studied in fungi than in bacteria, however some fungi may
489 produce Hg volatile compounds such as MeHg (Vonk and Sijpesteijn 1973). A study monitored
490 the production of MeHg in bacteria and fungi and revealed that *A. niger*, *Scopulariopsis*
491 *brevicaulis* and *Saccharomyces cerevisiae* were able to produce MeHg from sublethal HgCl₂
492 concentrations (Vonk and Sijpesteijn 1973). MeHg was essentially found in the mycelium in
493 contrast to bacteria, where the MeHg produced was mostly found in the media. For *A. niger*,

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

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

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

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

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

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

555 **Conclusions**

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

568 **Author contributions**

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

573 **Compliance with Ethical Statement**

574
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579

580 Conflict of Interest: Alexis Durand, François Maillard, Julie Foulon and Michel Chalot declare
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582

583 Ethical approval: This article does not contain any studies with human participants or animals
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585

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1039

1040 **Legends to figures**

1041 **Figure 1.** The effects of HgCl₂ on the radial growth of 6 selected fungal isolates. *P. involutus*
1042 He01, *P. involutus* Pi01, *P. tinctorius* Pt01, *Leptodontidium* sp. M10, *Helotiales* Pr01 and
1043 *Cadophora* sp. Pr29 were incubated on malt agar medium supplemented with 0 to 100 µM
1044 HgCl₂ for various periods of time. Means and standard deviations of at least five replicates are
1045 presented. Values designated by the same letters were not significantly different ($p < 0.05$)
1046 according to the Kruskal-Wallis test.

1047

1048 **Figure 2.** Peer reviewed publications on mercury in the bacterial or fungal kingdom and
1049 referenced in Google Scholar since 2000.

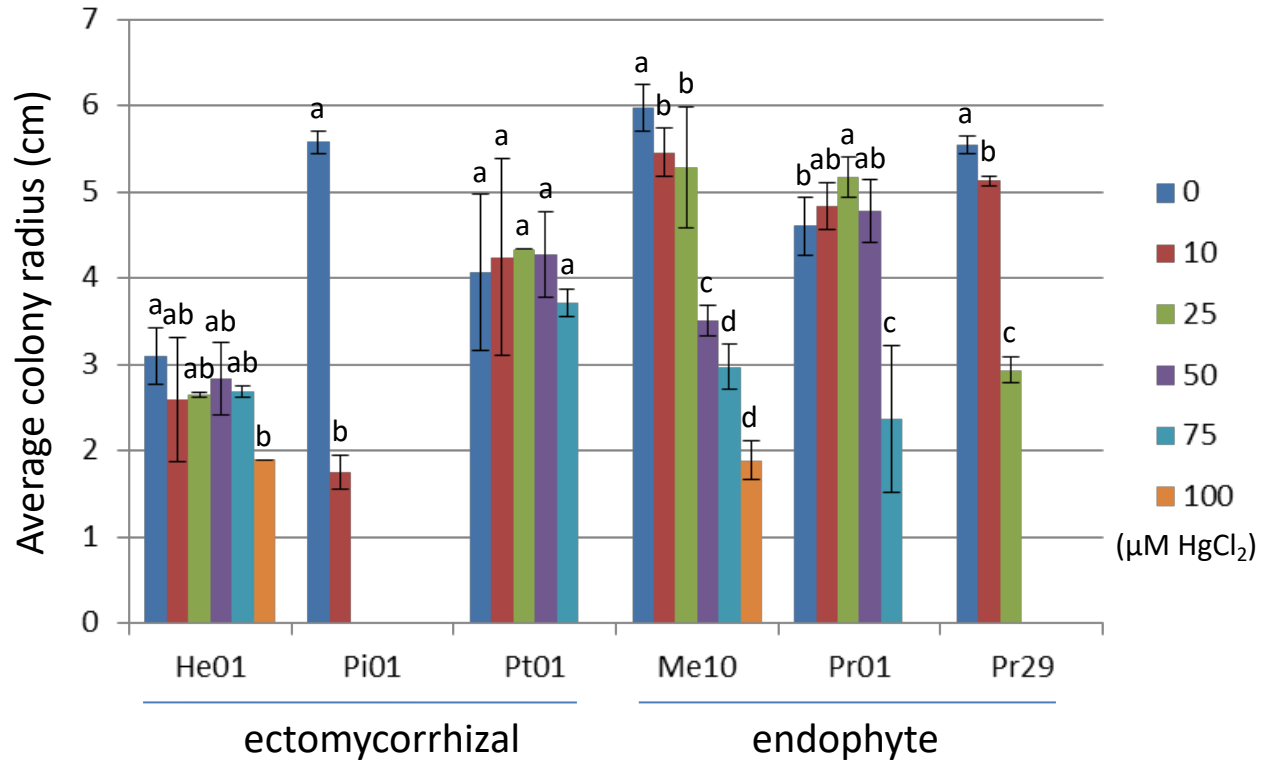
1050

1051 **Figure 3.** Comparison between the maximum Hg concentration and maximum Hg
1052 bioconcentration factor (BCF) of macromycetes genera reported in the literature. Smallest
1053 values are represented in detail on the right.

1054

1055 **Figure 4.** Schematic representation of the cellular mechanisms potentially involved in Hg
1056 tolerance in fungi. Extrahyphal immobilization of Hg occurs through the formation of
1057 secondary minerals by excreted ligands (1) and biosorption to cell wall constituents such as
1058 chitin and chitosan (2). Hg uptake could occur, for example, through specific transporters for
1059 the acquisition of other essential metals that have not yet been described (3). Hg transformation,
1060 such as reactions involving organometals (for example, methylations) and redox reactions (5),
1061 frequently result in metal volatilization (4). Intracellular Hg immobilization involves
1062 complexation by cytoplasmic phytochelatins (PC) (7) or glutathione (GSH). Hg–glutathione
1063 complexes can be further transferred to the vacuolar compartment by the *ycf1* transporter, for
1064 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

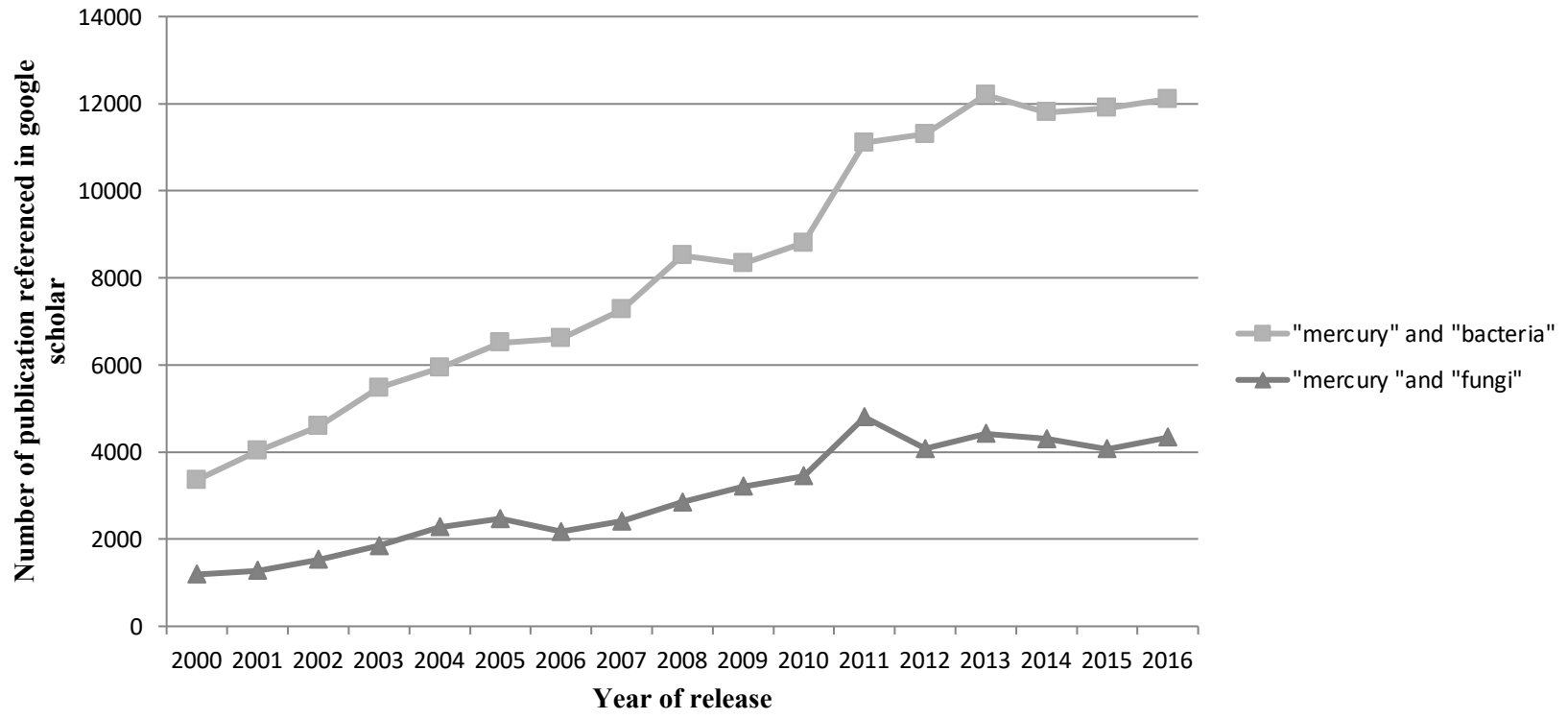


Figure 3

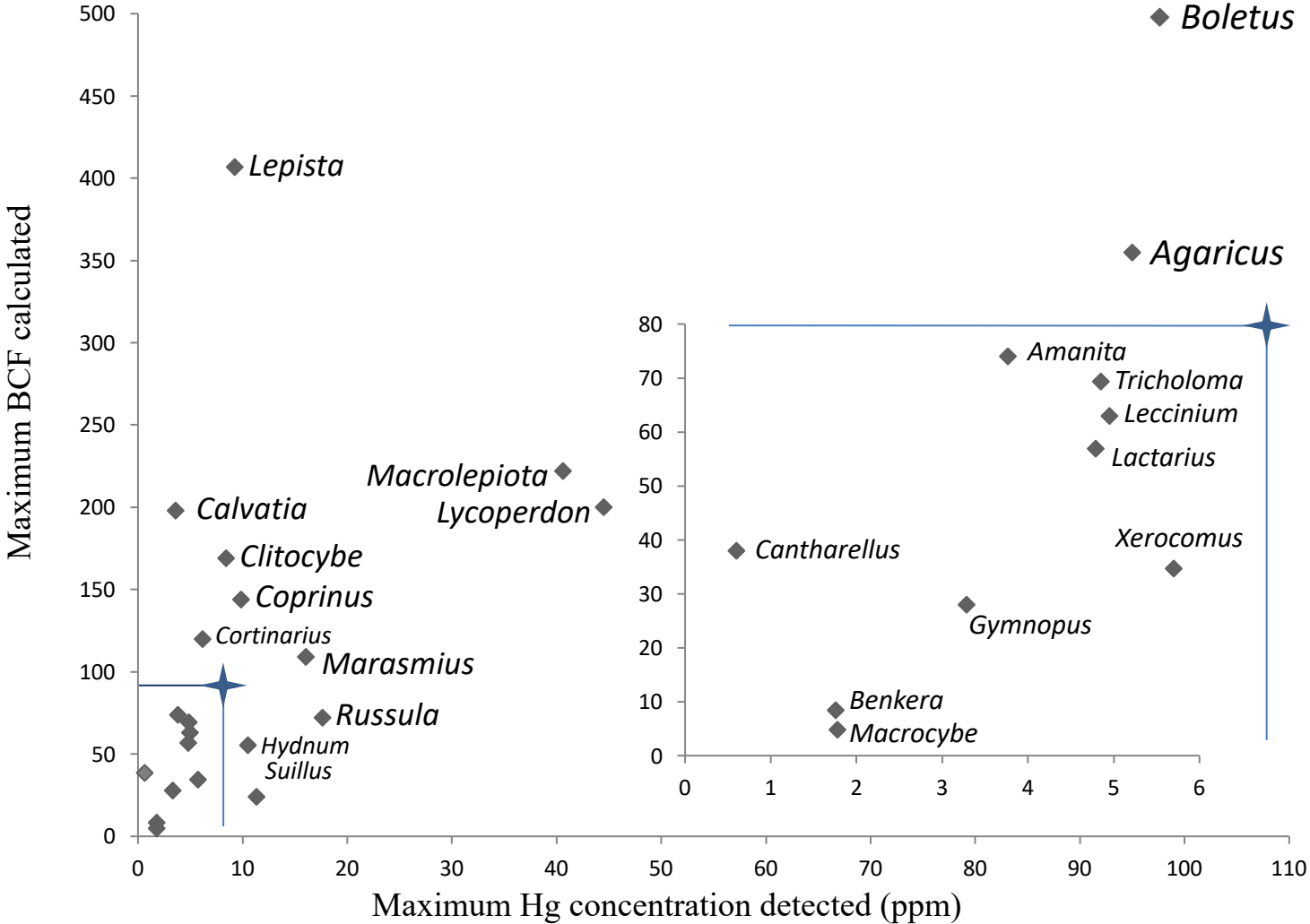


Figure 4

- Cytoplasm
- Cell wall
- Plasma membrane
- Vacuole
- Ligands (L)
- Phytochelatin (PC)
- Transporters (ycf1)
- Molecules

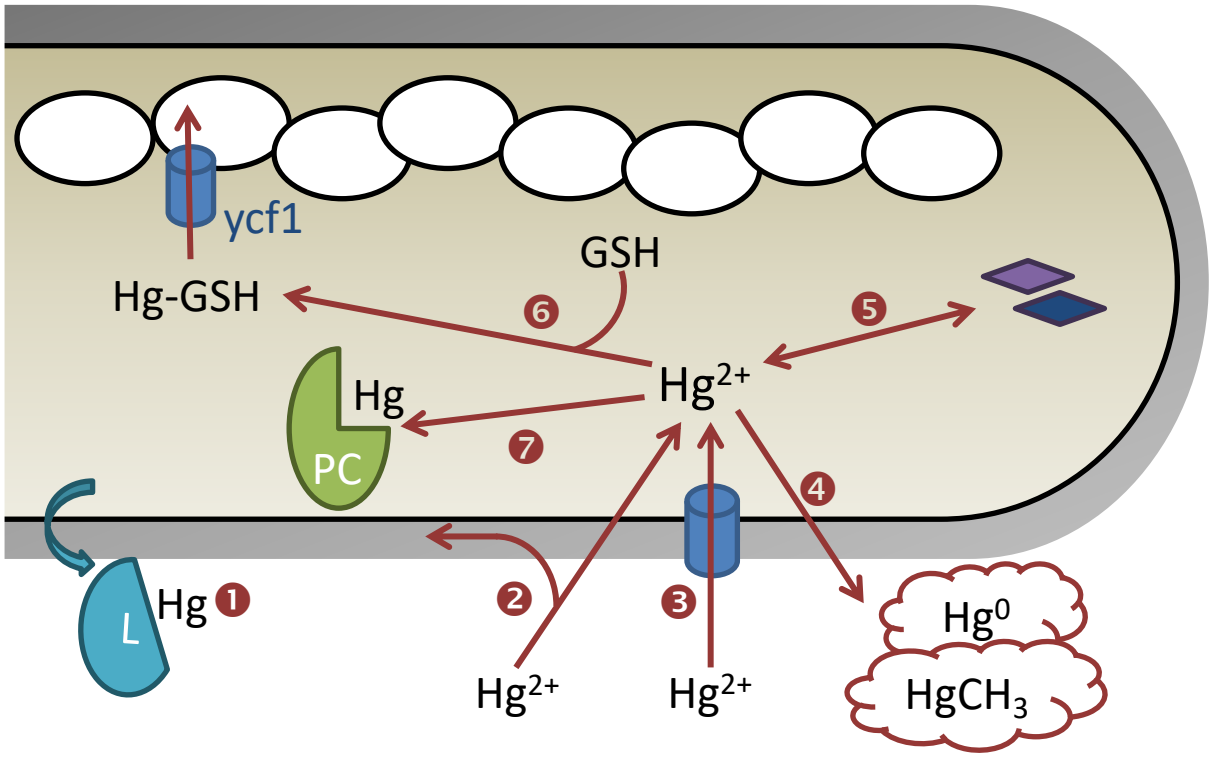


Table 1. Overview of tolerance of microbial communities towards Hg. The main effects are provided for the listed microbial communities, together with Hg concentrations in soils and references.

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
								-	basal respiration	respirometry
									change	bacterial community structure
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

								change	bacterial community structure	16S rRNA gene metabarcoding	
								change	fungal community structure	ITS rRNA gene metabarcoding	
		controlled conditions						acute	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	16S quantitative PCR	
								+	positiv correlation between MHg and bacterial abundance		
								+	Gemmatimonadetes (phylum lvl), Anaerolineales, envOPS12, Hydrogenophilales and SBR1031 (genus lvl)	454 pyrosequencing	
								-	<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	fungus 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	
								o	fungus 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	CO ₂ 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
								+	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	