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1 **Bacteria in decomposing wood and their interactions with wood-decay fungi**

2

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10

11 **Running head:** Bacteria in wood

12

13 **Keywords:** bacteria; fungi; wood; decomposition; community ecology; wetwood

14

15 **Single-sentence summary:**

16 Bacteria and fungi both live in wood, but not much is known about how they interact - this article

17 reviews what is already known about them and what is yet to be found out.

18 **Abstract**

19           The fungal community within dead wood has received considerable study, but far less  
20 attention has been paid to bacteria in the same habitat. Bacteria have long been known to inhabit  
21 decomposing wood, but much remains underexplored about their identity and ecology. Bacteria  
22 within the deadwood environment must interact with wood decay fungi, but again, very little is  
23 known about the form this takes; there are indications of both antagonistic and beneficial  
24 interactions within this fungal microbiome. Fungi are hypothesised to play an important role in  
25 shaping bacterial communities in wood, and conversely, bacteria may affect wood-decay fungi in a  
26 variety of ways. This mini-review considers what is currently known about bacteria in wood and their  
27 interactions with fungi, and proposes possible associations based on examples from other habitats.  
28 It aims to identify key knowledge gaps and pressing questions for future research.

29

30 *141 words*

## 31 **1. Introduction**

32 Globally, fallen wood stores more than 73 billion tonnes of carbon (Pan *et al.* 2011) and  
33 provides habitat for a wide range of saproxylic (*i.e.* deadwood-inhabiting) organisms (Stokland *et al.*  
34 2012). Understanding the rate, mechanisms and control of wood decomposition is of major  
35 ecological and economic importance, and the key to doing so lies in understanding the microbial  
36 communities that effect and regulate decomposition. Fungi are the dominant agents of wood  
37 decomposition, but it has long been known that bacteria also inhabit dead wood (Greaves, 1971).  
38 There are indications of great bacterial diversity within wood (Zhang *et al.* 2008; Větrovský *et al.*  
39 2011; Sun *et al.* 2014; Hoppe *et al.*, 2015), but bacteria are very poorly understood compared with  
40 fungi in the same environment. Wherever bacteria and fungi co-occur they must interact with and  
41 influence each other (Fig.1), yet although wood-decay fungi are well-known for being highly  
42 competitive (Boddy 2000) relatively little attention has been paid to the fungus-bacteria relationship  
43 (de Boer *et al.* 2005). Fungal-bacterial interactions have already been studied in other contexts for  
44 their importance in medicine, agriculture, and food and drink (Frey-Klett *et al.* 2011), but have been  
45 explored far less with respect to decomposition. The suite of bacteria that surround and interact  
46 with a fungus effectively constitute its microbiome, and as such, they must be considered together.  
47 The aim of this mini-review is to synthesise the current state of knowledge about bacteria in wood  
48 and how they interact with wood decay fungi, so as to identify key areas for future exploration.

49

## 50 **2. Diversity of bacterial communities in wood**

51 Information on bacterial communities in decomposing wood is surprisingly scarce, given how  
52 well saproxylic fungal communities have been studied. This disparity is doubtless partially due to the  
53 greater propensity of fungi to enter culture – there is a long history of successful isolation of fungal  
54 decay communities from wood (*e.g.* Boddy *et al.* 1987). In contrast, whilst there are studies that  
55 have looked at the culturable fraction of saproxylic bacteria (*e.g.* Murray & Woodward 2007; van der  
56 Wal *et al.* 2007), a large and variable proportion are unculturable (Folman *et al.* 2008). Culture-based  
57 studies can thus, at best, only indicate part of the bacterial community. Because the culturable  
58 *proportion* of total bacteria varies, plate counts can never be used for quantitative comparison in  
59 this context. For example, a microcosm experiment recorded that in the absence of wood-decay  
60 fungi, 61% of bacteria colonising wood blocks could be cultured; when a white-rot fungus was  
61 introduced, the culturable proportion dropped to 1% (Folman *et al.* 2008). Unfortunately, the  
62 limitations of culture-based surveys mean that much older literature in this field is of restricted  
63 usefulness. Whilst culture-based approaches can no longer be used for whole-community  
64 characterisation, they remain highly useful for exploring specific relationships (*e.g.* Nazir *et al.*,

65 2014). Culture-based studies have also succeeded in isolating new genera from dead wood, including  
66 members of the difficult-to-culture phylum Acidobacteria (*e.g.* Folman *et al.*, 2008). The accessibility  
67 and high throughput of next-generation DNA sequencing and associated metagenomics opens the  
68 door to more comprehensive study of saproxylic bacterial communities. This review will therefore  
69 pay special attention to studies that have used molecular methods to assess bacterial diversity in  
70 wood (Table 1), drawing on culture-based studies as well where applicable.

71 Bacterial diversity is far lower in wood than in soil (Hervé *et al.* 2014; Sun *et al.* 2014), and is  
72 highly influenced by the underlying soil type; nonetheless, there is a high level of intra-site  
73 heterogeneity (Sun *et al.* 2014). The bacterial community varies dependent on the wood's state of  
74 decay, with bacterial richness increasing as the wood decomposes (Hoppe *et al.* 2015). Heartwood  
75 and sapwood contain markedly different bacterial communities, but communities in heartwood are  
76 apparently more diverse (Zhang *et al.* 2008); nonetheless, bacteria may be more abundant in  
77 sapwood (Jeremic *et al.* 2004). There are indications that bacterial communities differ between tree  
78 species (Folman *et al.* 2008; Hoppe *et al.* 2014, 2015; Prewitt *et al.* 2014). The water content, pH,  
79 and C:N ratio of the wood affect the bacterial community, as does the forest management regime  
80 (Hoppe *et al.* 2015). Bacterial abundance and richness is highest at advanced stages of wood decay,  
81 but does not show a clear pattern for phylum-level community composition (Kielak *et al.* 2016b;  
82 Rinta-Kanto *et al.* 2016). These studies offer a tantalising insight into saproxylic bacterial  
83 communities, but the field is still young and the conclusions are tentative.

84 There are parallels between the microbial decomposer communities in wood and leaf litter.  
85 In leaf litter, bacterial and fungal communities show linked dynamics and both are also influenced by  
86 the same abiotic drivers of C:N ratio, nutrient availability, water content and pH (Purahong *et al.*,  
87 2016). In another study on deciduous leaf litter, fungi showed less dependence than bacteria on  
88 environmental variables, such as water availability and ambient temperature (Liu *et al.* 2016).  
89 However, it is very difficult to extrapolate results from one habitat or taxonomic group to another.  
90 For example, dominant tree identity is a major fungal community driver in both soil and litter, but  
91 less important for bacteria in litter and unimportant for bacteria in soil (Urbanová *et al.* 2015).

92 In functional terms, Greaves (1971) classified saproxylic bacteria into four groups based on  
93 their role in decomposition: bacteria that make wood more water-permeable without affecting its  
94 structural integrity; bacteria with (albeit limited) decomposition ability; bacteria that stimulate  
95 fungal decomposition; and bacteria that inhibit fungal decomposition. These classes maintain their  
96 relevance today, but present a challenge: how best to relate broad-scale, whole sample taxonomic  
97 information from sequencing to fine-scale functional abilities. Even the bacteria amenable to culture  
98 can show vastly different properties depending on medium, *etc.* (Murray and Woodward 2003).

99 Truly making sense of the bacterial communities in wood will depend upon linking their identity and  
100 function, even for species that can be cultivated.

101 Any consideration of bacteria in wood should take into account the presence and identity of  
102 wood decay fungi, as current evidence strongly indicates that they greatly influence the bacterial  
103 community (Folman *et al.* 2008; Sun *et al.* 2013; Hoppe *et al.* 2014). In the soil environment, areas  
104 under close fungal influence have distinctive bacterial communities (Warmink and van Elsas 2008).  
105 In *Picea abies* logs, fungal diversity correlated negatively with bacterial abundance, and there are  
106 indications that certain bacterial taxa co-occur preferentially with particular fungi (Rinta-Kanto *et al.*  
107 2016). Discerning ecologically realistic patterns is challenging, due to the huge number of potentially  
108 significant variables; for example, the effects of fungal inoculation on bacteria alter over time (Sun *et al.*  
109 *et al.* 2013). It is also virtually impossible to establish fungus-free bacterial controls when inoculating  
110 wood from soil (de Boer *et al.* 2010).

111 Fungi profoundly influence the wood physical environment by lowering the pH, excreting  
112 metabolites such as oxalic acid and translocating nitrogen and phosphorus into the resource  
113 (Watkinson *et al.* 2006; de Boer *et al.* 2010; Rudnick *et al.* 2015). It should be noted that whilst  
114 translocation increases the bulk N and P content of the wood, they are contained within hyphae and  
115 only available to bacteria that can access the hyphal contents. Experimental evidence shows that  
116 dead mycelium also provides a rich and largely labile nutrient source which supports a distinct  
117 bacterial community (Brabcová *et al.* 2016). However, in the environment fungi recycle cytoplasm  
118 from senescent hyphae to other parts of the mycelium, so not all of these nutrients are available to  
119 other decomposers (Watkinson *et al.* 2006).

120 Wood-decay fungi have repeatedly been associated with Burkholderiaceae (Seigle-Murandi  
121 *et al.* 1996; Lim *et al.* 2003; Yara *et al.* 2006; Folman *et al.* 2008; Valášková *et al.* 2009; Leveau *et al.*  
122 2010; Sato *et al.* 2010; Hervé *et al.* 2014; Prewitt *et al.* 2014; Sun *et al.* 2014). A widespread and  
123 versatile family of bacteria, it crops up alongside fungi with remarkable regularity, and not only in  
124 wood (de Boer *et al.* 2005; Frey-Klett *et al.* 2011). Moreover, there are indications of close,  
125 specialized associations between fungi and the genus *Burkholderia* involving collaborative  
126 pathogenicity (Partida-Martinez and Hertweck 2005); intimate mycelial associations (Lim *et al.*  
127 2003); endosymbiosis (Sato *et al.* 2010); co-migration and detoxification of antimicrobials (Nazir *et al.*  
128 *et al.* 2014); and successional persistence (Hervé *et al.* 2014). An analysis of global soil microbiota  
129 found significant co-occurrence between *Burkholderia* and fungi (Stopnisek *et al.* 2015). The same  
130 study also analysed the proteome of *B. glathei* when grown alone or with fungi, and found that  
131 when fungi were present the bacteria expressed fewer proteins associated with starvation, but

132 upregulated its stress response, suggesting that the bacteria gained nutrients from the fungus but  
133 experienced antibiosis and/or unfavourable chemical conditions (Stopnisek *et al.* 2015).

134 It has been suggested (Greaves 1971; Frey-Klett *et al.* 2011) that bacterial activity in the  
135 earliest stages of decay renders the wood more accessible to fungi. Whilst bacteria may detoxify  
136 certain compounds inhibitory to fungi, notably in treated wood (Greaves 1971; Clausen 1996),  
137 experiments using fresh, sterile wood show that fungi are competent wood decayers in the absence  
138 of bacterial conditioning (*e.g.* Hiscox *et al.* 2010). Similarly, although it is sometimes suggested that  
139 bacteria are the earliest colonists of dead wood, there is little evidence on whether or not that is the  
140 case (van der Wal *et al.* 2007). Given that wood decay fungal propagules are latently present in  
141 functional wood (Parfitt *et al.* 2010), for this to hold true bacteria would likewise have to be latently  
142 present, and/or colonise wood very rapidly once conditions were favourable.

143

### 144 **3. Bacterial colonisation of wood**

145 The provenance of saproxylic bacteria communities and their means of colonisation are  
146 largely unknown. Bacteria have limited motility and are unable to cross air voids, meaning that  
147 colonisation is likely to be slow without some means of carriage into the wood. Essentially, bacteria  
148 in a woody resource have four possible points of origin: the soil; the air; the wood itself; and fungi or  
149 other organisms colonising the wood. The relative importance of these sources is likely to vary under  
150 different conditions; the bacterial community in attached dead branches is probably very different  
151 from that in wood on the forest floor.

#### 152 *3.1. Edaphic and atmospheric sources of bacteria*

153 Soil represents a rich source of potential colonists for wood in ground contact, and the  
154 underlying assumption of many studies is that it is the main point of origin for bacteria in wood (*e.g.*  
155 van der Wal *et al.*, 2007; Folman *et al.*, 2008; Hervé *et al.*, 2014). These show that a subset of soil  
156 bacteria are competent to colonise wood, but do not indicate to what extent this occurs under  
157 natural conditions. Underlying soil type was a good predictor of bacterial assemblage in  
158 experimental wood blocks (Sun *et al.* 2014), which suggests either an edaphic origin of saproxylic  
159 bacteria, or an indirect influence of soil: for example, via an altered fungal community.

160 Movement via airborne spores and other propagules is a major means of bacterial dispersal,  
161 which has led to the widespread view that all bacteria are, or have the potential to be, ubiquitous: a  
162 view that has since been challenged (Green and Bohannan 2006). Nevertheless, the air could  
163 represent another means for bacteria to arrive at decomposing wood. In woodlands, rainfall creates  
164 bio-aerosols of bacteria and fungal spores, presumably contributing to their dispersal (Huffman *et al.*  
165 2013). An experiment on bacteria in woodland pools indicated that the community composition was

166 not dispersal limited, suggesting that airborne dispersal is effective at least across local scales (Bell  
167 2010).

### 168 3.2 Bacterial endophytes

169 As mentioned above, wood decay fungi exist in living trees as latent propagules which  
170 spread as mycelia when the branch or trunk is no longer functional in water conduction (Parfitt *et al.*  
171 2010). Scanning electron microscopy indicates that at least some, if not all, living trees also host  
172 abundant bacterial endophytes in their wood (Jeremic *et al.* 2004). However, there is very little  
173 literature on bacterial endophytes in wood, and the identity of these endophytes is as yet uncertain.

### 174 3.3. Bacteria co-colonisation with other organisms

175 *Burkholderia terrae* BS001 has been shown to migrate across soil with wood-decay fungi,  
176 including the aggregated mycelial cords of *Phanerochaete velutina* (Nazir *et al.* 2014). This  
177 demonstrates active bacterial movement, as the apical growth of fungal hyphae rules out the  
178 possibility of passive carriage. *P. velutina* had a lower bacterial 'carrying capacity' than several other  
179 fungi, suggesting that cords may be less conducive to migration than are fine hyphae. The presence  
180 of *B. terrae* BS001 can also facilitate the movement of other bacteria which would otherwise not be  
181 competent to migrate along hyphae (Warmink *et al.* 2011). Independent hyphal migration has also  
182 been observed for several other members of the Burkholderiales and some strains of *Dyella japonica*  
183 (Warmink and van Elsas 2009; Nazir *et al.* 2012). It has been suggested that other fungus-associated  
184 bacteria such as *Collimonas* may share this migratory ability (Leveau *et al.* 2010). Such behaviour  
185 raises the possibility that when fungi colonise a resource, they bring a suite of bacterial travelling  
186 companions. In this manner saproxylic bacteria could use foraging fungal mycelium as a conduit to  
187 new resources.

188 Other saproxylic organisms, particularly invertebrates, may transfer bacteria from one  
189 woody resource to another. Bark beetles can carry bacteria phoretically (Mercado *et al.* 2014), and  
190 introduce them into trees during the construction of galleries. This has also been suggested as a  
191 source of nitrogen-fixing bacteria in wood (Griffiths *et al.* 1993).

192

## 193 4. Wetwood

194 The presence of bacteria in living trees is most obvious in bacterial wetwood. Wetwood, also  
195 known as wet-heartwood or watermark, is a condition where the heartwood of a living tree  
196 becomes saturated and discoloured. This change may be accompanied by blocked vessels, gas build  
197 up, and the presence of a fetid liquid. The term refers to a suite of phenomena, probably with  
198 multiple causal agents but broadly similar manifestations, making it hard to disentangle the exact  
199 role bacteria play. Whilst in some tree species (*e.g. Salix sachalinensis*) wetwood is a serious disease,



200 spreading to sapwood and ultimately killing the tree (Sakamoto and Sano 2000), in others it seems  
201 to be an almost-ubiquitous part of maturation (*e.g. Ulmus americana*) (Murdoch and Campana  
202 1983). Wetwood is often attributed to bacterial activity, but there is no clear evidence whether this  
203 is true for this latter form, where there are no apparent ill-effects to the tree: it could equally be  
204 caused by physical processes, and bacteria secondarily colonise and modify the habitat.

205 Wetwood is frequently associated with the presence of anaerobic, methanogenic,  
206 pectinolytic prokaryotes, which could account for many of the observed symptoms (Schink *et al.*  
207 1981a). Although wetwood can form around the site of fungal infections, within the wetwood itself  
208 fungi are likely to be excluded by low O<sub>2</sub> concentrations, large amounts of organic acids and  
209 inhibitory metabolites (Worrall and Parmeter 1983). If fungi are indeed absent from wetwood, it  
210 represents an almost unique wood habitat in this respect.

211

## 212 **5. Bacterial metabolism in wood**

### 213 *5.1 Bacterial nitrogen fixation in wood*

214 It has long been recognised that dead wood plays host to nitrogen-fixing (diazotrophic)  
215 bacteria, which provide an independent source of nitrogen to the system (Cornaby and Waide 1973;  
216 Sharp and Millbank 1973). Many studies have focussed on coniferous forests of the Pacific  
217 Northwest, and used acetylene reduction as a measure of nitrogenase activity (reviewed by Son,  
218 2001). Interpretation and comparison of these results requires caution, as the exact methodology  
219 used varies; acetylene reduction has been criticised for its sensitivity to experimental parameters  
220 (Giller 1987), although the effects may not be as serious as suggested (Son 2001). Additionally, the  
221 conversion factor used to calculate N-fixation from acetylene reduction is not consistent (Son 2001;  
222 Brunner and Kimmins 2003), and there is evidence to suggest that the true conversion rate may vary  
223 between sample types (Hicks *et al.*, 2003b). In light of these difficulties, acetylene reduction should  
224 perhaps be regarded as semi-quantitative, suitable for comparison within but not between studies.

225 The picture that emerges of N-fixation in dead wood suggests a highly dynamic process,  
226 influenced by many factors (Hicks *et al.*, 2003a). Wood water content is consistently positively  
227 correlated with N-fixation (Larsen *et al.*, 1978; Jurgensen *et al.*, 1984; Brunner & Kimmins, 2003;  
228 Hicks *et al.*, 2003a), possibly because it creates better microhabitats for the  
229 anaerobic/microaerophilic diazotrophs (Spano *et al.*, 1982; Hicks *et al.*, 2003a). The optimum  
230 temperature for fixation is 30°C (Hicks *et al.*, 2003a), which may explain higher N-fixing activity in  
231 summer than in winter (Jurgensen *et al.* 1984; Sollins *et al.* 1987). The requirements for high  
232 temperature and high moisture suggest an interplay of factors that determine seasonal fixation  
233 patterns (Hicks *et al.*, 2003a). The effect of tree species on fixation is unclear, with some authors

234 reporting significant differences between species (Jurgensen *et al.* 1989; Griffiths *et al.* 1993; Hoppe  
235 *et al.* 2014), and others reporting none (Sollins *et al.*, 1987; Hicks *et al.*, 2003b). Nitrogen fixation in  
236 forest ecosystems is likely to be limited by the availability of molybdenum, which is necessary for  
237 nitrogenase synthesis, and possibly also by other micronutrients (Silvester, 1989).

238 Nitrogen fixation increases as decay proceeds (Larsen *et al.* 1978; Spano *et al.* 1982;  
239 Jurgensen *et al.* 1984), although two studies found that fixation peaked before dropping off in the  
240 most advanced stage of decay, perhaps because the latter studies included more decayed wood  
241 than the former (Hicks *et al.* 2003b). An experiment using a finer resolution time-series over 6 years  
242 revealed considerable variation within the overall increase in N fixation (Griffiths *et al.*, 1993). In the  
243 very early stages of decay, N fixation will be limited by the rate at which diazotrophs can colonise the  
244 resource. If nitrogen-fixing bacteria rely on carbon from fungal activity (see section 6.1), they may  
245 also experience a growth lag whilst fungi colonise and start to decompose the wood. Diazotrophic  
246 activity is higher in sapwood than in heartwood, and higher again in bark; low fixation has been  
247 recorded in heartwood, possibly because it is the fraction most refractory to decomposition  
248 (Griffiths *et al.*, 1993; Brunner & Kimmins, 2003; Hicks *et al.*, 2003b) and often contains inhibitory  
249 extractives.

250 The identity of the saproxylic diazotrophs is underexplored, but *Clostridium* and *Klebsiella*  
251 have been cultured (Spano *et al.* 1982). A survey of *nifH* nitrogenase genes in decaying wood  
252 indicated Rhizobiales was the predominant identifiable order, with Rhodocyclales,  
253 Pseudomonadales, Rhodospirillales, Sphingomonadales and Burkholderiales also present; however,  
254 most of the saproxylic *nifH* variants could not be matched to known bacteria (Hoppe *et al.* 2014).  
255 These bacterial orders have also been identified previously in 16S rRNA gene surveys of decaying  
256 wood (Folman *et al.* 2008; Valášková *et al.* 2009).

## 257 5.2 Bacterial wood decomposition

258 Bacteria are well known to be capable of cellulose decomposition, although their  
259 contribution to overall wood decay is restricted by small size and limited movement (Greaves 1971;  
260 Clausen 1996) unlike fungi with mycelial growth (de Boer *et al.* 2005). Various bacteria from  
261 woodland soil possess enzymes involved in the breakdown of cellulose/ cellulose products, including  
262 members of the Acidobacteria, a common phylum in dead wood (Lladó *et al.* 2016; Table 1). Some  
263 cellulolytic bacteria apparently use new, uncharacterised means of metabolising cellulose without  
264 expressing the usual enzymes (López-Mondéjar *et al.* 2016). Certain bacteria in wood break down  
265 pectin (Schink *et al.* 1981b; Clausen 1996), although in some cases this may be a strategy to access  
266 cellulose (Lynd *et al.* 2002). Evidence has emerged of bacteria with lignin-decomposing abilities,  
267 albeit to a lesser extent than fungi (Bugg *et al.* 2011; Brown and Chang 2014). An Actinobacterium,

268 *Amycolatopsis* sp. 75iv2, can use lignin as a sole carbon source (Brown and Chang 2014). Previously-  
269 unknown ligninolytic bacterial enzyme systems have been found, unlike those deployed by fungi,  
270 and environmental metagenomics may reveal more (Brown and Chang 2014). Lignin-model  
271 compounds are frequently used to screen for activity, and whilst they may not be fully  
272 representative, there is also evidence of bacterial depolymerisation of natural lignin (Salvachúa *et al.*  
273 2015).

274 Many bacteria are thought to favour easily accessible, low molecular weight compounds  
275 present during early decay, or released by fungal activity (de Boer and van der Wal 2008). Under  
276 such a scenario, it would be expected that bacteria would be most numerous at the start of decay,  
277 and would be displaced by fungi as the latter become established and the most labile components  
278 are used up (Clausen 1996). Conversely, the absolute number of bacteria may be maintained or even  
279 increase, but shift towards bacteria adapted to fungal co-existence, living on the products of fungal  
280 decomposition. Fungi may affect bacterial decomposition in other ways, too: for example, *in vitro* a  
281 forest soil bacterium, *Clostridium phytofermentans*, lyses fungal hyphae to increase its own cellulose  
282 decomposition, presumably due to acquisition of fungal nutrients (Tolonen *et al.* 2015).

283 Again, work on forest soils and leaf litter can offer clues as to the roles of fungi and bacteria  
284 in complex polymer decomposition. Acidobacteria from a forest soil showed a range of enzymatic  
285 abilities, including the capacity to break down chitin (a fungal cell wall component) and cellobiose (a  
286 cellulose breakdown product) (Lladó *et al.* 2016). Importantly, the dominant taxa in terms of DNA  
287 abundance do not necessarily match the most active taxa based on RNA transcripts (Žifčáková *et al.*  
288 2016). Fungal and bacterial biomass in soil does not vary greatly between seasons, but their patterns  
289 of transcription activity do show strong seasonal effects (Žifčáková *et al.* 2016). There is evidence for  
290 some degree of functional redundancy in litter-decomposing communities (Purahong *et al.* 2014).

291 Mixed communities of bacteria show greater decomposition ability in wood than individual  
292 species (Schmidt and Liese 1994), which implies that bacterial contributions to wood decomposition  
293 may have been underestimated. Nonetheless, total bacterial decomposition is likely to remain  
294 negligible compared to fungi, due to the latter's size and superior access to material: factors which  
295 would also allow fungi to decompose wood at a faster rate. One situation in which bacteria do play a  
296 major role in wood decomposition is in wet/waterlogged wood such as cooling towers and  
297 archaeological structures; the low oxygen concentrations under these conditions are inhibitory to  
298 most fungi, leaving bacteria as major agents of decomposition (Kim and Singh 2000). A fluid-filled  
299 environment is also far more conducive to bacterial movement (facilitating colonisation) than a dry  
300 material. Bacterial wood decomposition is usually slow and incomplete, and thus wooden artefacts  
301 can be preserved for centuries under these conditions (Björdal 2012).

302 Bacterial wood decomposition is often described based on the physical patterns produced in  
303 the wood ultrastructure, and is can be grouped into four main types (reviewed Greaves, 1971;  
304 Clausen, 1996; Kim & Singh, 2000). These categories are based on the morphology of wood  
305 substratum following decay, rather than the taxonomic affiliations of the bacteria involved.  
306 'Tunnelling' bacteria decay a convoluted path inside the cell walls (Kim and Singh 2000), which they  
307 may enter via pit chambers (Greaves 1969). They can act on all components of the cell wall and may  
308 be able to degrade/modify lignin, at least to some extent (Kim and Singh 2000). 'Erosion' bacteria  
309 create depressions in the wall from inside the lumen, which follow the path of cellulose microfibrils;  
310 they rarely affect the middle lamella, and probably lack the ability to degrade lignin (Greaves 1969;  
311 Kim and Singh 2000). 'Pitting' bacteria produce small, shallow indentations (Greaves 1971); the term  
312 is somewhat confusing, given that bacteria often are associated with pits connecting cells.  
313 'Cavitation' bacteria cause diamond-shaped cavities inside cell walls, possibly involving the  
314 production of diffusible enzymes (Kim and Singh 2000). Bacteria are often associated with pits  
315 between wood cells, and decomposition activity in these areas can greatly increase the permeability  
316 of the wood (Greaves 1969).

317

## 318 **6. Bacterial-fungal community interactions**

### 319 *6.1 Community competition and co-operation*

320 It is not difficult to envisage why fungal-bacterial co-existence in wood could lead to conflict.  
321 Both may compete for the same substrates; bacteria may remove the products of fungal  
322 extracellular enzyme decomposition (effectively microbial kleptoparasitism); and either group may  
323 regard the other as a food resource. Certainly wood-decay fungi have an arsenal of competitive  
324 strategies capable of deployment (Boddy 2000). Bacteria described as closely associated with  
325 *Phanerochaete chrysosporium* were all proficient at utilising lignin breakdown products *in vitro*,  
326 supporting the idea that they gained nutrition from fungal activity (Seigle-Murandi *et al.* 1996).

327 Studies show that the introduction of *Hypholoma fasciculare* can alter the abundance and  
328 community composition of bacteria within wood (Folman *et al.*, 2008; de Boer *et al.*, 2010), and  
329 rapid pH change has been suggested as a possible mechanism (de Boer *et al.* 2010). Whether this is  
330 representative of a natural situation is uncertain: bacteria were very abundant in more decayed *H.*  
331 *fasciculare*-colonised wood in a field scenario, which could be due to bacterial recovery over time, or  
332 the proliferation of fungus-tolerant bacteria (Valášková *et al.* 2009). Inoculation with *Phlebiopsis*  
333 *gigantea* lowered bacterial species richness in stumps after 12 months, although the effect had  
334 disappeared by 6 years post-inoculation (Sun *et al.* 2013). It is possible that direct fungal-bacterial  
335 competition occurs in wood similar to that observed in soil, where experimental inhibition of

336 bacteria results in accelerated fungal growth indicative of competitive release (Rousk *et al.*, 2008,  
337 2010). Intriguingly, the competitive outcome appears to depend on the ambient pH: fungi prevail at  
338 low pH, bacteria at higher pH (Rousk *et al.* 2010). This is salient in light of the major pH modification  
339 – typically lowering – that fungi effect in wood (de Boer *et al.* 2010).

340         There is much *in vitro* evidence for antagonism amongst saproxylic micro-organisms, both of  
341 fungi against bacteria (Janes *et al.* 2006; Popova *et al.* 2009) and of bacteria against fungi (Murray  
342 and Woodward 2003; de Boer *et al.* 2007; Caldeira *et al.* 2008; Boaisha 2012). This is not necessarily  
343 evidence for antagonism *in situ*, given that the effect can depend on the culture medium (Murray  
344 and Woodward 2003; Boaisha 2012). In addition, soil bacteria with little or no anti-fungal activity on  
345 their own (*Pedobacter* sp. and *Pseudomonas* sp.) can show considerable fungal inhibition when in  
346 combination, either as a collaborative effort or a by-product of antagonism towards each other (de  
347 Boer *et al.* 2007).

348

349         Conclusive evidence of fungal-bacterial mutualism requires demonstration of a benefit to  
350 both partners. Although this has been demonstrated in a variety of habitats (Frey-Klett *et al.* 2011),  
351 there is a shortage of clear examples in terrestrial deadwood. There are reports of basidiomycetes  
352 gaining more biomass and decaying wood faster in the presence of yeasts and nitrogen-fixing  
353 bacteria than in their absence (Blanchette and Shaw 1978). Moreover, SEM revealed close physical  
354 association between the mycelial fungi, yeasts and bacteria (Blanchette and Shaw 1978). *H.*  
355 *fasciculare* and *Resinicium bicolor* decompose wood significantly faster in the presence of bacteria  
356 than alone; *Heterobasidion annosum* displayed the same effect only if bacteria were added after the  
357 fungus had become established (Murray and Woodward 2003). However, in other instances,  
358 bacteria had no effect on *H. fasciculare* decomposition (Weißhaupt *et al.* 2013). Such variability  
359 could be influenced by bacterial community composition, fungal intra-specific variation, or  
360 environmental conditions. Increased decomposition may be attributable to bacterial nutrient  
361 provision (*e.g.* vitamin production (Ghignone *et al.* 2012) or N-fixation), or up-regulation of fungal  
362 enzymes due to the removal of breakdown products (Murray and Woodward 2003; de Boer *et al.*  
363 2005). Whilst the latter scenario would represent facilitation in ecosystem process terms, the benefit  
364 to the fungus is questionable, depending on whether faster decomposition translates to increased  
365 fungal growth, or simply to decreased efficiency due to bacterial consumption of breakdown  
366 products. This could be particularly disadvantageous to fungi with an ecological strategy that  
367 involves slowly decomposing wood over a long period, as with some xylariaceous ascomycetes  
368 (Boddy *et al.* 1989).

369           There are examples of bacterial-fungal interactions that benefit at least one party with  
370 (currently) no evidence of harm to the other, suggesting at least a commensal association. There is  
371 also *in vitro* evidence for growth enhancement, which should be regarded with the same caveats as  
372 *in vitro* antagonism. For example, a bacterium of the *Burkholderia cepacia* complex, isolated from a  
373 *Pleurotus ostreatus* fruit body, showed increased growth in the presence of *P. ostreatus* mycelium  
374 (Yara *et al.* 2006). A *Curtobacterium* sp. from dead wood promoted growth of *Stereum* sp. –  
375 although it was the only one out of 24 culturable strains to do so (Kamei *et al.* 2012). Notably,  
376 *Streptomyces* from woodland soil showed negative or neutral influences on mycorrhizal and  
377 pathogenic fungi, yet all consistently and markedly promoted growth of the white-rot fungus  
378 *Phanerochaete chrysosporium*; it may be salient that none of these *Streptomyces* strains showed  
379 ligninolytic activity themselves (Bontemps *et al.* 2013).

380           The fungal-migratory bacterium *Burkholderia terrae* BS001 (see section 3.3) has been  
381 demonstrated to protect a (non-wood decay) fungus from inhibition by the fungicide cycloheximide  
382 or metabolites from the antagonistic bacterium *Pseudomonas fluorescens* strain CHA0 (Nazir *et al.*  
383 2014). This raises the possibility of a true mutualism, whereby *B. terrae* BS001 gains access to  
384 resources and in return affords protection to its fungal host. The level of protection depended on the  
385 identity of the fungus, and, for reasons unknown, the timing of bacterial arrival (Nazir *et al.* 2014).

#### 386 6.2 Bacterial endosymbiosis and intimate hyphal associations

387           Bacteria co-exist endosymbiotically with arbuscular mycorrhizal fungi (Bonfante and Anca  
388 2009), but such an association has yet to be conclusively demonstrated for wood-decay fungi. It is  
389 likely that bacteria do occur within the hyphae of wood decay fungi, as they have also been found  
390 inside ectomycorrhizal hyphae (Bertaux *et al.* 2005), plant-pathogenic fungi (Partida-Martinez and  
391 Hertweck 2005), a range of endophytic fungi (Hoffman and Arnold 2010) and the soil saprotroph  
392 *Mortierella elongata* (Sato *et al.* 2010). Intrahyphal existence does not necessarily indicate true  
393 endosymbiosis, which implies active interaction between living cells (Lumini *et al.* 2006). Rather,  
394 bacteria may enter compromised or senescent hyphae opportunistically and without vertical  
395 transmission (de Boer *et al.* 2005; Lumini *et al.* 2006). This distinction is not always made clearly in  
396 the literature on fungal ‘endosymbionts’, nor is it always recognised that bacteria may associate  
397 intimately but extracellularly with mycelium.

398           Where true endosymbiosis does occur, the extent of its implications are illustrated by the  
399 well-characterised association between the plant-pathogenic fungus *Rhizopus microsporus* and its  
400 bacterial endosymbiont, *Burkholderia rhizoxinica* (Partida-Martinez and Hertweck 2005). The toxin  
401 rhizoxin forms a key part of *R. microsporus* pathogenicity, yet is synthesised not by the fungus but by  
402 the bacteria within it. Vertical transmission of the bacteria is guaranteed, as *R. microsporus* has lost

403 the ability to sporulate in the absence of *B. rhizoxinica* (Partida-Martinez *et al.*, 2007). *B. rhizoxinica*  
404 is also highly competent to colonise *R. microsporus* hyphae from the outside by localised chitinase  
405 activity that does not cause fungal lysis (Moebius *et al.* 2014). Colonisation relies on both the type II  
406 and type III secretion systems (Lackner *et al.* 2011; Moebius *et al.* 2014). Pertinently, these secretion  
407 systems have been implicated in other fungal-bacterial interactions, such as mycorrhiza formation,  
408 described as the 'helper bacteria effect' (Cusano *et al.* 2011); mycophagy (Mela *et al.* 2012); co-  
409 migration (Warmink & van Elsas, 2009; Nazir *et al.*, 2012, 2013, 2014); and an undefined bacteria-  
410 fungus association (Warmink and van Elsas 2008).

411         Aside from true endosymbiosis, there is evidence that wood decay fungi form intimate  
412 mycelial associations with bacteria (Seigle-Murandi *et al.* 1996; Lim *et al.* 2003; Yara *et al.* 2006). For  
413 example, bacteria have been observed to co-exist with ten strains of *Phanerochaete chrysosporium*  
414 (Seigle-Murandi *et al.* 1996), although Janse *et al.*, (1997) failed to isolate bacteria from five strains  
415 of the same fungus, including one described by Seigle-Murandi *et al.* (1996). Thirty-two other wood-  
416 rot fungi tested negative, but where bacteria were present on *P. chrysosporium*, pure cultures of the  
417 fungus could not be established even from conidiospores, suggesting that bacteria may be within the  
418 hyphae and vertically transmitted (Seigle-Murandi *et al.* 1996). Similarly, *Burkholderia sordidicola*  
419 was isolated from two strains of *P. sordida*, and bacteria-free fungal cultures could not be  
420 established (Lim *et al.* 2003).

### 421 6.3 Mycophagy and predation

422         From mycelial associations, it is a small step to bacterial mycophagy (fungus-eating): the  
423 active utilisation of living fungal matter for bacterial growth (Leveau and Preston 2008). Given that  
424 bacteria are smaller than fungi, and do not kill the entire host organism, bacterial mycophagy is  
425 more analogous to parasitism than predation. There is also potential for mutualistic mycophagy,  
426 where bacteria 'pay their way' by provision of specific nutrients or degrading toxins (Leveau and  
427 Preston 2008). Endosymbiosis can be regarded as a specialised form of mycophagy (Leveau and  
428 Preston 2008).

429         An increasing body of evidence suggests that glycerol is a favoured carbon source for many  
430 mycophagous bacteria, although so far none of this evidence is derived directly from wood. In liquid  
431 culture *Burkholderia terrae* strain BS001 stimulates glycerol release by the fungus *Lyophyllum* sp.  
432 strain Karsten, and the glycerol is apparently consumed by the bacteria (Nazir *et al.* 2013). Whilst  
433 this ability has not yet been tested in an ecologically realistic situation, the *B. terrae* BS001 genome  
434 encodes glycerol transporters that are unique among the *Burkholderia*, possibly linked to its fungus-  
435 associated lifestyle (Haq *et al.* 2014). *B. rhizoxinica*, the *Rhizopus* endosymbiont, likewise possesses  
436 genes involved in glycerol metabolism and can utilise glycerol as a carbon source (Partida-Martinez

437 *et al.*, 2007; Lackner *et al.*, 2011). The mycophagous bacterium *Collimonas fungivorans* is also  
438 capable of metabolising glycerol (de Boer *et al.* 2004). In several *Burkholderia* species glycerol  
439 induces production of antibiotics, including the antifungal pyrrolnitrin (Depoorter *et al.*, 2016).

440 True mycophagy can be difficult to demonstrate, as many bacteria may feed saprotrophically  
441 on dead hyphae or passively on fungal exudates, whilst others may lyse hyphae for reasons other  
442 than nutrition (Leveau and Preston 2008). Evidence for mycophagy in wood is limited. A strain of  
443 *Streptomyces violaceusniger* isolated from bark inhibited fungi by endochitinase production, but only  
444 after being 'conditioned' by exposure to chitin (a major component of fungal cell walls) (Shekhar *et al.*  
445 *al.* 2006). This is an example of probable mycophagy where it has not yet been demonstrated that  
446 the bacteria fulfil the criterion of using fungal material for growth. Bacteria closely related to the  
447 mycophagous *Collimonas fungivorans* have been found on mycelial cords of the white-rot fungus *R.*  
448 *bicolor* (Folman *et al.* 2008). *Collimonas* is able to use fungal hyphae as a sole carbon source, and  
449 apparently uses the fungal exudate oxalic acid as a signal molecule to locate hyphae (Rudnick *et al.*  
450 2015). The abundance of *Collimonas* cells has been observed to be higher in forest soils than in  
451 either grassland or ex-arable soils (Höppener-Ogawa *et al.* 2007). The further observation that  
452 collimonads can alter the fungal community composition in soil microcosms indicates their  
453 potentially far-reaching importance (Höppener-Ogawa *et al.* 2009).

454 Conversely, there is also evidence for wood decay fungi feeding on bacteria; for example,  
455 the physical disappearance of bacteria cells following fungal inoculation, and/or the appearance of  
456 bacterial nutrients in mycelium under starvation conditions (Folman *et al.* 2008; Weißhaupt *et al.*  
457 2011). Wood decay fungi have been observed to lyse bacterial colonies in culture, including  
458 consumption of the bacteria that were decomposing dead nematodes (Tsuneda and Thorn, 1994).  
459 Again, such associations could be mutualistic if the fungus, despite consuming some bacterial cells,  
460 provided bacteria with nutrition and/or habitat. This seems to be the case for the soil saprotroph  
461 *Morchella crassipes*, which showed reciprocal carbon exchange with *Pseudomonas putida* but lysed  
462 some of the bacteria to feed the nutrient-intensive process of sclerotia formation: a situation that  
463 has been described, controversially, as fungal farming of bacteria (Pion *et al.* 2013).

464

## 465 **7. Conclusions and future perspectives**

466 Despite the many gaps in our knowledge of wood-dwelling bacteria, a picture emerges of a  
467 diverse and dynamic community, intimately linked to their physical habitat and the fungi they share  
468 it with. The complexity of these potential interactions, and the challenges associated with wood as a  
469 study system, mean that gaining a clear understanding of this environment will require the assembly  
470 of many 'jigsaw pieces' of information. The ultimate goal in researching fungal-bacterial interactions



471 in wood is a functional understanding of how fungi and prokaryotes interact, in terms of outcome  
472 for each partner, mechanisms of interaction, and effects on the process of wood breakdown. Before  
473 such questions can be addressed, it is first necessary to ascertain which organisms are present and  
474 their activities within the deadwood environment. Outstanding questions include:

- 475 - What is the origin of bacteria in wood; how and over what time-scale does colonisation occur?
- 476 - What are the major biotic and abiotic determinants of bacterial communities, and by what  
477 mechanisms do these operate?
- 478 - Are interactions with fungi predominantly beneficial or antagonistic? Does one partner  
479 consistently benefit at the expense of the other?
- 480 - How, and to what extent, do bacteria influence ecosystem-level flows of carbon and nitrogen in  
481 the context of dead wood?

482

483 One of the major features that emerges with regard to fungal-prokaryote interactions is just  
484 how hard it can be, in any given case, to distinguish the exact identity of the association. If fungal  
485 growth increases in the presence of a bacterium (or *vice versa*), is it mutualism, commensalism or  
486 parasitism? Do we truly see mycophagy rather than saprotrophy, endosymbiosis rather than  
487 opportunism? When fungi alter the bacterial community, are they selecting for their specific  
488 symbionts or simply unable to out-compete the remaining bacteria – or a mixture of the two? Such  
489 associations can be deceptively hard to disentangle.

490 Happily, a suite of methods is coming of age that will hopefully assist in answering such  
491 questions. Metagenomics gives a snapshot not just of the taxonomic identities of the community,  
492 but also of their genomic potential (although it still has limited ability to marry the two).  
493 Metatranscriptomics and metaproteomics offer insight into which of these potential abilities are  
494 realised in a particular situation. Metabolomics explores the complete metabolic signature of a  
495 microbial community under given conditions. At the same time, new culture methods offer hope for  
496 isolating key community players, allowing physiological characterisation and manipulative  
497 experiments (Ling *et al.*, 2015; Oberhardt *et al.*, 2015; Kielak *et al.* 2016a). Each of these techniques  
498 comes with associated limitations, pitfalls and benefits, and it will require judicious use of these  
499 approaches, combined with appropriate statistical and mathematical methods, to pick apart fungal-  
500 prokaryote associations.

501 The overwhelming conclusion regarding the current state of knowledge is that, despite the  
502 work already done on saproxylic bacteria and their interactions with fungi, we have still barely  
503 scratched the surface. Results can be disparate or even contradictory depending on the  
504 environmental conditions, identity of the organisms involved, or methods employed, frustrating the

505 chance of drawing together a robust theoretical framework. With so much ground still to cover, the  
506 microbiota of dead wood remains a lively and under-explored area of ecological research, but one  
507 that is likely to be highly rewarding and will be furthered by deployment of modern genomic and  
508 post-genomic approaches.

509

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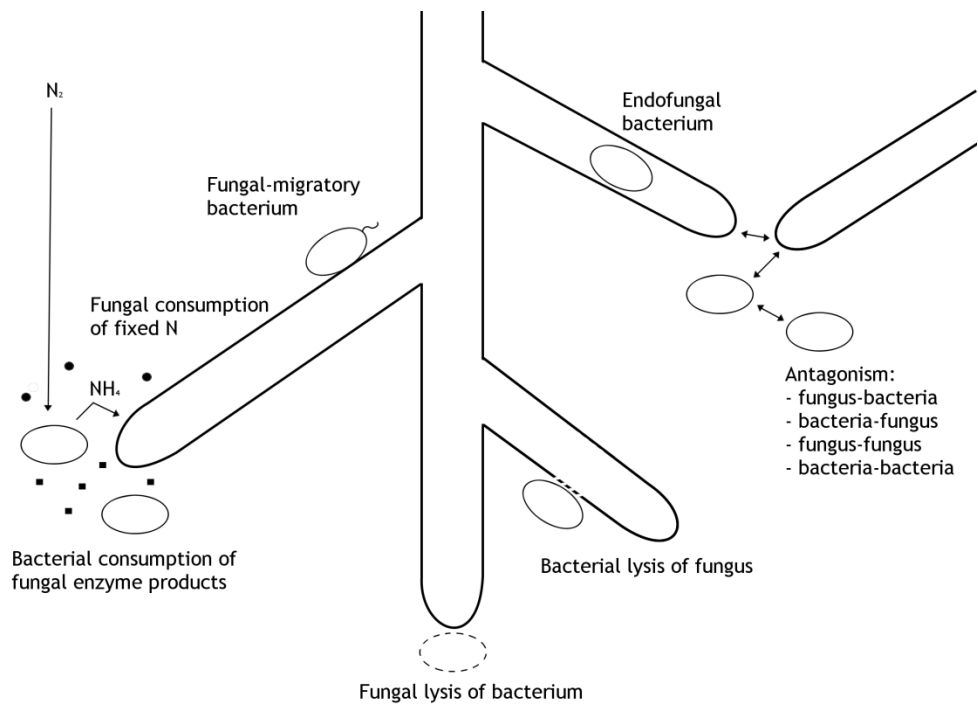
513

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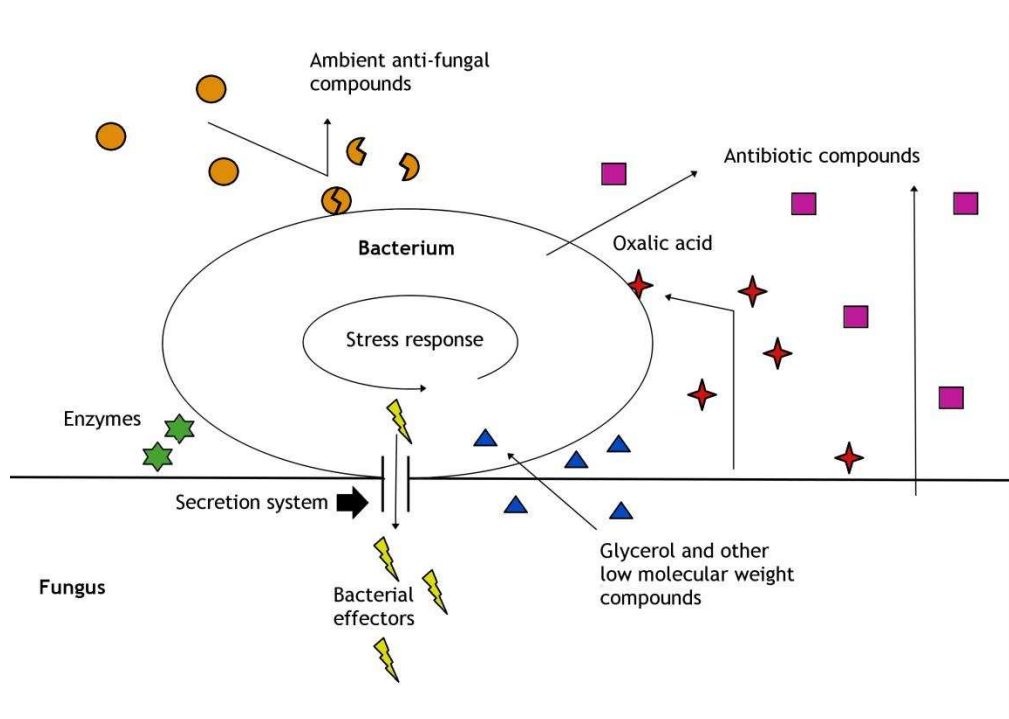
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517

518 **Fig. 1** Potential fungus-bacteria interactions occurring in wood; not all have so far been observed.  
 519 The interactions may be obligate (*e.g.* some endosymbioses) or facultative (*e.g.* predation). In many  
 520 cases it is not clear whether a given interaction is beneficial to one, both or neither of the partners.  
 521 The outcomes indicated may occur via more than one route: for example, fungi could receive fixed N  
 522 by mutualism with diazotrophs, by lysing the bacteria, or by predated on nematodes *etc.* that had in  
 523 turn predated on bacteria. A) Whole-organism level interactions. B) Molecular mechanisms of  
 524 interaction; see main text for details of each.



525



526

527 **Table 1** Marker gene-based studies of bacteria in wood, and the major phyla reported in each.

Study	Wood species	State of decay	Location	Marker gene	Method	Major bacterial phyla
Folman <i>et al.</i> , 2008	<i>Fagus sylvatica</i>	7-10 months' colonisation	Lab	16S rRNA	DGGE and sequencing	Betaproteobacteria; Gammaproteobacteria; Acidobacteria; Bacilli
Hervé <i>et al.</i> , 2014	<i>Fagus sylvatica</i>	Sawdust, 3-5 months' colonisation	Lab	16S rRNA	NGS amplicons	Alpha-, beta- and gamma-proteobacteria
Hoppe <i>et al.</i> , 2014	<i>Fagus sylvatica</i> , <i>Picea abies</i>	Not reported	Temperate woodland (Germany)	<i>nifH</i>	NGS amplicons	Alphaproteobacteria
Hoppe <i>et al.</i> , 2015	<i>Fagus sylvatica</i> , <i>Picea abies</i>	Kahl (2012) decay class 1-4 (3-27 years)	Temperate woodland (Germany)	16S rRNA	NGS amplicons	Alphaproteobacteria; Actinobacteria; Acidobacteria
Kielak <i>et al.</i> , 2016	<i>Pinus sylvestris</i>	Classified as early, middle or late decay based on density	Temperate woodland (The Netherlands)	16S rRNA	NGS amplicons	Alphaproteobacteria; Acidobacteria
Rinta-Kanto <i>et al.</i> , 2016	<i>Picea abies</i>	Range from "recently dead" to "almost decomposed" (Mäkinen <i>et al.</i> , 2006)	Boreal forest (Finland)	16S rRNA	NGS amplicons	Alphaproteobacteria; Acidobacteria

Sun <i>et al.</i> , 2014	<i>Picea abies</i>	2-4 months' colonisation	Boreal forest (Finland)	16S rRNA	NGS amplicons	Proteobacteria; Bacteroidetes; Acidobacteria; Actinobacteria
Valášková <i>et al.</i> , 2009	<i>Betula sp.</i> , <i>Fagus sylvatica</i> , <i>Quercus robur</i> , <i>Pinus sylvestris</i>	Reported only as "high"	Temperate woodland (The Netherlands)	16S rRNA	Clone library	Alpha-, beta- and gamma-proteobacteria; Acidobacteria; Firmicutes
Zhang <i>et al.</i> , 2008	<i>Keteleeria evelyniana</i>	Not reported	Not reported; sub-tropical?	16S rRNA	Clone library	Alpha-, beta-, gamma- and delta-proteobacteria; Actinobacteria; Acidobacteria

528

529

530 **References**

- 531 Bell T. Experimental tests of the bacterial distance-decay relationship. *ISME J* 2010;**4**:1357–65.
- 532 Bertaux J, Schmid M, Hutzler P *et al.* Occurrence and distribution of endobacteria in the plant-  
533 associated mycelium of the ectomycorrhizal fungus *Laccaria bicolor* S238N. *Environ Microbiol*  
534 2005;**7**:1786–95.
- 535 Blanchette R, Shaw C. Associations Among Bacteria, Yeasts and Basidiomycetes During Wood Decay.  
536 *Phytopathology* 1978;**68**:631–7.
- 537 Björdal, C, Microbial degradation of waterlogged archaeological wood. *J Cult Herit* 2012;**13S**:S118-  
538 S122
- 539 Boaisa O. *Burkholderia cepacia* complex bacteria and their antimicrobial activity. 2012. PhD thesis,  
540 Cardiff University
- 541 Boddy L, Bardsley DW, Gibbon OM. Fungal communities in attached ash branches. *New Phytol*  
542 1987;**107**:143–54.
- 543 Boddy L, Owens EM, Chapela IH. Small scale variation in decay rate within logs one year after felling:  
544 Effect of fungal community structure and moisture content. *FEMS Microbiol Ecol* 1989;**62**:173–  
545 83.
- 546 Boddy L. Interspecific combative interactions between wood-decaying basidiomycetes. *FEMS*  
547 *Microbiol Ecol* 2000;**31**:185–94.
- 548 de Boer W, Folman LB, Klein Gunnewiek PJA *et al.* Mechanism of antibacterial activity of the white-  
549 rot fungus *Hypholoma fasciculare* colonizing wood. *Can J Microbiol* 2010;**56**:380–8.
- 550 de Boer W, Folman LB, Summerbell RC *et al.* Living in a fungal world: impact of fungi on soil bacterial  
551 niche development. *FEMS Microbiol Rev* 2005;**29**:795–811.
- 552 de Boer W, Leveau JHJ, Kowalchuk GA. *et al.* *Collimonas fungivorans* gen. nov., sp. nov., a chitinolytic  
553 soil bacterium with the ability to grow on living fungal hyphae. *Int J Syst Evol Microbiol*  
554 2004;**54**:857–64.
- 555 de Boer W, Wagenaar A-M, Klein Gunnewiek PJA *et al.* *In vitro* suppression of fungi caused by  
556 combinations of apparently non-antagonistic soil bacteria. *FEMS Microbiol Ecol* 2007;**59**:177–  
557 85.
- 558 de Boer W, van der Wal A. Interactions between Saprotrophic Basidiomycetes and Bacteria. In:  
559 Boddy L., Frankland JC., van West P. (Eds.), *Ecology of Saprotrophic Basidiomycetes*.  
560 Amsterdam: Elsevier, 2008, 143–53.
- 561 Bonfante P, Anca I-A. Plants, mycorrhizal fungi, and bacteria: a network of interactions. *Annu Rev*  
562 *Microbiol* 2009;**63**:363–83.
- 563 Bontemps C, Toussaint M, Revol P-V *et al.* Taxonomic and functional diversity of *Streptomyces* in a  
564 forest soil. *FEMS Microbiol Lett* 2013;**342**:157–67.
- 565 Brabcová V., Nováková M., Davidová A. *et al.* Dead fungal mycelium in forest soil represents a  
566 decomposition hotspot and a habitat for a specific microbial community. *New Phytol*  
567 2016;**210**:1369–1381
- 568 Brown ME, Chang MCY. Exploring bacterial lignin degradation. *Curr Opin Chem Biol* 2014;**19**:1–7.

- 569 Brunner A, Kimmins JP. Nitrogen fixation in coarse woody debris of *Thuja plicata* and *Tsuga*  
570 *heterophylla* forests on northern Vancouver Island. *Can J For Res* 2003;**33**:1670–82.
- 571 Bugg TD, Ahmad M, Hardiman EM *et al.* The emerging role for bacteria in lignin degradation and bio-  
572 product formation. *Curr Opin Biotechnol* 2011;**22**:394–400.
- 573 Caldeira AT, Feio SS, Arteiro JMS *et al.* Environmental dynamics of *Bacillus amyloliquefaciens* CCM1  
574 1051 antifungal activity under different nitrogen patterns. *J Appl Microbiol* 2008;**104**:808–16.
- 575 Clausen CA. Bacterial associations with decaying wood: a review. *Int Biodeterior Biodegradation*  
576 1996;**37**:101–7.
- 577 Cornaby BW, Waide JB. Nitrogen fixation in decaying chestnut logs. *Plant Soil* 1973;**39**:445–8.
- 578 Cusano AM, Burlinson P, Deveau A *et al.* *Pseudomonas fluorescens* BBc6R8 type III secretion mutants  
579 no longer promote ectomycorrhizal symbiosis. *Environ Microbiol Rep* 2011;**3**:203–10.
- 580 Depoorter E, Bull M, Peeters C *et al.* Burkholderia: an update on taxonomy and biotechnological  
581 potential as antibiotic producers. *Appl Microbiol Biotechnol* 2016;**100**:5215–5229
- 582 Folman LB, Klein Gunnewiek PJ, Boddy L *et al.* Impact of white-rot fungi on numbers and community  
583 composition of bacteria colonizing beech wood from forest soil. *FEMS Microbiol Ecol*  
584 2008;**63**:181–91.
- 585 Frey-Klett P, Burlinson P, Deveau A *et al.* Bacterial-fungal interactions: hyphens between agricultural,  
586 clinical, environmental, and food microbiologists. *Microbiol Mol Biol Rev* 2011;**75**:583–609.
- 587 Ghignone S, Salvioli A, Anca I *et al.* The genome of the obligate endobacterium of an AM fungus  
588 reveals an interphylum network of nutritional interactions. *ISME J* 2012;**6**:136–45.
- 589 Giller KE. Use and abuse of the acetylene reduction assay for measurement of “associative” nitrogen  
590 fixation. *Soil Biol Biochem* 1987;**19**:783–4.
- 591 Greaves H. Micromorphology of the bacterial attack of wood. *Wood Sci Technol* 1969;**3**:150–66.
- 592 Greaves H. The Bacterial Factor in Wood Decay. *Wood Sci Technol* 1971;**5**:6–16.
- 593 Green J, Bohannan B. Spatial scaling of microbial biodiversity. *Trends Ecol Evol* 2006;**21**:501–7.
- 594 Griffiths RP, Harmon ME, Caldwell BA. *et al.* Acetylene reduction in conifer logs during early stages of  
595 decomposition. *Plant Soil* 1993;**148**:53–61.
- 596 Haq IU, Graupner K, Nazir R *et al.* The Genome of the Fungal-Interactive Soil Bacterium *Burkholderia*  
597 *terrae* BS001-A Plethora of Outstanding Interactive Capabilities Unveiled. *Genome Biol Evol*  
598 2014;**6**:1652–68.
- 599 Hervé V, Le Roux X, Uroz S *et al.* Diversity and structure of bacterial communities associated with  
600 *Phanerochaete chrysosporium* during wood decay. *Environ Microbiol* 2014;**16**:2238–52.
- 601 Hicks WT, Harmon ME, Griffiths RP. Abiotic controls on nitrogen fixation and respiration in selected  
602 woody debris from the Pacific Northwest, U.S.A. *Ecoscience* 2003a;**10**:66–73.
- 603 Hicks WT, Harmon ME, Myrold DD. Substrate controls on nitrogen fixation and respiration in woody  
604 debris from the Pacific Northwest, USA. *For Ecol Manage* 2003b;**176**:25–35.
- 605 Hiscox J, Hibbert C, Rogers HJ *et al.* Monokaryons and dikaryons of *Trametes versicolor* have similar  
606 combative, enzyme and decay ability. *Fungal Ecol* 2010;**3**:347–56.
- 607 Hoffman MT, Arnold AE. Diverse bacteria inhabit living hyphae of phylogenetically diverse fungal  
608 endophytes. *Appl Environ Microbiol* 2010;**76**:4063–75.
- 609 Hoppe B, Kahl T, Karasch P *et al.* Network Analysis Reveals Ecological Links between N-Fixing

610 Bacteria and Wood-Decaying Fungi. *PLoS One* 2014;**9**:e91389.

611 Hoppe B, Krger K, Kahl T *et al.* A pyrosequencing insight into sprawling bacterial diversity and  
612 community dynamics in decaying deadwood logs of *Fagus sylvatica* and *Picea abies*. *Sci Rep*  
613 2015;**5**:9456.

614 Höppener-Ogawa S, Leveau JHJ, Hundscheid MPJ *et al.* Impact of *Collimonas* bacteria on community  
615 composition of soil fungi. *Environ Microbiol* 2009;**11**:1444–52.

616 Höppener-Ogawa S, Leveau JHJ, Smart W *et al.* Specific detection and real-time PCR quantification  
617 of potentially mycophagous bacteria belonging to the genus *Collimonas* in different soil  
618 ecosystems. *Appl Environ Microbiol* 2007;**73**:4191–7.

619 Huffman JA, Prenni AJ, DeMott PJ *et al.* High concentrations of biological aerosol particles and ice  
620 nuclei during and after rain. *Atmos Chem Phys* 2013;**13**:6151–64.

621 Janes D, Umek A, Kreft S. Evaluation of antibacterial activity of extracts of five species of wood-  
622 colonizing fungi. *J Basic Microbiol* 2006;**46**:203–7.

623 Janse B, Gaskell J, Cullen D *et al.* Are Bacteria Omnipresent on *Phanerochaete chrysosporium*  
624 Burdsall ? *Appl Environ Microbiol* 1997;**63**:2913–5.

625 Jeremic D, Cooper P, Srinivasan U. Comparative analysis of balsam fir wetwood, heartwood and  
626 sapwood properties. *Can J For Res* 2004;**24**:1241–50.

627 Jurgensen MF, Larsen MJ, Spano SD *et al.* Nitrogen Fixation Associated with Increased Wood Decay  
628 in Douglas-fir Residue. *For Sci* 1984;**30**:1038–44.

629 Jurgensen MF, Larsen MJ, Wolosiewicz M *et al.* A comparison of dinitrogen fixation rates in wood  
630 litter decayed by white-rot and brown-rot fungi. *Plant Soil* 1989;**115**:117–22.

631 Kahl T, Mund M, Bauhus J, Schulze E-D. Dissolved organic carbon from European beech logs:  
632 Patterns of input to and retention by surface soil. *Ecoscience* 2012;**19**:1-10.

633 Kamei I, Yoshida T, Enami D *et al.* Coexisting *Curtobacterium* bacterium promotes growth of white-  
634 rot fungus *Stereum* sp. *Curr Microbiol* 2012;**64**:173–8.

635 Kielak A, Barreto C, Kowalchuk G *et al.* The ecology of Acidobacteria: moving beyond genes and  
636 genomes. *Front Microbiol* 2016a;**7**: 00744

637 Kielak A, Scheublin T, Mendes L *et al.* Bacterial Community Succession in Pine-Wood Decomposition.  
638 *Front Microbiol* 2016b; <http://dx.doi.org/10.3389/fmicb.2016.00231>

639 Kim YS, Singh AP. Micromorphological characteristics of wood biodegradation in wet environments:  
640 A review. *IAWA J* 2000;**21**:135–55.

641 Lackner G, Moebius N, Hertweck C. Endofungal bacterium controls its host by an hrp type III  
642 secretion system. *ISME J* 2011;**5**:252–61.

643 Lackner G, Moebius N, Partida-Martinez LP *et al.* Evolution of an endofungal Lifestyle: Deductions  
644 from the *Burkholderia rhizoxinica* Genome. *BMC Genomics* 2011;**12**:210.

645 Larsen MJ, Jurgensen MF, Harvey AE. N<sub>2</sub> fixation associated with wood decayed by some common  
646 fungi in western Montana. *Can J For Res* 1978;**8**:341–5.

647 Leveau JHJ, Preston GM. Bacterial mycophagy: definition and diagnosis of a unique bacterial-fungal  
648 interaction. *New Phytol* 2008;**177**:859–76.

649 Leveau JHJ, Uroz S, de Boer W. The bacterial genus *Collimonas*: mycophagy, weathering and other  
650 adaptive solutions to life in oligotrophic soil environments. *Environ Microbiol* 2010;**12**:281–92.



- 651 Lim YW, Baik KS, Han SK *et al.* *Burkholderia sordidicola* sp. nov., isolated from the white-rot fungus  
652 *Phanerochaete sordida*. *Int J Syst Evol Microbiol* 2003;**53**:1631–6.
- 653 Ling L., Schneider T., Peoples T *et al.* A new antibiotic kills pathogens without detectable resistance.  
654 *Nature* 2015;**517**:455–459 Liu D, Keiblinger K, Leitner S, *et al.* Is there a convergence of  
655 deciduous leaf litter stoichiometry, biochemistry and microbial population during  
656 decay? *Geoderma* 2016;**272**:93–100
- 657 Lladó S, Baldrian P, Žifčáková L *et al.* Functional screening of abundant bacteria from acidic forest soil  
658 indicates the metabolic potential of Acidobacteria subdivision 1 for polysaccharide  
659 decomposition. *Biol Fertil Soils* 2016;**52**:251–260
- 660 López-Mondéjar R, Zühlke D, Becher D *et al.* Cellulose and hemicellulose decomposition by forest  
661 soil bacteria proceeds by the action of structurally variable enzymatic systems. *Sci Rep* 2016;**6**:  
662 25279
- 663 Lumini E, Ghignone S, Bianciotto V *et al.* Endobacteria or bacterial endosymbionts? To be or not to  
664 be. *New Phytol* 2006;**170**:205–7.
- 665 Lynd LR, Weimer PJ, van Zyl WH *et al.* Microbial Cellulose Utilization: Fundamentals and  
666 Biotechnology. *Microbiol Mol Biol Rev* 2002;**66**:506–77.
- 667 Mäkinen H, Hynynen, J, Siitonen J *et al.*, Predicting the decomposition of Scots pine, Norway spruce,  
668 and birch stems in Finland. *Ecol Appl* 2006;**16**:1865–1879
- 669 Mela F, Fritsche K, De Boer W *et al.* Comparative genomics of bacteria from the genus *Collimonas*:  
670 Linking (dis)similarities in gene content to phenotypic variation and conservation. *Environ*  
671 *Microbiol Rep* 2012;**4**:424–32.
- 672 Mercado JE, Hofstetter RW, Reboletti DM *et al.* Phoretic symbionts of the mountain pine beetle  
673 (*Dendroctonus ponderosae hopkins*). *For Sci* 2014;**60**:512–26.
- 674 Moebius N, Üzüm Z, Dijksterhuis J *et al.* Active invasion of bacteria into living fungal cells. *Elife*  
675 2014:e03007.
- 676 Murdoch CW, Campana RJ. Bacterial Species Associated with Wetwood of Elm. *Phytopathology*  
677 1983;**73**:1270–3.
- 678 Murray AC, Woodward S. In vitro interactions between bacteria isolated from Sitka spruce stumps  
679 and *Heterobasidion annosum*. *For Pathol* 2003;**33**:53–67.
- 680 Murray AC, Woodward S. Temporal changes in functional diversity of culturable bacteria populations  
681 in Sitka spruce stumps. *For Pathol* 2007;**37**:217–35.
- 682 Nazir R, Tazetdinova DI, van Elsas JD. *Burkholderia terrae* BS001 migrates proficiently with diverse  
683 fungal hosts through soil and provides protection from antifungal agents. *Front Microbiol*  
684 2014;**5**:1–10.
- 685 Nazir R, Warmink JA., Voordes DC *et al.* Inhibition of Mushroom Formation and Induction of Glycerol  
686 Release–Ecological Strategies of *Burkholderia terrae* BS001 to Create a Hospitable Niche at the  
687 Fungus *Lyophyllum* sp. Strain Karsten. *Microb Ecol* 2013;**65**:245–54.
- 688 Nazir R, Zhang M, de Boer W *et al.* The capacity to comigrate with *Lyophyllum* sp. strain Karsten  
689 through different soils is spread among several phylogenetic groups within the genus  
690 *Burkholderia*. *Soil Biol Biochem* 2012;**50**:221–33.
- 691 Oberhardt M, Zarecki R, Gronow S, *et al.* Harnessing the landscape of microbial culture media to  
692 predict new organism–media pairings. *Nat Comm* 2015;**6**:8493
- 693 Pan Y, Birdsey RA, Fang J *et al.* A large and persistent carbon sink in the world’s forests. *Science*

694 2011;**333**:988–93.

695 Parfitt D, Hunt J, Dockrell D *et al.* Do all trees carry the seeds of their own destruction? PCR reveals  
696 numerous wood decay fungi latently present in sapwood of a wide range of angiosperm trees.  
697 *Fungal Ecol* 2010;**3**:338–46.

698 Partida-Martinez LP, Groth I, Schmitt I *et al.* *Burkholderia rhizoxinica* sp. nov. and *Burkholderia*  
699 *endofungorum* sp. nov., bacterial endosymbionts of the plant-pathogenic fungus *Rhizopus*  
700 *microsporus*. *Int J Syst Evol Microbiol* 2007a;**57**:2583–90.

701 Partida-Martinez LP, Hertweck C. Pathogenic fungus harbours endosymbiotic bacteria for toxin  
702 production. *Nature* 2005;**437**:884–8.

703 Partida-Martinez LP, Monajembashi S, Greulich KO *et al.* Endosymbiont-Dependent Host  
704 Reproduction Maintains Bacterial-Fungal Mutualism. *Curr Biol* 2007b;**17**:773–7.

705 Pion M, Spangenberg JE, Simon A *et al.* Bacterial farming by the fungus *Morchella crassipes*. *Proc R*  
706 *Soc B* 2013;**280**:20132242.

707 Popova M, Trusheva B, Gyosheva M *et al.* Antibacterial triterpenes from the threatened wood-decay  
708 fungus *Fomitopsis rosea*. *Fitoterapia* 2009;**80**:263–6.

709 Prewitt L, Kang Y, Kakumanu ML *et al.* Fungal and Bacterial Community Succession Differs for Three  
710 Wood Types during Decay in a Forest Soil. *Microb Ecol* 2014;**68**:212–21.

711 Purahong W, Schloter M, Pecyna M, *et al.* Uncoupling of microbial community structure and function  
712 in decomposing litter across beech forest ecosystems in Central Europe. *Sci Rep* 2014;**4**:7014

713 Purahong W, Wubet T, Lentendu G *et al.* Life in leaf litter: novel insights into community dynamics of  
714 bacteria and fungi during litter decomposition. *Molec Ecol* 2016;doi 10.1111/mec.13739

715 Rinta-Kanto J, Sinkko H, Rajala T, *et al.* Natural decay process affects the abundance and community  
716 structure of Bacteria and Archaea in *Picea abies* logs. *FEMS Microbiol Ecol* 2016;**92**:403-  
717 410Rousk J, Brookes PC, Bååth E. Investigating the mechanisms for the opposing pH  
718 relationships of fungal and bacterial growth in soil. *Soil Biol Biochem* 2010;**42**:926–34.

719 Rousk J, Demoling LA, Bahr A *et al.* Examining the fungal and bacterial niche overlap using selective  
720 inhibitors in soil. *FEMS Microbiol Ecol* 2008;**63**:350–8.

721 Rudnick MBB, van Veen JA., de Boer W. Oxalic acid: a signal molecule for fungus-feeding bacteria of  
722 the genus *Collimonas* ? *Environ Microbiol Rep* 2015;**31**:709-14

723 Sakamoto Y, Sano Y. Inhibition of water conductivity caused by watermark disease in *Salix*  
724 *sachalinensis*. *IAWA J* 2000;**21**:49–60.

725 Salvachúa D, Karp E, Nimlos C, *et al.* Towards lignin consolidated bioprocessing: simultaneous lignin  
726 depolymerization and product generation by bacteria. *Green Chem* 2015;**17**:4951-4967

727 Sato Y, Narisawa K, Tsuruta K *et al.* Detection of Betaproteobacteria inside the Mycelium of the  
728 Fungus *Mortierella elongata*. *Microbes Environ* 2010;**25**:321–4.

729 Schink B, Ward JC, Zeikus JG. Microbiology of Wetwood: Role of Anaerobic Bacterial Populations in  
730 Living Trees. *Microbiology* 1981a;**123**:313–22.

731 Schink B, Ward JC, Zeikus JG. Microbiology of wetwood: importance of pectin degradation and  
732 *Clostridium* species in living trees. *Appl Environ Microbiol* 1981b;**42**:526–32.

733 Schmidt O, Liese W. Occurance and significance of bacteria in wood. *Holzforschung* 1994;**48**:271–7.

734 Seigle-Murandi F, Guiraud P, Croize J *et al.* Bacteria Are Omnipresent on *Phanerochaete*  
735 *chrysosporium* Burdsall. *Appl Environ Microbiol* 1996;**62**:2477–81.

- 736 Sharp RF, Millbank JW. Nitrogen fixation in deteriorating wood. *Experientia* 1973;**29**:895–6.
- 737 Shekhar N, Bhattacharya D, Kumar D *et al.* Biocontrol of wood-rotting fungi with *Streptomyces*  
738 *violaceusniger* XL-2. *Can J Microbiol* 2006;**52**:805–8.
- 739 Silvester W. Molybdenum limitation of asymbiotic nitrogen fixation in forests of Pacific Northwest  
740 America. *Soil Biol Biochem* 1989;**21**:283–9.
- 741 Sollins P, Cline SP, Verhoeven T *et al.* Patterns of log decay in old-growth Douglas-fir forests. *Can J*  
742 *For Res* 1987;**17**:1585–95.
- 743 Son Y. Non-symbiotic nitrogen fixation in forest ecosystems. *Ecol Res* 2001;**16**:183–96.
- 744 Spano SD, Jurgensen MF, Larsen MJ *et al.* Nitrogen-fixing bacteria in Douglas-fir residue decayed by  
745 *Fomitopsis pinicola*. *Plant Soil* 1982;**68**:117–23.
- 746 Stokland JN, Siitonen J, Jonsson BG. *Biodiversity in Dead Wood*. Cambridge: Cambridge University  
747 Press, 2012.
- 748 Stopnisek N, Zühlke D, Carlier A *et al.* Molecular mechanisms underlying the close association  
749 between soil *Burkholderia* and fungi. *ISME J* 2015:1–12.
- 750 Sun H, Terhonen E, Kasanen R *et al.* Diversity and Community Structure of Primary Wood-Inhabiting  
751 Bacteria in Boreal Forest. *Geomicrobiol J* 2014;**31**:315–24.
- 752 Sun H, Terhonen E, Koskinen K *et al.* The impacts of treatment with biocontrol fungus (*Phlebiopsis*  
753 *gigantea*) on bacterial diversity in Norway spruce stumps. *Biol Control* 2013;**64**:238–46.
- 754 Tolonen AC, Cerisy T, El-Sayyed H *et al.* Fungal lysis by a soil bacterium fermenting cellulose. *Environ*  
755 *Microbiol* 2015;**17**:2618–27.
- 756 Tsuneda A., Thorn RG. Interactions of wood decay fungi with other microorganisms, with emphasis  
757 on the degradation of cell walls. *Can J Bot* 1994;**73**(S1):S1325-S1333
- 758 Urbanová M, Šnajdr J, Baldrian P. Composition of fungal and bacterial communities in forest litter  
759 and soil is largely determined by dominant trees. *Soil Biol Biochem* 2015;**84**:53-64
- 760 Valášková V, de Boer W, Klein Gunnewiek PJA *et al.* Phylogenetic composition and properties of  
761 bacteria coexisting with the fungus *Hypholoma fasciculare* in decaying wood. *ISME J*  
762 2009;**3**:1218–21.
- 763 Větrovský T, Voříšková J, Snajdr J *et al.* Ecology of coarse wood decomposition by the saprotrophic  
764 fungus *Fomes fomentarius*. *Biodegradation* 2011;**22**:709–18.
- 765 van der Wal A, de Boer W, Smant W *et al.* Initial decay of woody fragments in soil is influenced by  
766 size, vertical position, nitrogen availability and soil origin. *Plant Soil* 2007;**301**:189–201.
- 767 Watkinson S., Bebber D., Darrah P. *et al.* The role of wood decay fungi in the carbon and nitrogen  
768 dynamics of the forest floor. In Gadd, M. (Ed.), *Fungi in Biogeochemical Cycles*. Cambridge:  
769 Cambridge University Press, 2006, 151-181
- 770 Warmink JA., Van Elsas JD. Migratory response of soil bacteria to *Lyophyllum* sp. strain Karsten In soil  
771 microcosms. *Appl Environ Microbiol* 2009;**75**:2820–30.
- 772 Warmink J a., Nazir R, Corten B *et al.* Hitchhikers on the fungal highway: The helper effect for  
773 bacterial migration via fungal hyphae. *Soil Biol Biochem* 2011;**43**:760–5.
- 774 Warmink JA, van Elsas JD. Selection of bacterial populations in the mycosphere of *Laccaria proxima*:  
775 is type III secretion involved? *ISME J* 2008;**2**:887–900.
- 776 Weißhaupt P, Naumann A, Pritzkow W *et al.* Nitrogen uptake of *Hypholoma fasciculare* and

- 777 coexisting bacteria. *Mycol Prog* 2013;**12**:283–90.
- 778 Weißhaupt P, Pritzkow W, Noll M. Nitrogen metabolism of wood decomposing basidiomycetes and  
779 their interaction with diazotrophs as revealed by IRMS. *Int J Mass Spectrom* 2011;**307**:225–31.
- 780 Worrall JJ, Parmeter JR. Inhibition of Wood-Decay Fungi by Wetwood of White Fir. *Phytopathology*  
781 1983;**73**:1140–5.
- 782 Yara R, Maccheroni W, Horii J *et al.* A bacterium belonging to the *Burkholderia cepacia* complex  
783 associated with *Pleurotus ostreatus*. *J Microbiol* 2006;**44**:263–8.
- 784 Zhang H-B, Yang M-X, Tu R. Unexpectedly high bacterial diversity in decaying wood of a conifer as  
785 revealed by a molecular method. *Int Biodeterior Biodegradation* 2008;**62**:471–4.
- 786 Žifčáková L, Větrovský T, Howe A *et al.* Microbial activity in forest soil reflects the changes in  
787 ecosystem properties between summer and winter. *Environ Microbiol* 2016;**18**:288–301