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1 **Title : Forest plant cover and mineral type determine the diversity and composition**
2 **of mineral-colonizing fungal communities**

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22 **ABSTRACT**

23 Soil fungi play a fundamental role in the cycling of nutrients and tree nutrition in forests.
24 As mycorrhizal fungi are closely associated with their host trees and provide them essential
25 base cations and phosphorus, we hypothesize that they actively mine soil minerals and
26 transfer their nutritive content to their host. Therefore, mycorrhizal fungi are expected to be
27 important colonizers of soil mineral surfaces relative to other fungal trophic guilds. To test
28 this hypothesis, 50 μm nylon mesh bags were filled with three different mineral types (*i.e.*
29 calcite, apatite and obsidian) and buried in the same soil colonized by three forest stands (*i.e.*
30 beech, Corsican pine and coppice with standards). After an *in situ* incubation period of 29
31 months in the topsoil, mineral dissolution was detectable in the mesh bags, and the analysis of
32 the fungal communities was therefore undertaken. Minerals presented a lower fungal biomass
33 than the surrounding bulk soil and no difference between the three mineral types tested was
34 observed. The high-throughput sequencing (HTS) approach showed that the fungal
35 communities differed among the three forest stands, but in each case, mineral associated
36 fungal taxa differed significantly from those in the bulk soil. To a lesser extent, fungal
37 communities further varied between the three mineral types. Overall, trophic inference
38 analyses suggested that two groups of plant-associated fungi, namely the ectomycorrhizal and
39 endophytic fungi, were the major fungal mineral colonizers. Saprophytes also appeared
40 significantly enriched on minerals comparatively to the surrounding bulk soil. Together, our
41 data reveal at local scale that the mineral-associated fungal communities are first determined
42 by the forest plant cover and then by the type of mineral.

43

44 **Key words:** forest; minerals; fungi; tree stand; ITS sequencing

45 **1. INTRODUCTION**

46 Soil minerals and rocks play a fundamental role in the long-lasting functioning of nutrient-
47 poor ecosystems with low-human impact, where they represent the main source of inorganic
48 nutrients (i.e., K, Mg, Ca, P)[1]. This is especially the case in temperate forests, which are
49 usually developed on acidic and nutrient-poor soils, while the fertile and easily manageable
50 soils have been dedicated to agriculture [2]. The access to these inorganic nutrients is
51 especially important for the trees that require long periods of time to grow and significant
52 amount of nutrients. Therefore their full development relies on the inorganic nutrients
53 released from the soil minerals or coming from organic matter decomposition and
54 atmospheric deposition [3]. However, each mineral is characterized by its own physico-
55 chemical properties (i.e., composition, weatherability, size, age) and its dissolution depends
56 on its properties and the local conditions. In acidic soils, minerals are mainly represented by
57 phyllosilicates (*e.g.*, biotite) or tectosilicates (*e.g.*, K feldspar, quartz), which are the most
58 recalcitrant to dissolution [4]. Consequently, their nutritive content is not directly accessible
59 to tree roots, underlining the pivotal role of soil mineral weathering processes in tree nutrition
60 and ecosystem functioning. Mineral weathering occurs through a combination of abiotic and
61 biotic reactions [5-8]. Abiotic weathering operates mostly through the flow of water and
62 carbon dioxide occurring into the soil, the soil acidification and the freeze-thaw changes that
63 progressively break down and dissolve minerals and rocks [9]. Plants, macro- and micro-
64 organisms can also physically break down the mineral particles through the pressure exerted
65 (*e.g.*, root and mycelium) or directly solubilise minerals through their activities. Plants can
66 also locally change the soil properties (i.e., pH) and promote mineral weathering [7, 10-16].
67 However, we are far from knowing which microbial taxa are involved in the mineral
68 weathering process.

69 Plants themselves can physically disrupt mineral particles through the pressure exerted by
70 their roots on mineral surfaces or chemically through the action of chelating and acidifying
71 molecules contained in root exudates [17,18]. Higher mineral weathering rates have been
72 reported for minerals collected in the rhizosphere than in the surrounding bulk soil [19-25].
73 However, significant differences were observed between plant species growing in a same soil,
74 suggesting a direct species effect or an indirect effect linked to their associated microbiota
75 [19,24]. In this sense, the presence of effective mineral weathering microorganisms (i.e.,
76 bacteria and fungi) was reported in the rhizosphere of different plants [7,14], suggesting that
77 the ability of plants to weather minerals is not purely a function of their own activity, but a
78 joint activity of the roots and their microbiota.

79 The ability to weather minerals has been reported for a broad range of microorganisms
80 including soil bacteria, lichen and fungi [6,7,14,26-28]. Fungi are major actors in forest
81 ecosystem due to their ability to decompose complex organic compounds [29,30] and for
82 some of them, to establish symbiotic associations with plants [31]. Fungal hyphae can explore
83 important volume of soil and colonize pores non-accessible to the tree roots. For symbiotic
84 fungi, this ability improves the access and transfer of nutrients and water to the host plants.
85 The discovery of micrometer-size pores in mineral particles was attributed to the mineral
86 weathering activity of the fungal hyphae [14,32,33]. Although their real implication in the
87 formation of these pores is not established, several mycorrhizal and non-mycorrhizal species
88 have been reported as capable of weathering minerals through bio-mechanical forcing and/or
89 the production of protons and oxalate [14,28,34-39], and consecutively are likely to promote
90 nutrient transfer to plants [21,40,41]. In addition, mycorrhizal fungi with low mineral
91 weathering activities exhibit high-affinity ion transporter systems resulting in a greater
92 capacity to absorb inorganic nutrients from the soil [42].

93 In the soil environment, minerals represent a particular interface due to their physical
94 properties, but also their nutrient content and reactivity to the local conditions. Different
95 factors such as mineral composition, particle size and age have been suggested to condition
96 biomass and mineral weathering activity of fungi [40-46]. Such selective process was also
97 reported on rock surfaces, where significant changes of the fungal community composition
98 were observed according to the mineral composition [47-49]. However in the soil, few studies
99 have applied high-throughput sequencing to provide a good understanding of the composition
100 and potential drivers structuring mineral-colonizing fungal communities [49-53]. In this
101 context, our study aimed at investigating how the soil fungal communities adapt to different
102 types of minerals incubated *in situ* below different tree stands and which ecological guilds of
103 fungi are mainly associated with these different types of minerals. We hypothesized that (1)
104 the fungal biomass, diversity and community composition on mineral surfaces differ from the
105 surrounding soil (BS), (2) minerals result in an enrichment of different fungal communities
106 according to their physico-chemical properties, and (3) mycorrhizal fungi are major
107 colonizers of minerals particles. To test these hypotheses, pure minerals (*i.e.*, calcite, apatite,
108 and obsidian) enclosed in mesh bags were introduced in the topsoil of the long-term forest
109 observatory (LTO) of Breuil-Chenue (France) for an incubation period of 29 months. The
110 composition and structure of the fungal communities in the different mesh bags as well as of
111 the surrounding bulk soil were analyzed using high-throughput sequencing. The fungal
112 population sizes in mesh bags and in the soil were determined by quantitative PCR (qPCR).

113

114 2. MATERIALS AND METHODS

115 2.1 Sampling site description and experimental design

116 The present study was performed in the Long Term Observatory (LTO) of Breuil-Chenue
117 (Morvan region; 47°18'N, 4°5'E, France). This experimental site is characterized by
118 monospecific plots (0.1 ha) of different tree species planted in 1976 and growing under the
119 same climatic conditions. We obtained a permit from the LTO manager to work on the plots
120 planted with beech (*Fagus sylvatica* L.(Bc)), Corsican pine (*Pinus nigra* Arn. subsp. *laricio*
121 Poiret var. *Corsicana*, (Cp)) or colonized by the native forest (coppice with standards,
122 (CwS)). The term ‘coppice with standards’ refers to the forestry practice that consists in
123 regularly harvesting the coppice (*Quercus sessiliflora* Smith, *Betula verrucosa* Ehrh, and
124 *Corylus avellana* L.) of the native forest and the conservation of oldest trees (*Fagus*
125 *sylvatica*). The soil is classified as a Typic Dystrochrept [54] developed on the “Pierre qui
126 Vire” granite. The bulk soil is sandy-loam textured (60% sands and <20% clays) and acidic
127 (pH_{H2O} ca. 4)[55]. A thick layer of humus is present as moder on the site. The soil
128 characteristics are presented in Table S1.

129 To investigate the impact of mineral substrates on soil fungal community structure, three
130 mineral types (calcite, apatite, and obsidian) were selected. The minerals used in this work are
131 the same as those used in [11] to analyse the mineral-associated bacterial communities. The
132 chemical composition (Table S2) and the way of preparation of the minerals are described in
133 [11]. These minerals have been selected because of their differences of chemical composition
134 and weatherability. Apatite (P and Ca rich) is encountered in the Breuil-Chenue granite as an
135 accessory mineral, while obsidian (Si, Al and Fe rich) and calcite (Ca rich) are not naturally

136 present in this soil. For each mineral type, particles were subjected to a mechanical grinding
137 step followed by washing / sieving to conserve only particles of 100 to 200 μm in size. The
138 minerals were washed several times to remove any soluble fraction adsorbed on their surface,
139 according to [19]. This size was selected to allow an observable dissolution in few years in
140 our experimental conditions. Nylon bags (mesh size, 50 μm ; 4 by 10 cm) were filled with 3
141 grams of pure minerals (i.e., calcite or apatite or obsidian) calibrated in size following the
142 procedure described in references [56,57]. The mesh size (50 μm) was selected to prevent root
143 colonization and to allow microbial colonization and water circulation [58]. On June 13,
144 2012, mesh bags (n=4 per mineral type) were installed horizontally within the organo-mineral
145 layer (5-15 cm) below the three tree stands (Coppice, Beech and Corsican pine) as described
146 in [11]. Soil layers (i.e. litter, organic layer (0-5 cm) and organo-mineral layer (5-15 cm))
147 were removed one by one to install the mesh bags. The sampling date was determined on the
148 basis of preliminary experiments in order to obtain conditions where mineral dissolution was
149 observable [19,59] and to have established fungal mineral colonization.

150 On November 4, 2014 (29 months later), all the mesh bags (n=4 for each mineral) and the
151 surrounding bulk soil (BS; n=3 below each tree stand) were sampled. For each tree stand, soil
152 chemical properties (pH, total C and N, C/N ratio, organic matter content, phosphorus,
153 cationic exchange capacity and all the cations) were determined and are presented in [11].
154 After 29 months of incubation in the soil conditions of the Breuil-Chenue LTO, the relative
155 mass loss (final weight/initial weight x 100) was observable and quantifiable for calcite
156 minerals (~15%) and to a lesser extent for apatite and obsidian (~3%) (Figure 1). A
157 subsample of each mineral type was directly imaged by stereomicroscopy and scanning
158 electron microscopy in order to examine the potential presence of fungal hyphae on the
159 mineral particles (Figure 2).

160

161 *2.2 DNA extraction, quantitative PCR and ITS metabarcoding inventory*

162 The genomic DNA used in this study are the same than those analyzed in [11]. Total DNA
163 was used to quantify the total fungi 18S rRNA gene copies using the 18S rRNA gene-specific
164 primers [10 μ M each; FR1/FF390 (total fungi; [60]). The quantification performed by qPCR
165 gives a good approximation of the population size (i.e., 18S rRNA gene copies), a quantity
166 related to the fungal biomass. Absolute quantifications were performed using serial dilutions
167 of standard plasmids containing a total fungal 18S rDNA insert (from 10^9 to 10^2 gene
168 copies/ μ l) and the SsoAdvanced Universal SYBR Probes Supermix (classical qPCR) from
169 BioRad. Total fungal quantification was performed using the following cycle parameters: 40
170 cycles, with 95°C for 15 s, 50°C for 30 s and 70°C for 60 s. For each qPCR run, a melting
171 curve was performed at the end. The population sizes of total fungi are expressed as
172 log[number of 18S rRNA gene copies per gram dry weight soil]. Subsequently, amplicon
173 libraries were created using barcode-tagged primers for the primer pair ITS1F/ITS2. Each
174 reaction contained 1X PCR Mastermix (5 PRIME®), 500 nM ITS1F primer, 500nM ITS2
175 primer and 7 ng of DNA (as measured by a Nanodrop spectrophotometer). Pyrosequencing
176 was performed by Beckman Coulter Genomics (Danvers, MA, USA) on a Genome Sequencer
177 (GS) FLX 454 Titanium System (Roche).

178

179 *2.3 Bioinformatic analyses*

180 The sequencing effort resulted in 516,120 unidirectional ITS sequences across 9 bulk soil
181 samples and 36 mineral samples. The ITS sequences were sorted according to the samples
182 and adapters were deleted. Subsequently, ITS sequences shorter than 150 bp and with

183 expected error > 0.5 were removed. All chimeras and singletons were discarded before further
184 analysis using UPARSE [61]. Two mineral samples collected below the Coppice stand (1
185 mesh bag containing calcite and another containing apatite) resulted in few ITS sequences and
186 were thus discarded from downstream analyses. Overall, a total of 269,739 high-quality ITS
187 sequences were obtained. We rarefied the library size to 2,936 randomly selected reads per
188 sample to correct for differences in sequencing depth and to obtain unbiased non-parametric
189 richness estimates of microbial community diversity [62]. A total of 128,398 high quality ITS
190 sequences were subsequently analyzed and resulted in the identification of 1,295 fungal
191 OTUs. Using UPARSE algorithm in USEARCH, an OTU-based analysis was performed to
192 calculate alpha-diversity estimates in our samples with a cutoff of 3% dissimilarity. Then, ITS
193 sequences were assigned to taxonomic groups based on pairwise similarity searches against
194 the curated UNITE fungal ITS sequence database. Finally, the trophic mode was determined
195 for each OTU using the FUNGuild software [63]. Only the FUNGuild assignments with a
196 confidence score of “Probable” or “Highly Probable” were considered. The taxa with
197 assignment scores below these confidence scores were considered as ‘unassigned’. For our
198 analyses, we assigned taxa to one of the six guilds: symbiotroph, saprotroph, pathotroph,
199 pathotroph-saprotroph, unassigned and others. The category “others” grouped other modes
200 that represented a small percentage of sequence reads and were not analysed further.

201

202 *2.4 Statistical analyses*

203 Based on the fungal OTUs table, alpha-diversity estimates were calculated using the
204 function “rarefy” from the package ‘Vegan’ [64]. Richness (S_{obs}) was calculated as the
205 number of observed OTUs in each sample. The diversity within each individual sample was
206 estimated using the non-parametric Shannon index. Correlation analyses were done to

207 determine whether the soil chemical properties were linked to the different indices. We also
208 assessed whether fungal population size and alpha diversity varied using a Student's t-test.
209 One-factor analysis of variance (ANOVA) was done independently below each tree stand.
210 The factor considered was the compartment (*i.e.*, bulk soil vs mineral) or the sample type (*i.e.*,
211 bulk soil, calcite, apatite and obsidian). Similar analyses were performed to test the effect of
212 minerals and mineral type on the alpha-diversity within the two main fungal phyla (*i.e.*,
213 Basidiomycota and Ascomycota). Concerning the beta-diversity, we applied a Hellinger
214 transformation of the OTUs table and generated a pairwise distance matrix using Bray-Curtis
215 dissimilarity using the Vegdist function [64]. Samples were then compared to determine
216 whether there were significant differences in the variance and means between tree stands (*i.e.*,
217 Beech, Coppice and Corsican pine), compartments (*i.e.*, bulk soil vs mineral) and mineral
218 types (*i.e.*, calcite, apatite and obsidian) using Nonmetric multidimensional scaling (NMDS)
219 ordinations and permutational multivariate analysis of variance (PERMANOVA). Variance
220 partitioning analysis was performed using the 'varpart' function in the 'vegan' package. The
221 main contributing taxa for dissimilarity between bulk soils and minerals were identified at
222 different taxonomical levels through a similarity percentages (SIMPER) analysis using the
223 function 'simper' from the 'vegan' package [64]. In addition, changes in fungal taxonomical
224 composition and functional guilds (*i.e.*, FUNGuild) between bulk soils and minerals and
225 between the three mineral types were tested using the Student's t-test or ANOVA analysis.
226 When required, a p adjustment was done using the false-Discovery-Procedure (FDR) [65] to
227 determine the p-value threshold. All statistical analyses were carried out in R (v.3.5.1) (R
228 Core Team 2018).

229

230 *2.5 Accession numbers*

231 The ITS pyrosequences generated for this study were submitted to the Sequence Read

232 Archive (SRA) under the accession number PRJNA507076.

233 **3. RESULTS**

234 *3.1 Quantification of the fungal population sizes*

235 For each tree stand, lower fungal populations (i.e., biomass based on qPCR) were observed
236 on minerals compared to the surrounding bulk soil (BS; Student's t-test, $p < 0.05$; Figure 2A).
237 The stronger difference was observed between calcite samples and their related BS samples
238 below beech and Corsican pine stands (Figure 2A). No difference in population size was
239 observed for each tree stand between the different mineral types (i.e. calcite, apatite and
240 obsidian) (ANOVA; $p > 0.05$), excepted between calcite and apatite below beech stand (Figure
241 2A). Finally, a subsample of minerals was imaged using stereomicroscopy and scanning
242 electron microscopy (SEM), which confirmed fungal colonization of mineral surfaces (Figure
243 3).

244

245 *3.2 Fungal assemblage from metabarcoding inventory*

246 Almost 97% of the ITS sequences were classified into five different phyla, predominantly,
247 Basidiomycota (51.2%), Ascomycota (37.8%) and Zygomycota (7.5 %). At the order level, it
248 was possible to classify about 64% of sequences, the most common orders being *Russulales*,
249 *Boletales* and *Agaricales* among Basidiomycota; *Hypocreales* and *Helotiales* among
250 Ascomycota; and *Mortierellales* among *Zygomycota*. A total of 1,295 OTUs was generated
251 from this sequence dataset.

252

253 *3.3 Alpha diversity*

254 The fungal diversity was similar in the bulk soil samples of the different tree stands
255 ($H'_{\text{Beech}}: 2.3 \pm 0.1$; $H'_{\text{Coppice}}: 2.6 \pm 0.5$; $H'_{\text{Corsican pine}}: 2.7 \pm 0.5$) (Figure 2B and Table S3).
256 However, below the beech and Coppice with standards stands significantly higher diversity
257 values were observed for calcite samples than in the related BS samples (Student's t-test;
258 $p < 0.05$; $H'_{\text{Beech}}: 3.6 \pm 0.9$; $H'_{\text{Coppice}}: 4.1 \pm 0.2$), but not below Corsican pine ($H'_{\text{Corsican pine}}: 4.0$
259 ± 0.3 , $p > 0.05$; Figure 2B). This increase was mainly attributed to higher Shannon index
260 values in the Basidiomycota (Student's t-test; all $p < 0.05$; Figure S1). No significant
261 relationship was observed between the Shannon index or the observed number of OTUs and
262 the soil chemical properties ($p > 0.05$).

263

264 *3.4 Fungal community structure*

265 According to NMDS and PERMANOVA analyses, the tree stand was the main factor
266 explaining the fungal community structure (PERMANOVA : $F=9.0$; $p < 0.001$) (Figure 4).
267 Noticeably, for each tree stand, a significant compartment effect (*i.e.*, mineral vs BS) was
268 observed (PERMANOVA; Beech: $F=4.4$; $p < 0.01$; Coppice: $F=3.0$; $p < 0.01$ and Corsican pine:
269 $F=2.8$; $p < 0.01$) (Figures 4 and S4). In a lesser extent, the mineral type (*i.e.*, calcite, apatite and
270 obsidian) significantly impacts the structure of the mineral-associated fungal communities in
271 each tree stand (PERMANOVA ; Beech: $F=2.1$; $p < 0.01$; Coppice: $F=2.0$; $p < 0.01$ and
272 Corsican pine: $F=2.1$; $p < 0.01$) (Figures 4 and S4).

273 Together the tree stand and minerals explained 30.9% of the observed variation at the OTU
274 level as stated by a variance partitioning analysis. Tree stand effect was able to independently
275 explain 28.5% of the variation observed, while the compartment (mineral vs bulk soil) alone

276 explained only 3.2%. When the BS samples were excluded from the analysis to concentrate
277 on the potential effect of the mineral type (i.e., apatite vs obsidian vs calcite), the tree stand
278 and minerals explained 24% of the observed variation. Again, the tree stand effect was the
279 main factor explaining the variance (23%), while the type of mineral alone explained 2.3% of
280 the variation.

281

282 *3.5 Fungal assemblage changes between BS and mineral samples*

283 A similarity percentage analysis (SIMPER) determined that the changes in proportion of
284 the Basidiomycota and Ascomycota contributed respectively to 44.1 - 49.4% and 21.3 -
285 28.8% of the observed dissimilarity between BS and mineral samples (Table S5).
286 Basidiomycota were by far the most abundant phylum in the BS samples (relative abundance
287 in the BS samples below each tree stand: Beech: 87.4% \pm 2.4; Coppice: 72.4% \pm 10.0;
288 Corsican pine: 77.6% \pm 11.8) and their relative abundance strongly declined on mineral
289 surfaces (relative abundance in the mineral samples below each tree stand: Beech: 36.3% \pm
290 16.8; Coppice: 51.6% \pm 31.6; Corsican pine: 44.9% \pm 21.1) (Figure 5A). In contrast,
291 Ascomycota, whose importance was limited in BS (relative abundance: Beech = 8.9% \pm 2.3;
292 Coppice = 17.9% \pm 6.8; Corsican pine = 16.2% \pm 8.6), increased in relative abundance on
293 mineral surfaces (Beech = 56.5% \pm 15.1; Coppice = 40.4% \pm 24.8; Corsican pine = 34.4% \pm
294 16.3) (Figure 5A). Depending on the tree stand analysed, these compositional changes were
295 assessed as statistically significant for Basidiomycota (ANOVA; Beech: F=26.2, p<0.001;
296 Coppice: F=1.2, P=0.29; Corsican pine: F=6.4, p<0.05) and Ascomycota (ANOVA; Beech:
297 F=28.0, p<0.001; Coppice: F=2.3, P=0.16; Corsican pine: F=3.4, P=0.09) (Table S4).

298 At the order level, *Russulales* and *Agaricales* were responsible for respectively 15.6 -
299 31.9% and 5.1 – 7.0% of the observed dissimilarity (Table S5). These two orders were more
300 abundant in BS samples than on minerals (ANOVA; all $p < 0.05$, except for *Agaricales* below
301 Corsican pine) (Table S3). On the contrary, the *Hypocreales* and *Helotiales* orders each
302 responsible for nearly 3% of the observed dissimilarity (Table S5) were more abundant on
303 minerals.

304 When regarding the 25 most abundant species identified in our dataset, 13 were related to
305 ECM fungi, one was related to ericoid fungi and the other appeared related to
306 saprophytes/pathogens and potential endophytes. Notably, ITS sequences related to *Russula*
307 *ochroleuca*, *Russula puellaris*, *Lactifluus glaucescens* and *Amanita rubescens* were
308 significantly enriched in BS compared to minerals (Table S7).

309

310 3.6 Fungal assemblage changes between mineral types

311 When mineral samples were examined without the related BS samples in each tree stand,
312 the composition of fungal communities was shown to vary according to the mineral type. This
313 effect was observable at the phylum level, but was only statistically significant below the
314 Coppice with standards stand (*i.e.*, the native forest). In this tree stand, Basidiomycota
315 appeared more abundant on obsidian ($70.6\% \pm 16.2$) than on calcite ($15.5\% \pm 5.3$), while the
316 opposite trend was observed for Ascomycota (Obs = $26.6\% \pm 16.6$ and Cal = $67.5\% \pm 2.5$)
317 and Zygomycota (Obs = $1.9\% \pm 0.6$ and Cal = $11.3\% \pm 1.6$) (ANOVA, $p < 0.05$) (Figure 5A
318 and Table S7). At the order level, *Hypocreales* and *Tremellales* were more abundant on
319 calcite (9.2-20.8% and 1.4-7.1%, respectively) than on apatite (0.8-1.4% and 0.4-1.1%,
320 respectively) and obsidian (1.1-6.0% and 0.5-4.1%, respectively) (ANOVA, all $p < 0.05$,

321 except for Corsican pine *Hypocreales*) (Table S8). Noticeably, several fungal species belonging to
322 the *Mortierellales* (*Mortierella horticola*, *M. alpine*, *M. gamsii* and *M. macrocystis*) and
323 *Hypocreales* (*Ilyonectria radicola*) orders appeared more abundant on calcite than on other
324 minerals below the Beech and Coppice stands, some of them showing significant differences
325 (ANOVA, $p < 0.05$, Table S9).

326

327 *3.7 Trophic mode prediction of fungal communities*

328 A total of 419 fungal OTUs was successfully assigned to a trophic mode. These OTUs
329 represented 78.6-90.9% of the total ITS sequences in BS samples and 49.9-65.9% in the
330 mineral samples. Symbiotrophic fungi presented higher relative abundance in BS (Beech =
331 $84.5\% \pm 1.7$; Coppice = $64.6\% \pm 12.9$ and Corsican pine = $73.8\% \pm 11.4$) than on minerals
332 (Beech = $40.0\% \pm 18.2$; Coppice = $46.9\% \pm 32.8$ and Corsican pine = $31.5\% \pm 24.2$)
333 (ANOVA; Beech: $F=16.9$, $p=0.001$; Coppice: $F=0.8$, $p=0.39$ and Corsican pine: $F=8.3$,
334 $p=0.01$) (Figure 5B and Table 1). On the contrary, saprotrophic and pathogenic fungi
335 presented a lower relative abundance in the BS samples (saprotrophs: Beech = $3.5\% \pm 0.8$;
336 Coppice = $9.5\% \pm 5.0$; Corsican pine = $8.1\% \pm 3.8$ and pathotrophs: Beech = $0.9\% \pm 0.2$;
337 Coppice = $1.3\% \pm 0.5$; Corsican pine = $0.9\% \pm 0.3$) than on mineral surfaces (saprotrophs:
338 Beech = $8.8\% \pm 6.6$; Coppice = $8.6\% \pm 6.9$; Corsican pine = $23.8\% \pm 7.8$ and pathotrophs:
339 Beech = $2.35\% \pm 2.3$; Coppice = $7.12\% \pm 9.2$; Corsican pine = $4.7\% \pm 6.5$)(Figure 5B and
340 Table 1AB).

341 When mineral samples were examined without the related BS samples, both obsidian and
342 apatite were characterized by higher relative abundance of symbiotrophic fungi (36.3-64.8%
343 and 47.4-60.5%, respectively) than calcite (9.4-25.1%)(Figure 5B and Table 1B).

344 Pathotrophic fungi were significantly enriched on calcite (Beech: $4.9\% \pm 2.4$ and Coppice:
345 $20.3\% \pm 2.1$) compared to obsidian (Beech: $0.9\% \pm 0.6$ and Coppice: $1.1\% \pm 0.1$) and apatite
346 particles (Beech: $1.2\% \pm 1.0$ and Coppice: $2.0\% \pm 1.3$) (ANOVA, all $p < 0.05$). Higher
347 saprotrophic relative abundance was observed on calcite (Beech: $14.9\% \pm 7.3$; Coppice:
348 $16.4\% \pm 1.7$) than on obsidian particles (Beech: $4.5\% \pm 1.4$; Coppice: $3.9\% \pm 0.9$) (ANOVA,
349 all $p < 0.05$) (Figure 5B and Table 1B).

350

351 **4. DISCUSSION**

352 *4.1 Mineral chemistry does not determine fungal biomass*

353 The potential effect of the mineral chemistry on fungal colonization of minerals has been
354 reported previously, mostly in boreal forests [45,46,66-68]. Previous studies revealed an
355 increase of the fungal biomass in mesh bags amended with minerals carrying nutritive
356 elements (i.e., P-carrying minerals (i.e., apatite) or K- or Mg-carrying mineral (i.e.,
357 hornblende and biotite)). The preferential colonization of minerals carrying limiting nutrients
358 would represent an adaptation of fungal communities, or an adaptive trait of trees extended to
359 their symbiotic fungi, to the nutrient limitations occurring in forest soils. However, this
360 increase of biomass on the minerals was not observed in all the experimental sites studied and
361 was shown to vary from one year to the next one on a same site, suggesting combined effects
362 of mineral chemistry, nutrient availability into the soil and nutrient status of the considered
363 forests [43,45,66]. In our study, quantitative PCR analyses indicated that fungal population
364 sizes were lower on mineral surfaces than in surrounding bulk soil. Although the physical
365 differences between the two matrixes (i.e. mineral particles vs the bulk soil) may explain
366 these lower abundances on minerals, similar conclusions were obtained in previous studies

367 [51,53]. Apatite did not exhibit an increase in fungal biomass in comparison with obsidian
368 and calcite, and the lower fungal biomass was observed for calcite (Ca-carrying mineral).
369 Nevertheless, our results are hardly comparable with those of previous studies [43,45,66] due
370 to several differences in terms of fungal quantification methods (*i.e.*, ergosterol vs qPCR),
371 mesh bag strategy (*i.e.*, bags mainly filled with quartz and amended with limited quantity of
372 minerals vs bags fully filled with mineral), forest type (*i.e.*, boreal vs temperate), soil depth
373 (*i.e.*, different soil horizons) and incubation times of mineral in soils (*i.e.*, few months vs
374 years).

375

376 *4.2 Land cover primarily determines the structuration of mineral-associated fungal* 377 *communities*

378 The richness, diversity and fungal community composition are known to be driven by the
379 pedo-climatic parameters and land cover [69-71]. At local scale (*i.e.*, plot), fungal
380 communities are also vertically structured (*i.e.*, soil horizons)[72,73]. The the strong effect of
381 the land cover (*i.e.*, tree stand effect) on the composition of soil fungal communities observed
382 in our study was expected and confirmed the important relationship existing between the tree
383 species and their associated fungi [69,74]. *Russulales*, *Agaricales*, *Boletales*, *Atheliales*,
384 *Thelephorales*, *Mortierellales*, *Pezizales* represented the main orders identified in bulk soil
385 samples and differences in taxonomic composition according to tree species were consistent
386 with previous studies carried out on the same experimental site [69,75]. Notably, our results
387 highlighted that the soil fungal community structure was significantly impacted by minerals
388 and that this compartment effect (*i.e.*, minerals vs bulk soil) was first conditioned by the land
389 cover. These results are relatively new as most of our knowledge on the mineral-colonizing
390 fungal communities comes from mesh bag studies done below *Picea abies* stands and in

391 boreal forests [44-46,66]. The differences observed may be due to the sampling strategy used
392 in our study. The small-scale approach we used permitted to limit the effects of different
393 confounding factors, especially the soil heterogeneity. On the contrary, the previous studies
394 used a large-scale sampling strategy where the soil heterogeneity was higher, hiding probably
395 the mineral type effect. Interestingly, other recent studies [51,53] reported a mineral type
396 effect using a small-scale approach.

397

398 *4.3 Taxonomic modification of the fungal communities colonizing minerals compared to* 399 *the surrounding bulk soil*

400 HTS results revealed that minerals, and especially calcite, tended to harbour more diverse
401 fungal communities than the surrounding bulk soil. A net increase of the relative abundance
402 of ITS sequences assigned to Ascomycota and Zygomycota was observed on minerals, while
403 the Basidiomycota orders *Russulales* and *Agaricales*, abundant in both compartments, were
404 significantly more abundant in the bulk soil. One may explain these fungal compositional
405 changes between BS and mineral samples by technical biases. The mesh size would favour
406 some taxa more than others (see the review of [76]). The use of fresh mineral surfaces (*i.e.*,
407 mineral particles generated by mechanical grinding; see Material and methods section) may
408 also favour opportunistic taxa (r-strategy) as it was suggested for bacteria [16]. On the other
409 hand, the minerals contained in the mesh bags contrast considerably with the surrounding
410 bulk soil in that they contain low levels of directly available organic and inorganic nutrients.
411 Therefore, these nutrient-poor conditions may limit the development of fungal biomass and
412 select for specific microorganisms capable of developing under such oligotrophic conditions
413 or of recovering the nutrients entrapped into the minerals. Although the mesh size and fresh
414 mineral surface biases cannot be completely excluded, previous studies validated the mesh-

415 bag use, including several studies on organic matter decomposition [77,78] or mineral
416 colonization [51,58]. Notably, Wallander *et al.* [58] evidenced that after a trenching
417 experiment, the dominant fungi colonizing mineral-amended mesh bags were mycorrhizal
418 ones as in our study. Interestingly, in our study, while all the mesh bags contained ECM
419 related taxa (*i.e.*, *Russulales*, *Agaricales*, *Boletales*), some were highly colonized and others
420 poorly colonized, confirming a patchy distribution of the fungi in the soil [79-81]. As an
421 example, *Boletales* related sequences appeared increased in abundance on minerals compared
422 to the bulk soil, but only below the coppice with standards stand (Table S6 and S10). In
423 addition, several OTUs affiliated to the *Archaeorhizomyces* genus were also detected in our
424 dataset, with some of them enriched on mineral surfaces, but only specifically below certain
425 tree species. As an example, the OTU47 was more abundant on apatite and obsidian than in
426 the bulk soil or on calcite, but only in the beech stand. Notably, Pinto-Figueroa *et al.* [82]
427 recently reported an increase of the abundance of *Archaeorhizomyces* in mineral rich
428 environment. These authors suggested that some representatives of this fungal class may be
429 adapted to mineral environment with potential capacities of mineral weathering. Together, our
430 results highlight that no specific fungal species is selected by the minerals whatever the tree
431 stand, but at the same time that the distribution of certain classes (*Agaricales*, *Helotiales*,
432 *Hypocreales*) is relatively well conserved.

433

434 *4.4 Mineral chemistry drives the structuration of the mineral-associated fungal* 435 *communities*

436 A separate analysis, comparing only the three different minerals types and excluding the
437 BS samples, revealed significant differences between mineral-associated fungal communities.
438 Overall, Ascomycota and Zygomycota tended to be more enriched on calcite, while

439 Basidiomycota were more abundant on obsidian and apatite. Similar structuring effects of the
440 mineral type have also been reported for the fungal communities colonizing the surface of a
441 granite outcrop, where certain fungal ribotypes were specifically associated with K-felspar,
442 plagioclase or quartz [48,49]. Noticeably, quartz was shown to select particular taxa, though it
443 is a nutrient-poor mineral mainly composed of silica [48,49]. By contrast, other studies
444 reported that the mineral type has no effect on the structuration of the fungal communities
445 [40, 43, 45]. These differences could be explained by the fact that previous studies used mesh
446 bags mainly filled with quartz particles and amended with only 1% of the mineral tested (*i.e.*,
447 apatite), while we filled mesh bags with 100% of the mineral tested. This is an important
448 difference as our conditions corresponded to an important hotspot of nutrients, while in the
449 previous conditions those nutritive elements were highly diluted in quartz. As quartz was
450 shown to have specific selective effect [48,49], the absence of difference observed in these
451 studies may be due to a major effect of quartz and a minor effect of the 1% amendment. The
452 differences in fungal assemblages observed on the surface of the three mineral types tested
453 here may be attributed to different intrinsic (*i.e.* chemical composition of the mineral
454 considered, their nutrient content, their weatherability) and extrinsic (*i.e.*, physico-chemical
455 conditions of the surrounding soil) factors. In this way, the strong balance differences
456 between Ascomycota and Basidiomycota measured on calcite, in comparison to those
457 observed on apatite and obsidian, could be attributed to the nutritive content of calcite (*i.e.*,
458 Ca) and / or by the potential increase of the local pH due to carbonates released during the
459 dissolution of this mineral [11]. At the order level, calcite particles were enriched in specific
460 taxa belonging to the *Hypocreales*, *Filobasidiales*, *Tremellales* or *Mortierellales*. Notably, the
461 *Hypocreales* order encompass taxa frequently identified as endophytes in plant roots [83] and
462 which has been shown to facilitate the uptake of micronutrients by host plants and were

463 suggested to weather mineral substrates through the production of siderophores [84-86].
464 Concerning the *Mortierellales* order, several species related to the genera *Mortierella* (*i.e.*, *M.*
465 *horticola*, *M. alpine*, *M. longigemmata*, *M. gamsii* and *M. macrocystis*) and *Ilyonectria* were
466 also enriched on calcite or apatite in our study. Notably, *Mortierella* possess functional
467 abilities related to organic matter decomposition [87] and mineral weathering [88,89], and
468 their presences in mesh bag amended with apatite has also been reported [40,44]. Together,
469 these results suggest that *Mortierella* species are well adapted to several environments,
470 including minerals, and are potentially capable of weathering minerals. As the representative
471 of this genus are culturable, it opens new perspectives in the understanding of their potential
472 role in nutrient cycling and mineral weathering.

473

474 4.5 Contrasted responses of the different trophic guilds of fungi to the mineral habitat

475 Fungal assemblage differences between the compartments (*i.e.*, mineral vs BS) or the
476 mineral type (*i.e.*, calcite, obsidian and apatite) were also illustrated by trophic mode analysis
477 (FUNguild). Symbiotrophic fungi represented the most abundant group among the assigned
478 trophic modes detected in the soil horizon considered and on the mineral surfaces. However,
479 symbiotrophs represented a lower fraction on minerals than in the surrounding bulk soil,
480 especially on calcite (Figure 5b). Previous study demonstrated *in vitro* the selective
481 colonization of ECM fungi associated to *Pinus sylvestris* in patches of nutrient-rich potassium
482 feldspar in comparison with patches of nutrient-poor quartz [68]. Recently, Sun *et al.* [52]
483 reported that after 6-month incubation in the E soil horizon of a mixed forest, mesh bags filled
484 with apatite, serpentine, quartz or feldspar were dominantly colonized by symbiotrophic
485 fungi. Together these data evidence both *in vitro* and *in situ* the ability of symbiotrophic fungi
486 to explore their environment and their potential key role in nutrient cycling and mineral

487 weathering [90]. Additionally, saprotrophic and pathotrophic fungi strongly increase in relative
488 abundance of ITS sequences in the mesh bags compared to the surrounding bulk soil,
489 suggesting an adaptation to the nutrient-poor conditions occurring in this mineral
490 environment. We cannot exclude that the incubation period (*i.e.*, 29 months) can be long
491 enough for accumulation of microbial necromass in the mesh bags due to the turnover of
492 ectomycorrhizal mycelia, resulting in a gradual increase in abundance of decomposer fungi
493 over time. It could also be suggested that the flux of dissolved organic matter produced when
494 percolating water passes through the forest floor could enter the mesh bag and thus represent
495 a source of energy and carbon for the microorganisms. In this sense, the presence of
496 heterotrophic bacteria isolated from the same mineral particles supports the presence of
497 available carbon substrates in the mesh bags [11]. However, the accumulation of organic
498 matter in the mesh bags was not assessed in the current study, precluding any conclusion on
499 this point. Alternatively, the presence of saprotrophic fungi on minerals may be due to their
500 mineral weathering ability. Indeed, some genera have been reported for their ability to
501 solubilize phosphate (*Aspergillus*, *Penicillium*, *Trichoderma*, *Mucor*, *Candida*, *Discosia*,
502 *Eupenicillium*, *Gliocladium*) [91-93]. Recently, Kirtzel *et al.* [94] revealed that the wood-
503 rotting basidiomycota *Schizophyllum commune* was capable of increasing mineral weathering
504 through a combined effect of organic acids, siderophores, enzymes and mechanical pressure.
505 The patterns observed and the potential role of these different guilds in the mineral
506 weathering process may differ according to the soil horizons considered. Indeed, fungal
507 communities are known to strongly differ across the soil profile [37,72,95]. Notably, topsoil
508 horizons are considered to be inhabited by communities more strongly involved in organic
509 matter recycling, while deeper soil horizons due to their low content of carbon and organic
510 matter are inhabited by oligotrophic communities more effective at mobilizing nutrients from

511 other sources (i.e., minerals). Complementary studies considering mesh bags introduced in
512 different soil horizons are required to test this functional distribution.

513

514 **5. CONCLUSIONS**

515 Our study highlights that minerals represent a specific habitat for fungi (i.e., the
516 mineralosphere; [8]), where particular taxa are enriched. While the physico-chemical
517 properties of the minerals impact the community composition of the fungi, no effect was
518 observed for the fungal biomass development. Our analyses also evidenced that
519 environmental conditions (i.e., pH, land cover) strongly condition the colonization of minerals
520 by fungi. Indeed, although the work was done on the same soil in our study, the land cover
521 remains the first driver of fungal community. The mineral type effect observed in our study
522 was probably made possible by the soil horizon considered (i.e. topsoil) and the small-scale
523 sampling strategy used in our study, which was determined to correspond to the scale of
524 mineral/microorganisms interaction (i.e., μm or mm) and to limit the soil heterogeneity at
525 both abiotic (i.e., pH, nutrient content) and biotic levels. Interestingly, a mineral type effect
526 was also demonstrated for bacteria, but with a stronger effect, suggesting that minerals are
527 active interfaces to consider in soil biology [11,16,51]. The next step will be to increase the
528 sampling scale to integrate the soil heterogeneity and to determine whether the mineral type
529 effect is conserved whatever the soil depth. Our data revealed that symbiotrophic fungi are the
530 main colonizers of most of the mineral types tested, confirming the key role played by
531 mycorrhizal fungi in nutrient cycling, tree nutrition and potentially in mineral weathering.
532 However, specific patterns of colonisation of the minerals by fungi have been observed below
533 each tree stand, suggesting a strong impact of the soil chemistry and/or of the nutritive
534 requirements of each tree species. Together the new data obtained in this study suggest a

535 contrasted response of the different guilds of fungi (*i.e.*, symbiotrophic, endophytic,
536 saprotrophic and pathotrophic fungi) according to the mineral type. A major objective will be
537 to investigate the role of the different guilds of fungi in mineral weathering. The culturable
538 fungi isolated from the Breuil-Chenue LTO will help to fill this gap. The impact of the soil
539 horizon considered on the distribution and functional role of these fungal communities will be
540 also a challenging question for future researches.

541

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553

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Figure legends

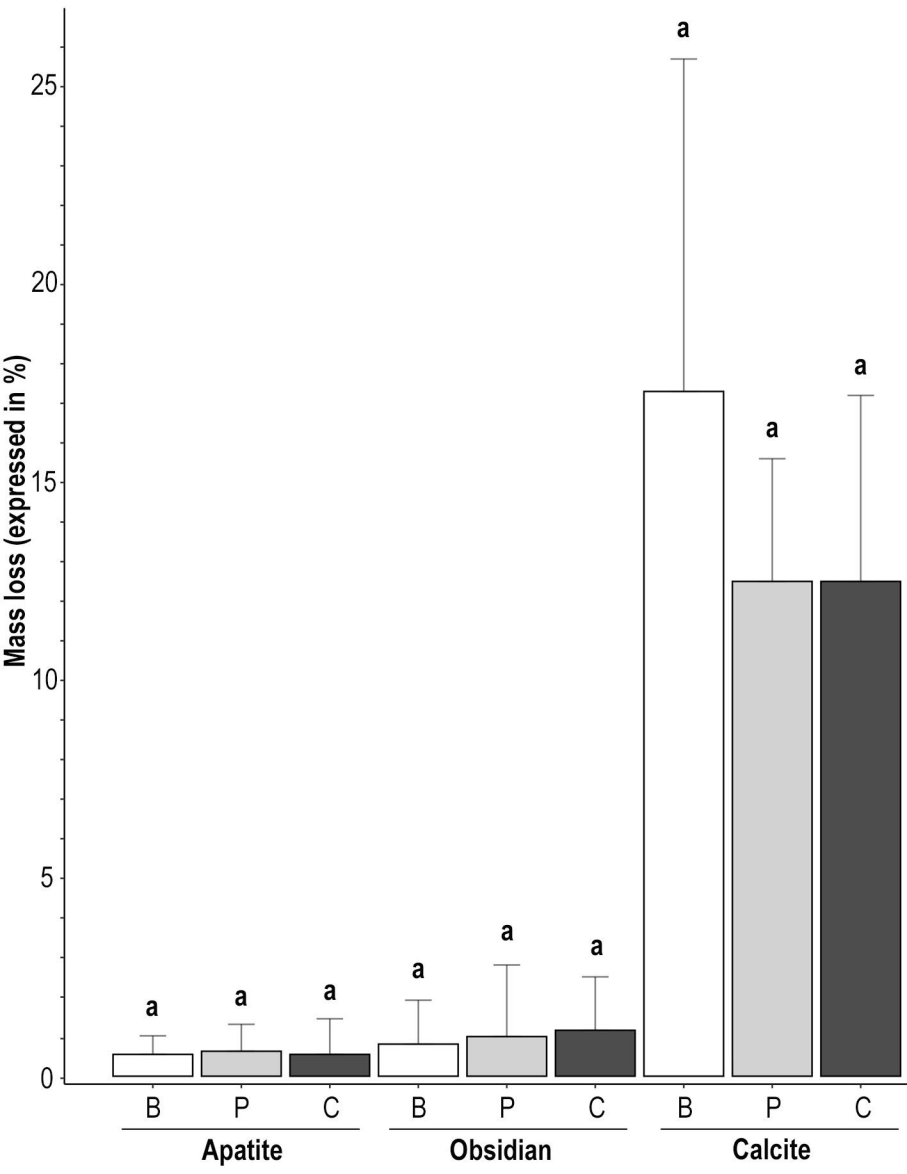
892 **Figure 1. Relative of mass loss of the mineral particles recovered in the mesh bags,**
893 **after 29 months of incubation in the different tree stands of the Breuil-Chenue forest**
894 **site.** Abbreviations were used as follows: B, Beech; P, Pine and C, Coppice with standards.
895 For each mineral type (apatite, obsidian, calcite), the percentage of mass loss was determined
896 and statistically compared between the different tree stands through an ANOVA test. Each
897 value presented is the mean \pm the standard error of the mean of four replicates. Different
898 letters indicate significant differences ($P < 0.05$).

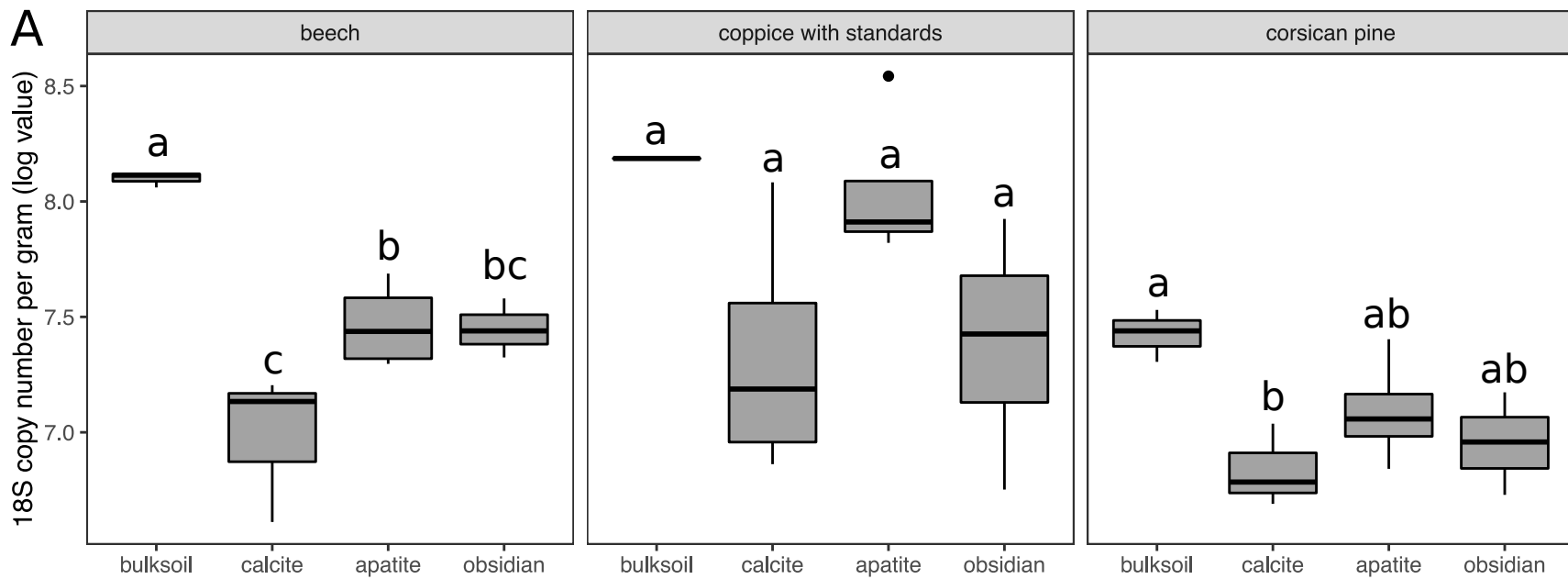
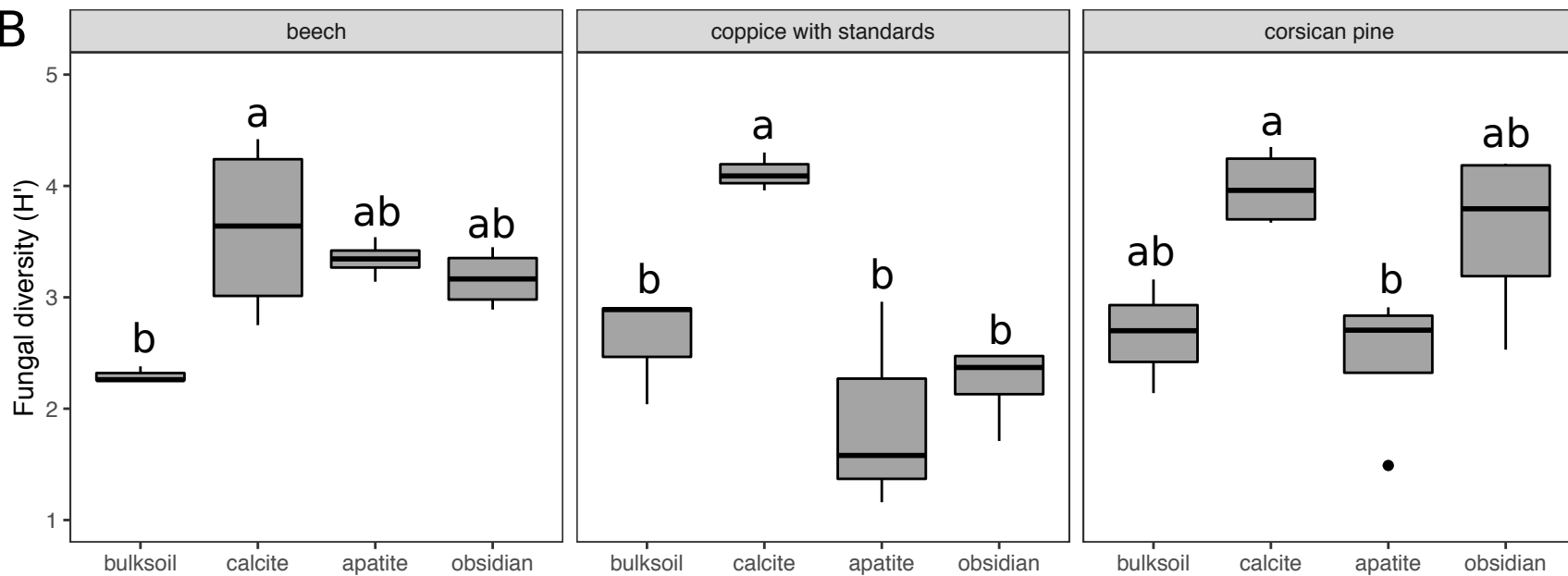
899 **Figure 2. Changes in fungal population size (A) and Shannon diversity (B) between**
900 **bulk soil and mineral samples below the different tree stands.** Fungal population size was
901 estimated based on 18SrRNA qPCR and data are presented as log-transformed [18S rRNA
902 gene copies per gram of soil or mineral]. Shannon index was calculated from the sequencing
903 data for the total fungal community. For both estimates, letters above the boxplots denote
904 significantly different groups from Tukey's post-hoc tests ($P < 0.05$). Boxplots indicate the
905 median, interquartile range, reasonable range of the data and outliers.

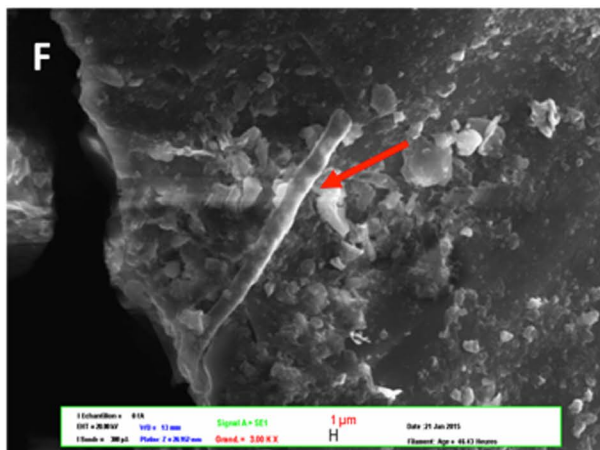
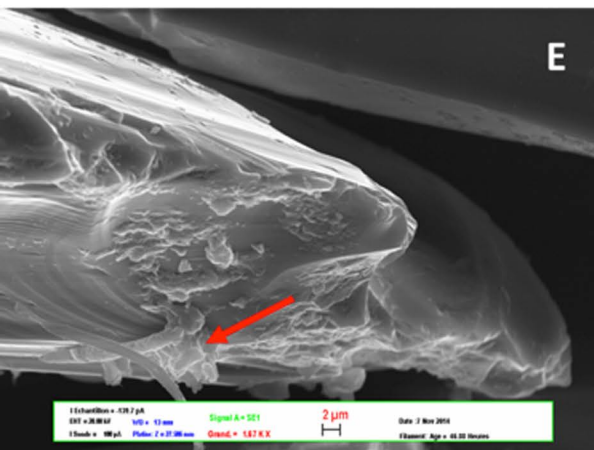
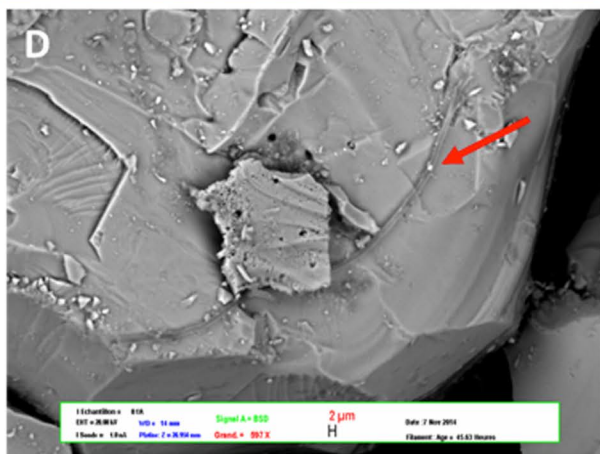
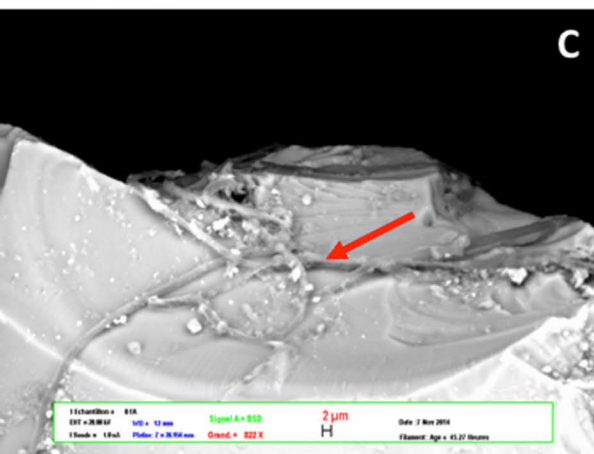
906 **Figure 3: Photographic and microscopy (SEM) images of mineral particles recovered**
907 **in the mesh bags, after 29 months of incubation in the different tree stands of the Breuil-**
908 **Chenue forest site.** A) White fungal hyphae colonizing apatite particles under Coppice stand;
909 B) Black fungal hyphae colonizing obsidian particles under Coppice stand; C) Direct
910 observation of an obsidian particle incubated in the Beech stand; D) Direct observation of an
911 apatite particle incubated in the Beech stand E) Direct observation of an obsidian particle
912 incubated in the Coppice stand; F) Direct observation of an obsidian particle incubated in the
913 Corsican pine stand. The red arrows indicate fungal hyphae. The mineral particles were
914 directly observed without any preparation.

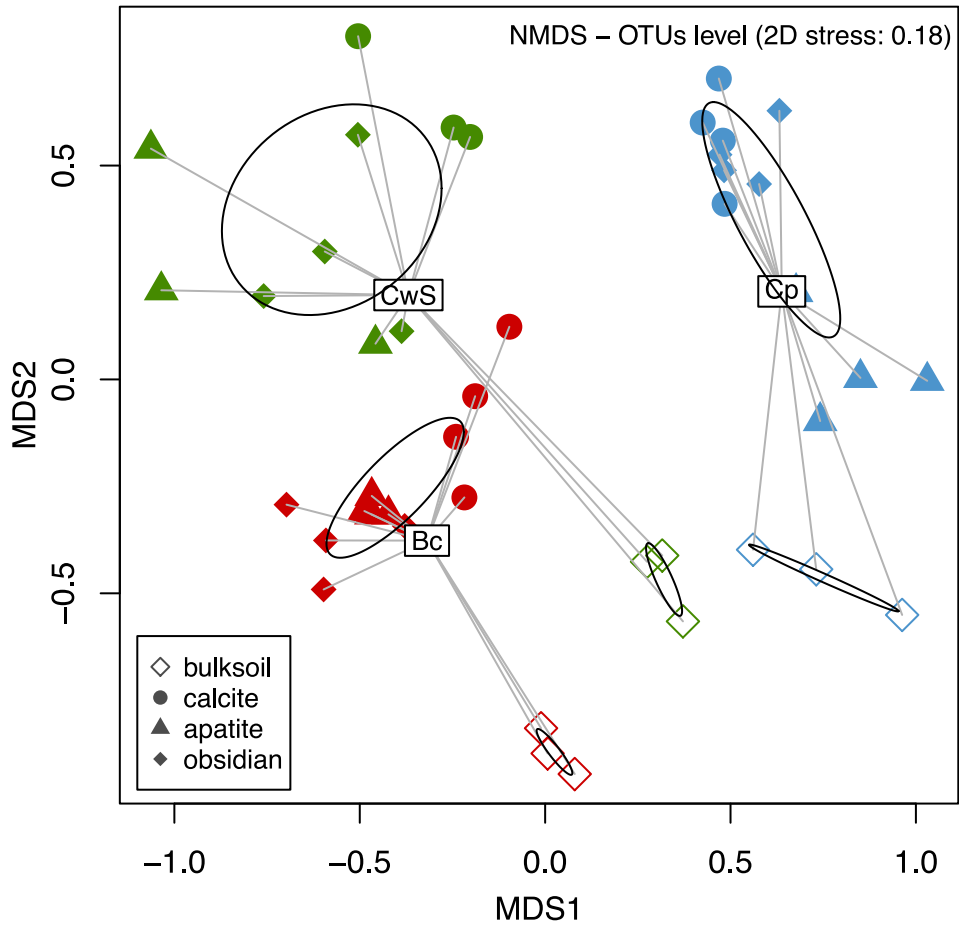
915 **Figure 4: Non-metric multidimensional scaling (nMDS) plot of fungal community**
916 **structure from bulk soil and mineral samples.** Ordination plot is based on based on *Bray-*
917 *Curtis* (*Hellinger*-transformed) dissimilarities. Symbols represent the different sample types
918 (bulk soil, calcite, apatite and obsidian) and colors reflect the different tree stands (beech: red,
919 coppice with standards: green and Corsican pine: blue). Ellipses represent 95% confidence
920 intervals of centroids.

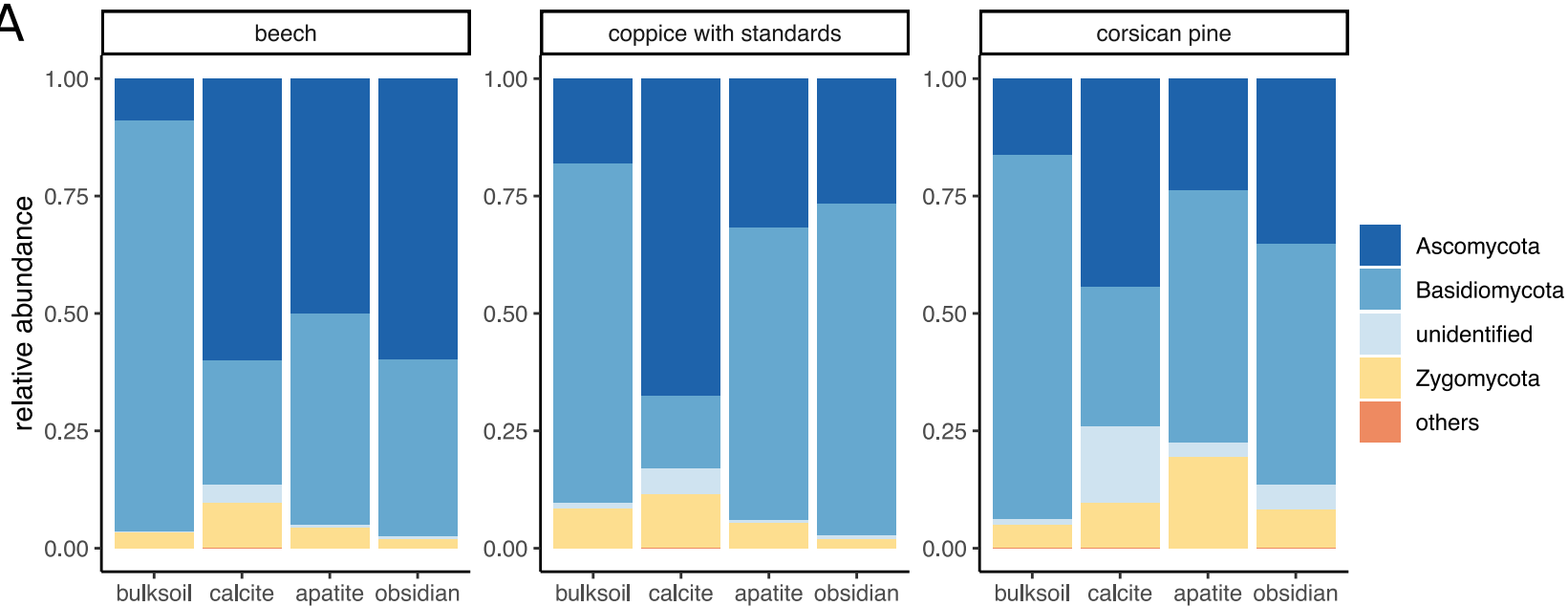
921 **Figure 5: Relative distribution of the major phyla (A) and fungal trophic modes (B)**
922 **detected in bulk soil and mineral samples below the different tree stands.** The values
923 presented are average values from the replicates. The category ‘other’ groups minor phyla or
924 minor trophic modes, while the ‘unassigned’ refer to the sequences only affiliated as fungi or
925 without known trophic mode.



A**B**





A**B**