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# Forest plant cover and mineral type determine the diversity and composition of mineral-colonizing fungal communities

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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  $\mu\text{m}$  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<sub>H2O</sub> 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  $\mu\text{m}$  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  $\mu\text{m}$ ; 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 $\mu\text{m}$ ) 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  $\mu$ 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/ $\mu$ 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 ( $S_{\text{obs}}$ ) 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         $\pm 0.3$ ,  $p > 0.05$ ; 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.,  $\mu\text{m}$  or  $\text{mm}$ ) 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

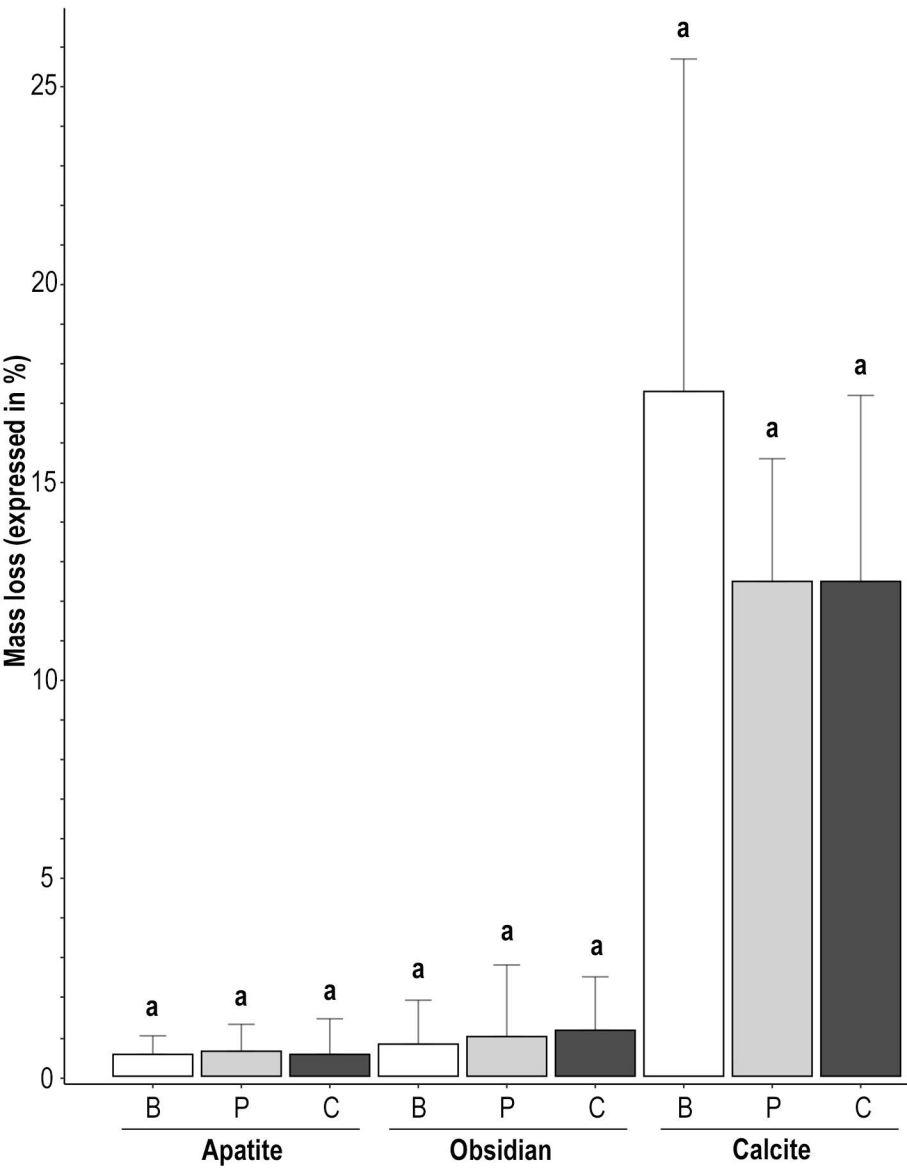
892 **Figure 1. Relative of mass loss of the mineral particles recovered in the mesh bags,**  
893 **after 29 months of incubation in the different tree stands of the Breuil-Chenue forest**  
894 **site.** Abbreviations were used as follows: B, Beech; P, Pine and C, Coppice with standards.  
895 For 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 ( $P < 0.05$ ).

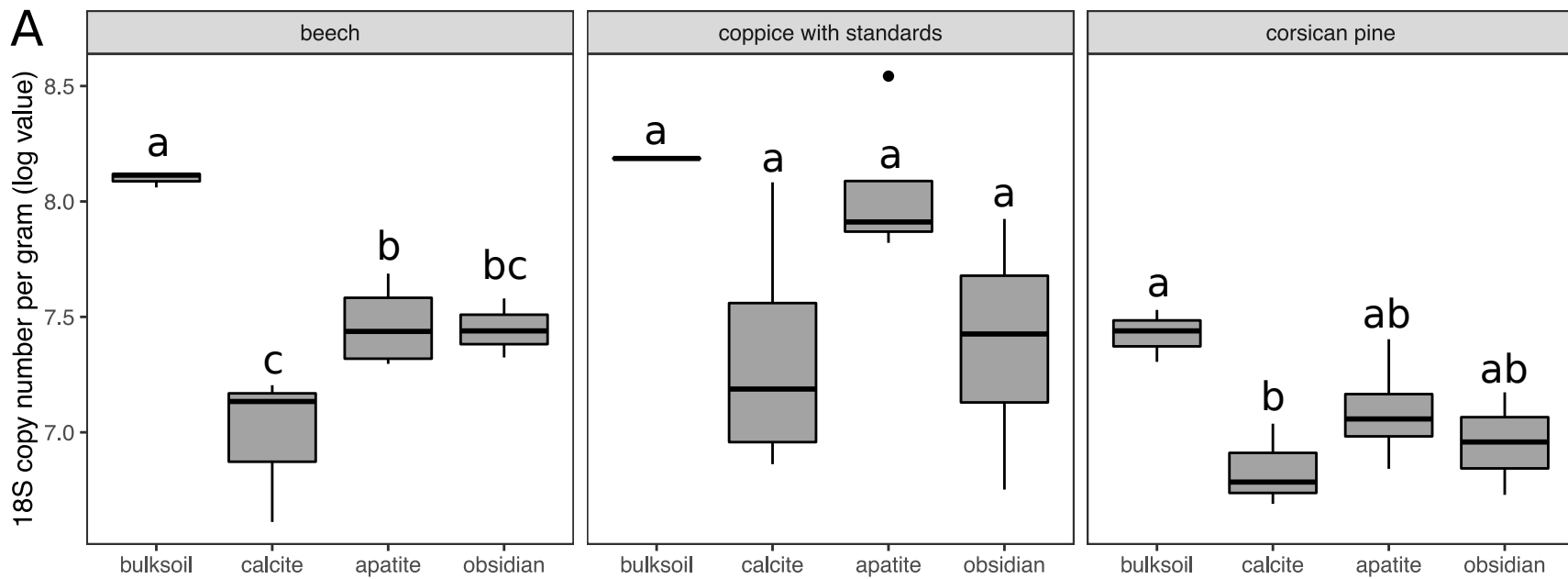
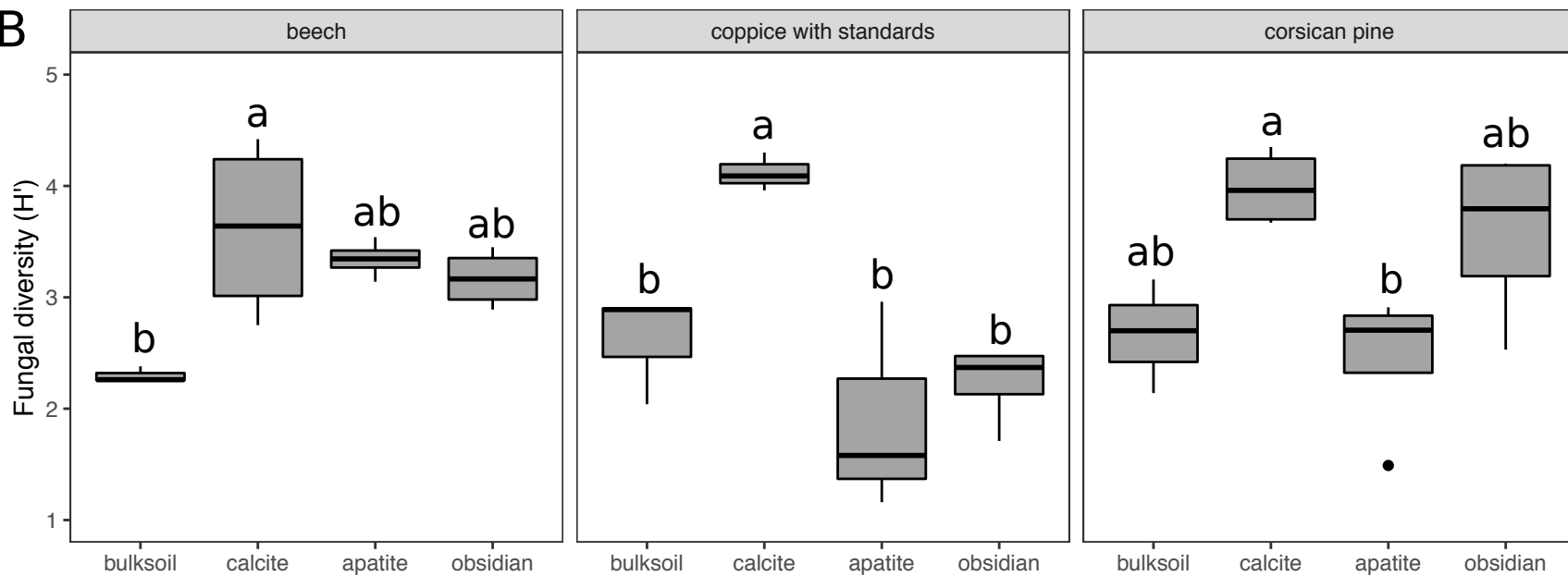
899 **Figure 2. Changes in fungal population size (A) and Shannon diversity (B) between**  
900 **bulk soil and mineral samples below the different tree stands.** Fungal population size was  
901 estimated based on 18SrRNA qPCR and data are presented as log-transformed [18S rRNA  
902 gene copies per 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.

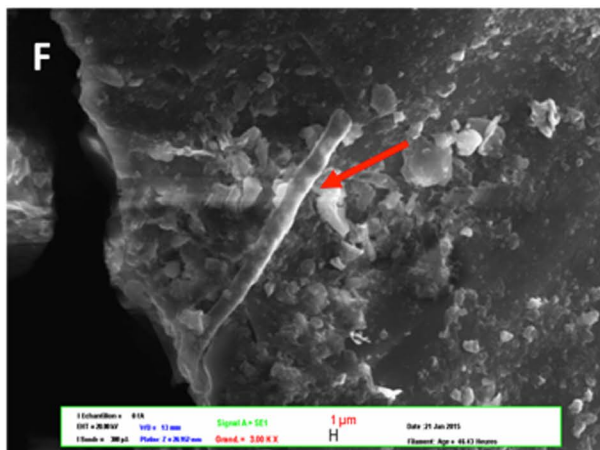
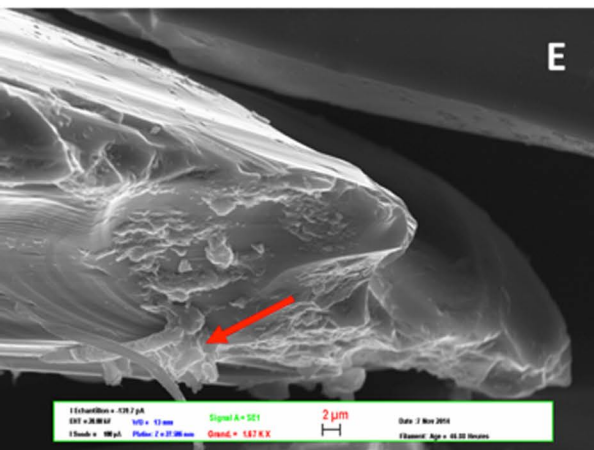
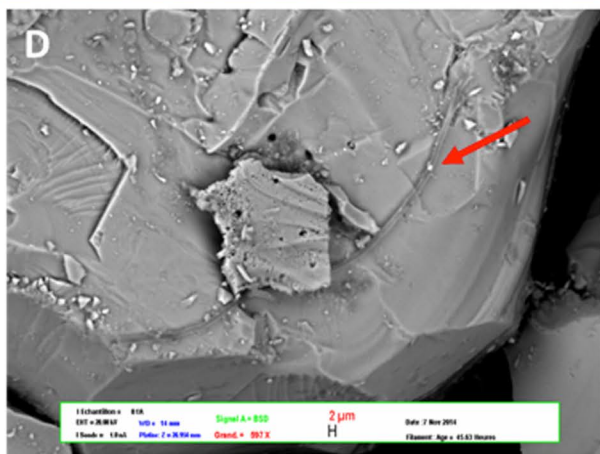
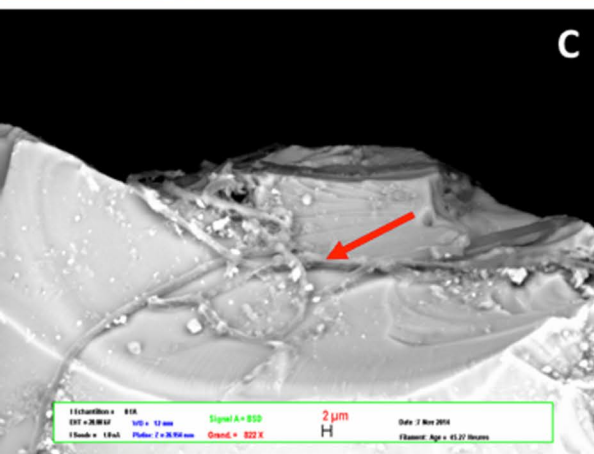
906 **Figure 3: Photographic and microscopy (SEM) images of mineral particles recovered**  
907 **in the mesh bags, after 29 months of incubation in the different tree stands of the Breuil-**  
908 **Chenue forest site.** A) White fungal hyphae colonizing apatite particles under Coppice stand;  
909 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.

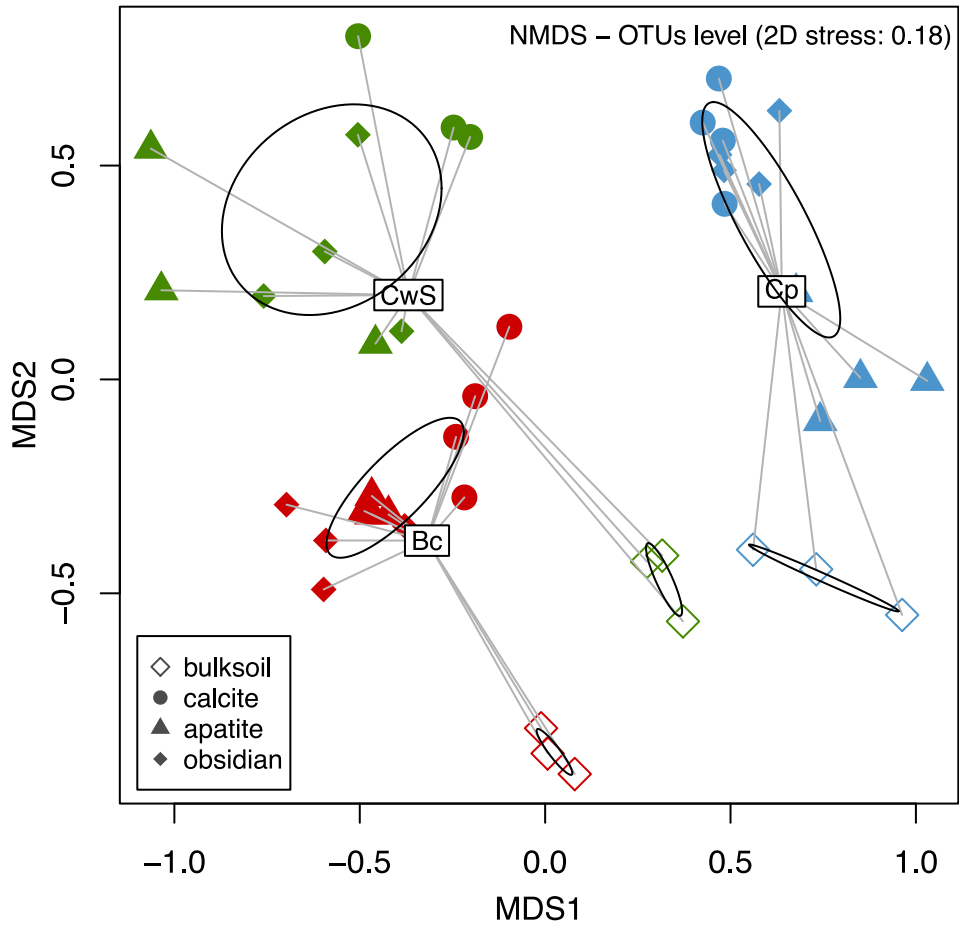
921 **Figure 5: Relative distribution of the major phyla (A) and fungal trophic modes (B)**  
922 **detected in bulk soil and mineral samples below the different tree stands.** The values  
923 presented are average values from the replicates. The category ‘other’ groups minor phyla or  
924 minor trophic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

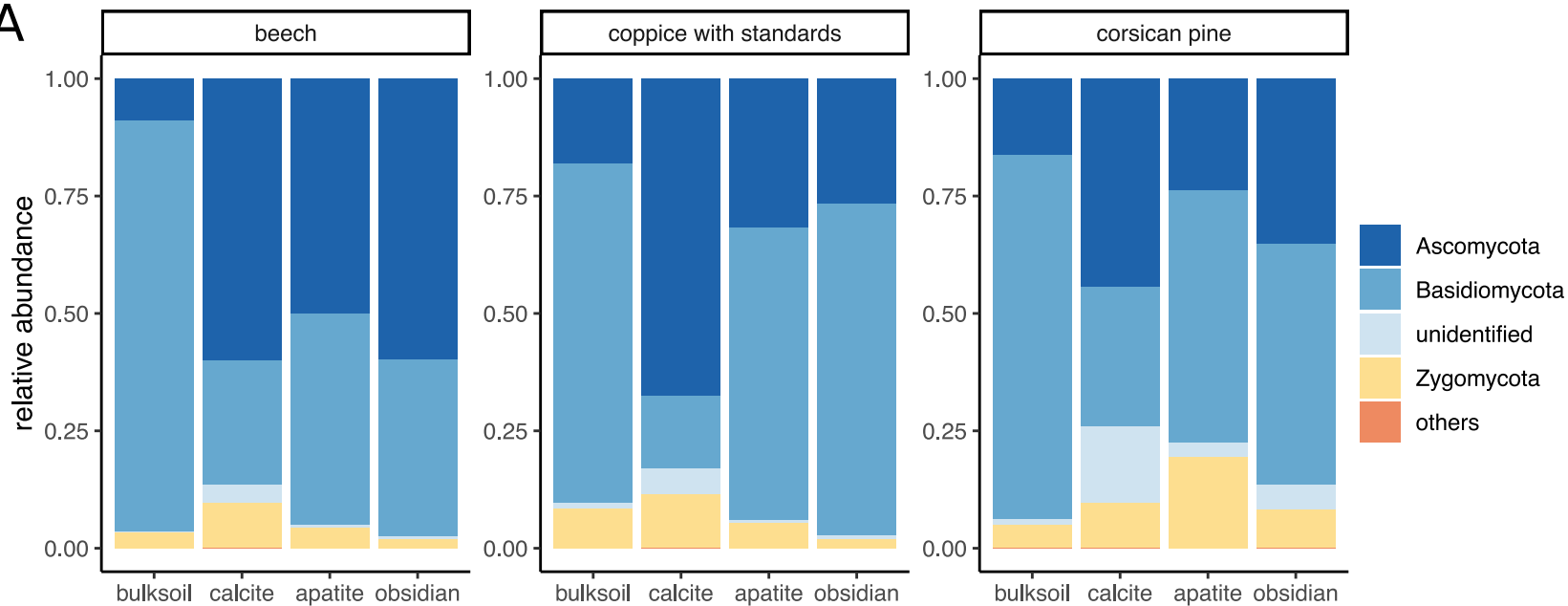
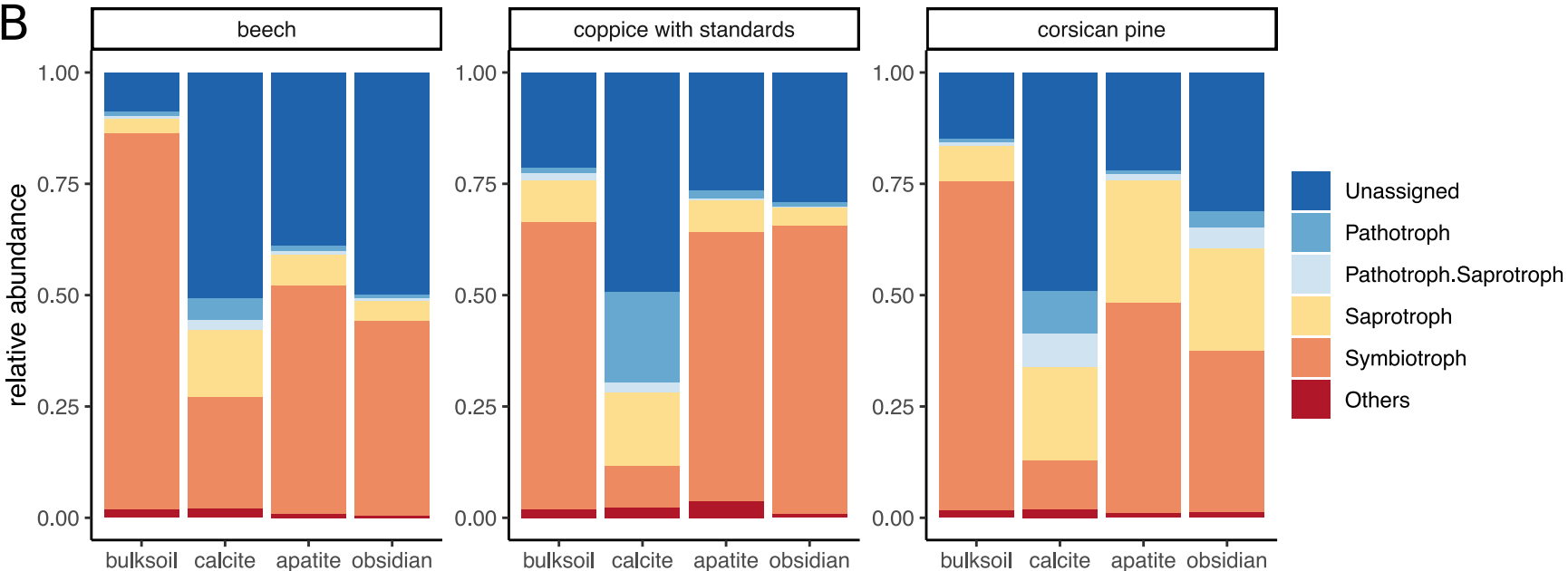


**A****B**







**A****B**

**Table 1: Relative distribution of the main fungal trophic modes detected A) in the bulk soil and mineral compartments below each tree stand or B) in the different mineral types below each tree stand.** The data presented are relative abundances (mean  $\pm$  standard deviation) based on ITS sequence distribution across the samples. Significant differences between bulk soil and mineral samples are indicated are presented by asterisks ('\*' means the p-value < 0.05, '\*\*' means the p-value < 0.01, '\*\*\*' means the p-value < 0.001). The term 'others' refers to the other minor trophic modes proposed by Funguild. Comparison symbols (< and >) were used to describe significant differences between calcite (c), apatite (a) and obsidian (o) samples.

**A)**

Trophic guilds	beech			Coppice with standards			Corsican Pine		
	bulk soil		minerals	bulk soil		minerals	bulk soil		minerals
	mean $\pm$ sd	mean $\pm$ sd	pval	mean $\pm$ sd	mean $\pm$ sd	pval	mean $\pm$ sd	mean $\pm$ sd	pval
Symbiotroph	84.46 $\pm$ 1.68	40.01 $\pm$ 18.22	**	64.57 $\pm$ 12.88	46.86 $\pm$ 32.77	0.391	73.78 $\pm$ 11.39	31.50 $\pm$ 24.23	*
Pathotroph	0.94 $\pm$ 0.24	2.33 $\pm$ 2.34	0.335	1.28 $\pm$ 0.49	7.12 $\pm$ 9.20	0.309	0.94 $\pm$ 0.31	4.75 $\pm$ 6.47	0.339
Saprotroph	3.46 $\pm$ 0.79	8.79 $\pm$ 6.06	0.163	9.51 $\pm$ 5.02	8.59 $\pm$ 6.86	0.835	8.07 $\pm$ 3.78	23.83 $\pm$ 7.82	**
Pathotroph/Saprotroph	0.59 $\pm$ 0.12	1.24 $\pm$ 1.13	0.351	1.43 $\pm$ 0.70	0.93 $\pm$ 1.03	0.454	0.67 $\pm$ 0.24	4.53 $\pm$ 3.40	0.078
Others	1.80 $\pm$ 0.98	1.25 $\pm$ 1.23	0.49	1.88 $\pm$ 0.77	2.24 $\pm$ 2.35	0.801	1.76 $\pm$ 0.57	1.47 $\pm$ 0.67	0.497
Unassigned	8.75 $\pm$ 1.83	46.38 $\pm$ 12.73	***	21.33 $\pm$ 10.49	34.26 $\pm$ 18.82	0.288	14.78 $\pm$ 7.08	33.93 $\pm$ 16.84	0.081

**B)**

	Beech							Coppice with standards							Corsican pine						
	calcite		apatite		obsidian		pval	calcite		apatite		obsidian		pval	calcite		apatite		obsidian		pval
	mean $\pm$ sd	mean $\pm$ sd	mean $\pm$ sd	mean $\pm$ sd	mean $\pm$ sd	mean $\pm$ sd	pval	mean $\pm$ sd	mean $\pm$ sd	mean $\pm$ sd	mean $\pm$ sd	mean $\pm$ sd	pval	mean $\pm$ sd	mean $\pm$ sd	mean $\pm$ sd	mean $\pm$ sd	mean $\pm$ sd	mean $\pm$ sd	pval	
<b>Symbiotroph</b>	25.10 $\pm$ 23.44	51.35 $\pm$ 10.00	43.58 $\pm$ 9.09	0.102	9.37 $\pm$ 5.99	60.49 $\pm$ 34.72	64.76 $\pm$ 19.36	o>c***	10.81 $\pm$ 8.70	47.37 $\pm$ 27.03	36.32 $\pm$ 20.19	0.076									
<b>Pathotroph</b>	4.89 $\pm$ 2.37	1.21 $\pm$ 0.97	0.90 $\pm$ 0.60	c>a=0*	20.33 $\pm$ 2.12	1.96 $\pm$ 1.33	1.09 $\pm$ 0.10	c>a=0**	9.68 $\pm$ 9.90	0.92 $\pm$ 0.40	3.65 $\pm$ 1.38	0.145									
<b>Saprotroph</b>	14.94 $\pm$ 7.29	6.92 $\pm$ 0.53	4.51 $\pm$ 1.36	c>o**	16.38 $\pm$ 1.68	7.08 $\pm$ 8.31	3.88 $\pm$ 0.95	c>o*	21.12 $\pm$ 2.10	27.50 $\pm$ 11.50	22.85 $\pm$ 7.66	0.536									
<b>Pathotroph.Saprotroph</b>	2.37 $\pm$ 1.41	0.73 $\pm$ 0.27	0.62 $\pm$ 0.11	c>o*	2.36 $\pm$ 0.57	0.30 $\pm$ 0.19	0.33 $\pm$ 0.14	c>a=0*	7.48 $\pm$ 1.21	1.38 $\pm$ 1.36	4.71 $\pm$ 3.76	c>a***									
<b>Unassigned</b>	50.53 $\pm$ 17.57	38.87 $\pm$ 10.34	49.75 $\pm$ 8.09	0.386	49.23 $\pm$ 3.25	26.39 $\pm$ 22.01	28.93 $\pm$ 20.20	0.280	48.87 $\pm$ 7.43	21.82 $\pm$ 18.63	31.10 $\pm$ 11.55	0.051									
<b>Others</b>	2.18 $\pm$ 1.92	0.92 $\pm$ 0.09	0.64 $\pm$ 0.32	0.179	2.34 $\pm$ 0.86	3.77 $\pm$ 4.12	1.01 $\pm$ 0.64	0.342	2.03 $\pm$ 0.78	1.00 $\pm$ 0.12	1.36 $\pm$ 0.54	0.071									