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1 **Differential effects of soil trophic networks on microbial decomposition**
2 **activity in mountain ecosystems**

3

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27

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29 appropriate public repository and the data DOI will be included at the end of the article should
30 the manuscript be accepted.

31 **ABSTRACT**

32 Soil trophic networks are key to biogeochemical cycles, in particular decomposition.
33 However, few studies have yet quantified how microbial decomposition activity along
34 environmental gradients is jointly driven by bacteria, fungi, and their respective consumers.
35 Here, we quantified these direct and indirect effects on decomposition and contrasted them
36 between forests and open habitats using multiple elevational gradients in the French Alps.

37 While environmental control on microbial decomposition activity was comparable in
38 the two habitats, the pathways and strengths of biotic predictors strongly differed. The fungal
39 channel composition played a moderate role in forests, while the bacterial channel
40 composition was critical in open habitats. Importantly, we found trophic regulation by
41 consumers to be a key modulator of the direct environmental effects on decomposition in
42 open habitats. These results highlight the need to integrate trophic regulation when predicting
43 future ecosystem functioning.

44 **1. INTRODUCTION**

45 Soil biodiversity underpins a range of ecosystem functions and services crucial to
46 human well-being, including carbon storage and litter decomposition (Bardgett and Putten,
47 2014; Smith et al., 2015). Predicting the consequences of environmental change on soil
48 biodiversity and associated ecosystem functions is therefore crucial (Jansson and Hofmockel,
49 2020; Wall et al., 2010). To do so, we need to better understand the regulatory pathways that
50 occur in soil trophic networks, and their changes along environmental gradients and habitats
51 (Thakur and Geisen, 2019; Wardle et al., 1998).

52 Bacteria and fungi are key decomposers of organic matter (De Boer et al., 2005; Swift
53 et al., 1979). Their activity is context-dependent and varies with climatic conditions, soil
54 physico-chemistry and vegetation structure. In forests, the litter coming from the trees is of
55 rather low quality, which generates rather acidic soils with high organic matter content.
56 Recycling organic matter thus requires the ability to use complex forms of carbon
57 immobilised in recalcitrant litter (Begon et al., 2006). This favours the dominance of many
58 fungal species but also certain bacterial clades that represent the slow cycling of organic
59 matter (López-Mondéjar et al., 2020; Wardle et al., 2004). In contrast, open habitats like
60 grasslands, mineral surfaces and, to a lesser extent, heathlands have a higher availability of
61 labile nutrients and a lower organic matter content (Fierer et al., 2007; Hagedorn et al., 2019).
62 They are therefore more suitable for the dominance of many bacterial species but also certain
63 groups of fungi representing the rapid cycling of organic matter (Ruess and Ferris, 2004;
64 Wardle et al., 2004). Following this observation, many studies have used the fungi to bacteria
65 biomass ratio to quantify the importance of primary decomposers (i.e. bacteria and fungi) in
66 relation to the environment for decomposition (Maassen et al., 2006; Malik et al., 2016). In
67 contrast, far fewer studies have compared the relative importance of bacterial community
68 composition, fungal community composition and the environment in forests and open

69 habitats. Even fewer studies have integrated and quantified the role of higher trophic levels
70 for decomposition (Thakur and Geisen, 2019).

71 Indeed, primary decomposers are part of a complex trophic network, which draws
72 energy from the decomposition of soil organic matter, and which can also influence microbial
73 decomposition activity. This trophic network is structured along two main channels and flows
74 of energy (Moore et al., 2002; Moore and William Hunt, 1988; Wardle et al., 2004). On the
75 one hand, the bacterial channel is based on bacterial communities and the organisms that feed
76 on bacteria, i.e. protists, nematodes and some micro-arthropods, and on the other hand, the
77 fungal channel is based on fungal communities and their consumers, i.e. micro-arthropods
78 (e.g. springtails and mites) and some nematodes and protists (Moore et al., 2002; Thakur and
79 Geisen, 2019; Wardle et al., 2004). Studies of trophic regulation on the biomass of primary
80 decomposers have shown varied results with either important or negligible top-down
81 regulation for both fungi and bacteria (Goncharov and Tiunov, 2014; Mikola and Setälä,
82 1998; Wardle et al., 1998). Moreover, the direct effects of this trophic regulation on the
83 composition and diversity of primary decomposer communities are poorly understood, as are
84 the indirect effects on microbial decomposition activity and the differences between channels
85 (Thakur and Geisen, 2019). The composition of consumer communities can be expected to
86 influence the composition of primary decomposer communities, for example when consumers
87 preferentially feed on certain groups of bacteria or fungi (A'Bear et al., 2014; reported for
88 nematodes, springtails and mites feeding on bacteria and fungi, Ruess et al., 2000; Schneider
89 and Maraun, 2005). Preferential feeding has the effect of relieving consumer pressure on the
90 non-preferred taxa of primary decomposers, which indirectly influences microbial
91 decomposition activity (Crowther et al., 2012; Thakur and Geisen, 2019; Trap et al., 2016).
92 The effect of indirect regulation by the consumers of bacteria and fungi may even be stronger
93 than their direct effects on ecosystem functions (Hättenschwiler et al., 2005). However, so far,

94 we still know little about how these trophic regulations influence microbial decomposition
95 activity, and even less about how this influence varies between habitats dominated by
96 different channels, such as forests or open habitats.

97 Finally, the existence of this trophic regulation could modulate the direct effects of the
98 environment on microbial decomposition activity. Indeed, since consumers are also structured
99 by the environment, their response could feed through to the composition of primary
100 producers (Xiong et al., 2021). So far, these indirect environmental effects have never been
101 quantified along varying environmental conditions and habitat types.

102

103 Here, we quantified the direct and indirect effects of the environment, primary
104 decomposers, and their respective consumers on decomposition along elevational gradients in
105 both forests and open habitats. We used extracellular enzymes to estimate microbial
106 decomposition activity and environmental DNA (*eDNA*) extracted from the same soil samples
107 to describe local compositions in fungi and bacteria, and their respective consumers among
108 protists, nematodes and arthropods. We then built structural equation models (*SEMs*) to
109 answer the following questions:

110

111 1- What are the main direct biotic and abiotic drivers of microbial decomposition activity and
112 how does their importance vary between habitats?

113 2- Is there a trophic regulation of microbial decomposition activity via the composition of
114 fungal and/or bacterial channels in both habitats?

115 3- Does the composition of the soil trophic network modulate the direct effect of the
116 environment on microbial decomposition activity?

117 **2. MATERIAL & METHODS**

118 **2.1. Study sites: Alpine elevation gradients characterised by two habitats**

119 We studied the composition of soil communities in the French Alps along 18
120 elevational gradients of the ORCHAMP observatory (www.orchamp.osug.fr, Appendix S1).
121 The gradients were continuous from about 900 m to 3000 m, had a homogeneous exposure
122 and slope, and were representative of the environmental and topographic variability of the
123 French Alps. Between 2016 and 2018, at least five sampling plots (30*30 m, see Fig. S1 for
124 details) were placed along each gradient, with an altitude difference of 200 m, resulting in a
125 total of 37 forest sites and 64 open habitat sites (such as meadows or heaths, see Fig. S2 for
126 details).

127

128 **2.2. Climatic data**

129 In mountain ecosystems, the presence of snow determines the start and length of the
130 vegetation growing season. During this growing season, heat accumulation (i.e. energy
131 available for growth) and soil exposure to frost (i.e. physiological limit of most metabolic
132 processes) shape the composition of plant and microbial communities (Choler, 2005; Edwards
133 et al., 2007; Zinger et al., 2009). In each plot, we calculated growing degree days (GDD) to
134 characterise heat accumulation, and freezing degree days (FDD) to characterise the intensity
135 of freezing events during the growing season (Fig. S3). They are the sum of average daily
136 degrees above (GDD) and below (FDD) zero accumulated over the growing season each year,
137 averaged over the period 1988-2018, and modelled in the first soil horizon (up to 10 cm
138 depth, see Martinez-Almoyna et al. (2020), Table 1 for details). As FDD is a sum of negative
139 degrees, the lowest FDD values correspond to the plots with the most frequent and intense
140 frost stress events. GDD and FDD were calculated from the SAFRAN- SURFEX/ISBA-

141 Crocus-MEPRA re-analysis (Durand et al., 2009), a model that deals with weather and snow
142 conditions in mountainous regions based on large-scale topographic features.

143

144 **2.3. Sampling, physicochemical properties and total potential extracellular enzyme** 145 **activity of the soil**

146 In each plot, we sampled soil in three 2×2 m subplots with homogeneous vegetation,
147 separated by a distance of 2 to 12 m (Fig. S1), taking particular care to avoid sample
148 contamination. In each sub-plot, we took about ten 5-cm-diameter cores of superficial soil (ca.
149 1-8 cm deep) and deeper soil (ca. 8-16 cm), in order to properly describe the first soil
150 horizons. The superficial soil cores were pooled and homogenised separately from the deeper
151 soil cores, resulting in two composite soil samples per subplot. In total, we collected 606 soil
152 samples over the three years, 222 in forest and 384 in open habitats.

153 We immediately recovered 15 g per soil sample for subsequent eDNA extractions, and sieved
154 the remaining parts to 5.6 mm. Then, we froze 2.75 g of the sieved sample for subsequent
155 analyses of extracellular enzyme activities, 5 g to quantify water content, and sieved the
156 remainder to 2 mm for analyses of the soil physico-chemistry (soil pH, soil organic matter
157 (SOM) and soil C/N as described in Martinez-Almoyna et al. (2020), Appendix S2).

158 We estimated the potential extracellular enzyme activity of six extracellular enzymes involved
159 in the decomposition of C-rich substrates (α -Glucosidase (AG, EC 3.2.1.20), β -1,4-
160 Glucosidase (BG, EC 3.2.1.21), β -D-Cellobiosidase (CB, EC 3.2.1.91) and β -Xylosidase
161 (XYL, EC 3.2.1.37)) and N-rich substrates (β -1,4-N-acetylglucosaminidase (NAG, EC
162 3.2.1.30) and leucine aminopeptidase (LAP, EC 3.4.11.1)) using standardised fluorimetric
163 techniques (Bell et al., 2013; see also Martinez-Almoyna et al., 2020 for more experimental
164 details). We calculated the total potential extracellular enzyme activity (*total EAA*) as the sum
165 of the raw potential activity values of the six extracellular enzymes, which had comparable

166 levels of potential activity (Fig. S4). We then standardized total EEA by soil organic matter
167 (*SOM*) to capture difference of *SOM* turnover between sites (German et al. 2011). *SOM*-
168 standardisation also has the advantage of limiting confounding effects due to the correlation
169 between total EEA and microbial biomass (Crowther et al., 2019; Piton et al., 2020).
170 Hereafter, we refer to this variable as *microbial decomposition activity*, as extracellular
171 enzymes are the functional tools by which microbes break down organic matter (Burns 2013).
172 Specifically, we address the enzymatic potential for depolymerization and recycling of
173 specific C- and N-rich substrates that dominate plant and microbial necromass (e.g., cellulose,
174 hemicellulose, proteins, chitin and peptidoglycan, German et al. 2011). Note that
175 investigating the whole decomposition process would require considering the action of other
176 drivers (e.g. mechanical action of other soil species, action of other enzymes), and is not
177 directly the subject of this article.

178

179 **2.4. Soil eDNA extraction, amplification, sequencing and curation**

180 From the 15 g per soil sample, we conducted the extraction of soil eDNA immediately
181 in the field following the protocol of Taberlet *et al.* (2012). This method was used due to its
182 easiness of implementation for large-scale samplings, and also because it produces ecological
183 patterns that are similar to those obtained with total DNA, although it may under-sample rare
184 taxa (Zinger et al., 2016). For eDNA amplification, we targeted Eukaryotes, Fungi and
185 Bacteria using the DNA markers Euka02 (18S rRNA), Fung02 (ITS) and Bact01 (16S rRNA)
186 described in Taberlet et al. (2018). We added unique eight-base long tags to the 5' end of each
187 primer in order to be able to find the original sample of each sequencing read after
188 sequencing. PCR reactions were conducted in quadruplicates for each DNA extract and
189 control. Finally, the PCR samples were pooled and purified prior to sequencing. We built one
190 library per marker in 2016 and 2018 and two libraries per marker in 2017, using the

191 METAFAST protocol. Sequencing was performed with pair-end sequencing technology on
192 the Illumina platform at FASTERIS, Geneva, Switzerland (2*125, HiSeq 2000, for Euka02, and
193 2*250 miseq, for Bact01 and Fung02).

194 We curated the sequencing reads using the obitools package (Boyer et al., 2016) and
195 the R metabar package (Zinger et al., 2021, Fig. S5). For each sequencing library, paired-end
196 reads were assembled, assigned to their original samples and markers, and dereplicated with
197 the OBITools package. We then removed PCR errors and grouped the remaining sequences
198 into molecular operational taxonomic units (MOTUs). MOTUs were assigned a taxonomy
199 using different databases depending on the marker. Cross-samples, reagents, sequencing
200 contaminants, dysfunctional PCRs and other artefacts were eliminated using metabar using
201 conservative quality criteria (Zinger et al., 2021). Next, we excluded samples for which only
202 two or fewer PCR replicates remained. 562 samples remained after this curation procedure, of
203 which 212 were from forest soils and 350 from open habitats. We finally performed a final
204 clustering step to unify the MOTUs across the libraries for each marker. For more details, see
205 Appendix S3 (1, Fig. S5 and Tables S1, S2)

206

207 **2.5. Trophic classes and groups of MOTUs**

208 In order to assess the importance of trophic regulation, we only considered organisms
209 directly involved in decomposition (i.e. fungi and bacteria) and their consumers. Finally, we
210 grouped them following their known role in the soil trophic network (i.e. according to their
211 resources and predators, Elton, 1927; Gauzens et al., 2015) and according to their function in
212 the ecosystem. MOTUs were therefore aggregated at two levels: first, at the level of their
213 *trophic class* (e.g. fungi), and second, at the level of a subgroup of this trophic class, which
214 we call a *trophic group* for simplicity (e.g. saprophytic fungi).

215

216 2.5.1. *At trophic class level:*

217 We separated bacterial MOTUs and fungal MOTUs into two different trophic classes,
218 which respectively form the basis of bacterial and fungal channels (Wardle et al., 2004). We
219 referred to the trophic classes of bacteria and fungi together as *primary decomposers*.
220 We then separated MOTUs feeding on bacteria from those feeding on fungi in two different
221 trophic classes, using literature, expert knowledge and databases (Fig. S6). Among the
222 bacterivores, we found mainly protists and nematodes, while among the fungivores, we found
223 mainly mites and springtails. We removed the MOTUs referenced as feeding on both bacteria
224 and fungi as they were very rare (~ 15 MOTUs and less 1 % of reads in forests and open
225 habitats). This classification represents the knowledge we have been able to extract from the
226 current literature and databases. We are aware that it may only represent the preferred diet
227 (and not obligate, Geisen, 2016). Details on the number of MOTUs within each trophic class
228 are in Appendix S3 (Table S3).

229

230 2.5.2. *At the trophic group level:*

231 We assigned MOTUs within each trophic class to more resolved trophic groups, to
232 facilitate interpretation of compositional variation within trophic classes. For fungi, we used
233 FUNGuild (Nguyen et al., 2016), FungalTraits (Pölme et al., 2020) and Tedersoo *et al.* (2014)
234 to divide the MOTUs into eleven trophic groups (Table S3). For bacteria, we used
235 FAPROTAX combined with expert knowledge to derive six trophic groups (Louca et al.,
236 2016; Sansupa et al., 2021, Table S3). Then, for the two consumer trophic classes,
237 bacterivores and fungivores, we used taxonomy to assign MOTUs to more resolved trophic
238 groups, as closely related taxa exhibit similar functions (Potapov et al., 2016; Schaefer and
239 Caruso, 2019; Wiens et al., 2010). Details on the number of MOTUs within each trophic
240 group are in Appendix S3 (Table S3).

241

242 **2.6. Statistical analyses**

243 To quantify the direct and indirect effects of the environment and the compositions of
244 the four trophic classes on microbial decomposition activity, we first constructed variables
245 representing the composition of each trophic class, and integrated these variables into a SEM.
246 This was done for both forest and open habitats independently to highlight differences in
247 decomposition regulation in the two habitats.

248

249 2.6.1. First step: Composition of each trophic class

250 *2.6.1.1. Variables construction*

251 To summarise the main variation of composition of a trophic class between samples of
252 a given habitat, we performed a correspondence analysis (CA) for each trophic class for each
253 habitat, using the *dudi.coa* function of the *ade4* package in R (R version 3.6.1., Core
254 Development Team, 2020; Dray and Dufour, 2007), and we kept the first axis. Two samples
255 with similar coordinates on the first axis had similar compositions of the trophic class
256 considered. To describe the composition of a trophic class in a sample, we therefore used its
257 coordinate on the first axis of the corresponding CA. CA is based on the chi2 distance, which
258 is hardly sensitive to sampling depth, allowing it to be performed directly on the numbers of
259 reads (Appendix S4, Figs. S7, S8).

260

261 *2.6.1.2. Interpretation of the compositional CA axes*

262 For each trophic class, we then used the more resolved information of the trophic
263 groups to facilitate the interpretation, the aim being to visualise which compositional
264 variations structure the position of the samples on the first CA axes. First, for each sample, we
265 calculated the relative abundance of each trophic group within each trophic class as the sum

266 of the number of reads of all MOTUs belonging to that trophic group standardised by the total
267 sum of the number of reads of all MOTUs in the same trophic class. We then fitted
268 generalised linear models to visualise the relative abundance of each trophic group as a
269 function of the sample coordinates on the first CA axis (Appendix S5, Figs. S9, S10). Second,
270 for each trophic class, we also used the variations in trophic diversity to interpret the
271 compositional variations represented by the first CA axes. To do this, we calculated the
272 trophic diversity of each trophic class in each sample, via the Shannon index applied to the
273 relative abundances of trophic groups (Figs. 1, 2).

274

275 2.6.2. Second step: Structural Equation Models

276 2.6.2.1. *Construction of the SEMs and evaluation of path coefficients*

277 For each habitat, we built a SEM to explain microbial decomposition activity. In this
278 SEM, we used the first CA axes to describe the compositions of the different trophic classes
279 and tested the existence of a trophic regulation of decomposition, through cascading links
280 between the compositions of the different trophic classes (i.e. representing their trophic
281 interactions). The SEM also allowed us to consider the direct effects of the environment on
282 the composition of the trophic classes and on decomposition (see Appendix S6 for the *a priori*
283 model).

284 We first tested the structure of the *a priori* model using the *sem* function in R (Lefcheck,
285 2016). This function locally estimates the path coefficients and then assesses the fit between
286 the *a priori* model and the data by testing the conditional independence of variables that are
287 not linked by a path (Shipley, 2000). Then, where necessary, we added some of the missing
288 paths based on their ecological relevance to our model (Grace et al., 2010). Finally, we
289 optimised the model structure through a stepwise procedure using the BIC criterium (Hertzog,
290 2018).

291

292 *2.6.2.2. Interpretation of the SEM in each habitat*

293 For interpretations, we used the standardised coefficients extracted from the most
294 parsimonious model (Grace et al., 2010). We also used the information on relative
295 abundances of trophic groups and trophic diversity within each trophic class to better
296 understand the direction of the effects of the composition of each trophic class on microbial
297 decomposition activity.

298 **3. RESULTS**

299 **3.1. The direct effects of abiotic and biotic predictors on microbial decomposition**
300 **activity varied between habitats**

301 The two SEMs for forest and open habitats explained a very similar percentage of the
302 total variation in microbial decomposition activity ($R^2=0.16$). Interestingly, although close in
303 terms of explained variance, the pathway strengths differed strongly between forests and open
304 habitats (Figs. 1 & 2). In forests, microbial decomposition activity was strongly influenced by
305 a direct and negative effect of GDD and FDD, to a lesser extent by a direct and negative effect
306 of soil C-N ratio, and less, but still significantly, by the composition of the fungal class (Fig.
307 1). In contrast, for open habitats, the composition of the trophic class of bacteria was the main
308 factor controlling microbial decomposition activity, while climate and soil played a similar
309 direct role as in forests, but to a lesser extent (Fig. 2).

310

311 **3.2. Different roles of biotic channels in decomposition activity in the two habitats**

312 To quantify the overall influence of fungal vs. bacterial channels, we extracted from
313 the SEMs the standardised direct and indirect effects through both the bacterial channel (i.e.,
314 bacterivores and bacteria), and the fungal channel (i.e., fungivores and fungi, Fig. 3).
315 Contrasting forests and open habitats, we found that the biotic effect on microbial
316 decomposition activity was due to different channels. In forests, it was the composition of the
317 fungi channel that influenced microbial decomposition activity, with a weak influence of
318 primary decomposers (i.e., fungi) and no trophic regulation by fungivores. In contrast, in open
319 habitats, the bacterial channel strongly influenced microbial decomposition activity, with a
320 strong effect of the compositions of the trophic classes of bacteria and bacterivores, but also
321 through strong trophic regulation, i.e. a strong indirect effect of bacterivores (Fig. 3).

322

323 **3.3. The composition of the trophic classes of primary decomposers and trophic**
324 **regulation modulate the effects of the environment on microbial decomposition**
325 **activity.**

326 Based on SEMs, we calculated the standardised indirect effects of the environment on
327 microbial decomposition activity through its direct effect on the composition of primary
328 decomposers, but also through its direct effect on the composition of consumers, which then
329 cascades indirectly on primary decomposers (i.e. trophic regulation, (Fig. 4)). The indirect
330 influence of the environment on microbial decomposition activity was much lower in forests
331 than in open habitats. This highlighted that the modulation of environmental effects by the
332 soil trophic network depended on the habitat type (Figs. 3, 4).

333 In forests, we found a weak indirect effect of the environment on decomposition
334 through its effect on the composition of primary decomposers. Acidic, rather cold soils with
335 poor organic matter slightly enhanced the presence of different groups of saprophytic fungi
336 (i.e. wood, soil and litter saprotrophs) compared to ectomycorrhizal fungi (*ECM*) in the fungal
337 composition (Fig. 1 (D)), which slightly increased the microbial decomposition activity. On
338 the other hand, the indirect effect of the environment via its effect on the composition of
339 consumers was minor in forests (Fig. 4), although the environment explained the composition
340 of consumers well ($R^2_{\text{bacterivores}} = 0.79$, $R^2_{\text{fungivores}} = 0.26$). The composition of fungivores was
341 mainly determined by the quality of soil organic matter, with a dominance of mites on low
342 fertility soils (i.e. high C/N ratio) and a co-dominance of mites and springtails on soils where
343 organic matter was of better quality (Figs. 1 (B), S9 (B)). However, fungivore composition
344 was not directly related to fungi composition, which negated the indirect effect of the
345 environment via fungivores. In addition, soil pH was the main predictor of the composition of
346 bacterivores, with Rhizaria-dominated communities occurring in acidic soils, and
347 communities with a co-dominance of Rhizaria and Ciliophora found in less acidic conditions

348 (Figs. 1 (A), S9 (A)). The indirect effect of the environment on microbial decomposition
349 activity in forests was only modulated via bacterivores and their weak effect on fungal
350 composition.

351 In open habitats, however, we found a strong indirect effect of the environment, both
352 through primary decomposers and their consumers (Fig. 4). Acidic soils favoured the
353 dominance of saprophytic bacteria, which clearly increased microbial decomposition activity
354 (Figs. 2 (C), 4). In contrast, the strong effect of pH on fungal composition resulted in a
355 dominance of soil saprophytes on acidic soils and arbuscular mycorrhizal fungi (*AMF*) under
356 less acidic conditions, but did not affect decomposition (Fig. 2 (D)). The indirect effect of the
357 environment via the consumers was explained on the one hand by the strong influence of
358 bacterivores on microbial decomposition activity and on the other hand by trophic regulation.
359 As in forests, the environment explained the composition of the consumer classes fairly well
360 ($R^2_{\text{bacterivores}} = 0.64$, $R^2_{\text{fungivores}} = 0.14$). In particular, pH was the main predictor of bacterivore
361 composition, leading to the same compositional trends as in forests (Figs. 2 (A), S10 (A)).
362 This effect cascaded to microbial decomposition activity, firstly because bacterivore
363 communities with a greater trophic diversity were themselves strongly associated with higher
364 microbial decomposition activity. On the other hand, the indirect effect of pH was moderated
365 by the effect of trophic regulation (Figs. 3, 4). In acidic soils, Rhizaria-dominated bacterivore
366 communities were associated with communities of bacteria dominated by saprophytic bacteria
367 and with increased microbial decomposition activity. In less acidic soils, where bacterivore
368 communities were more trophically diverse, bacterial communities were also characterised by
369 greater trophic diversity and associated with decreased decomposition activity (Figs. 2 (A, C),
370 S10 (A, C), 4).

371 **4. DISCUSSION**

372 While the importance of soil decomposers in ecosystem functioning is increasingly
373 acknowledged, the regulating effects of other trophic soil classes on microbial decomposition
374 remain poorly understood, as does their dependence on habitat (Thakur and Geisen, 2019).
375 Here, we compared the role of four environmental variables and of the consumers of primary
376 decomposers in structuring the composition and activity of primary decomposers in two
377 different habitats. In respect to our three initial questions, we found that (i) the environment,
378 in particular climate, have a stronger effect on microbial decomposition activity in forests
379 than in open habitats, where the biotic effect is more important. (ii) In forests, the composition
380 of the soil network, and primarily of fungal communities, was moderately linked to microbial
381 decomposition activity, whereas in open habitats the effects were much stronger, driven by
382 bacteria, but also strongly influenced by bacterivores. (iii) The environment influences the
383 composition of the different trophic classes, which indirectly influences the microbial
384 decomposition activity through trophic interactions.

385

386 Climate, much more than soil physico-chemistry, was an important direct driver of
387 microbial decomposition activity in both habitats. The negative relationships between GDD,
388 FDD and microbial decomposition activity showed that the investment of microbes in
389 extracellular enzyme production was favoured in difficult climatic conditions during the
390 vegetation season, i.e. low heat energy input (i.e. low GDD) and frequent and/or intense frost
391 events (i.e. low FDD). Lower (or more frequently negative) average temperatures can indeed
392 reduce (or even stop) extracellular enzyme activity *in situ* (Steinweg et al., 2012), thus
393 increasing the amount of extracellular enzymes needed to capture the same amount of
394 resource (Allison et al., 2010).

395 This study corroborates the hypotheses of Wardle et al. (2004) on a large scale, with a
396 complete shift from a moderate direct effect of the composition of fungi in forests to a strong
397 direct effect of the composition of bacteria in open habitats. In forests, our results are
398 supported by the work of Schneider et al. (2012, 2010), who showed that fungi produce most
399 extracellular enzymes in forest soils. Indeed, some trophic groups of fungi are key to forest
400 decomposition, because they open access to organic compounds, such as cellulose, blocked in
401 recalcitrant plant debris (e.g. wood and litter saprotrophs, De Boer et al. 2005). This could
402 explain why the increase in the relative abundance of saprophytic fungal groups compared to
403 ECM is associated with an increase in microbial decomposition activity in our study (Fig. 1).
404 In contrast, open habitats are characterised by plants with fewer recalcitrant compounds,
405 generally associated with less acidic soils (Appendix S2, Fig. S3). This could relieve bacteria
406 from the aforementioned constraints and a pH-related environmental stress, and make them
407 more competitive and active in open habitats overall (Rousk et al., 2010b). The increase in
408 relative abundance of parasitic and autotrophic bacterial groups (Figs. 1 (C), S9 (C)) is likely
409 driven by the presence of a mineral nutrient availability gradient in the mountainous open
410 habitats of our study (Fierer et al., 2007; Guo et al., 2015), and could explain the association
411 of the composition of bacteria with a decrease in microbial decomposition activity.

412 We also demonstrated the importance of a top-down regulation of the composition of
413 the consumer trophic classes on microbial decomposition activity. In particular, in line with
414 Xiong *et al.* (2021), the link between the composition of bacterivores and bacteria was central
415 in our two habitats (Figs. 1, 2). This can arise from the high degree of specificity of
416 bacterivores, which had already been observed for bacterivorous protists, dominant in our
417 study (Adl and Gupta, 2006; Trap et al., 2016). More generally, it is known that the presence
418 of specific groups of protists and nematodes influences the composition of primary
419 decomposer classes (Gao et al., 2019; Geisen et al., 2018; Griffiths et al., 1999). Furthermore,

420 we found a fairly strong link between the composition of bacterivores and fungi in forest
421 habitats, possibly due to the quite generalist feeding behaviour of some groups of protists
422 (Geisen, 2016). In the forests of our study, for example, Rhizaria-dominated bacterivore
423 communities seemed to favour the presence of saprophytic fungi over ECMs (Fig. 1). In
424 contrast, the effect of fungivore community composition on fungal community composition
425 and function was less clear in both habitats (Figs. 1, 2, 3). This lack of signal could be caused
426 by a biased representation of specific animal organisms in eDNA data, because it includes not
427 only signal from current communities, but also to a lesser extent, from those from the recent
428 past. For example, fungivores with stable bodies (e.g. mites) might be decomposed more
429 slowly and thus be slightly over-represented in fungivore communities (Table S3). However,
430 the literature also reports more contrasting effects of fungivores, suggesting that fungivores
431 are less specific (Crowther et al., 2012; Hanlon and Anderson, 1979; Maraun et al., 2003).
432 The weak links we found between the compositions of fungivores and fungi could also be
433 explained by the length and spatial extent of mycelia, which makes the effect of grazing by
434 fungivores less drastic. Up to a certain grazing pressure, fungivores do not suppress the whole
435 individual, which makes the trophic interaction less likely to influence the composition of the
436 fungal community (Crowther et al., 2012; Hanlon and Anderson, 1979).

437 Moreover, we provided new information on environmental drivers of the composition
438 of multi-trophic soil assemblages, and how environmentally induced compositional changes
439 can affect microbial decomposition activity. Soil physico-chemical properties had a stronger
440 effect on the composition of four soil trophic classes than climatic variables. In particular, soil
441 pH was a key predictor of the composition of bacteria, fungi and bacterivores (Figs. 1, 2).
442 This result is known for bacteria and fungi (Donhauser and Frey, 2018; Fierer and Jackson,
443 2006; Griffiths et al., 2011; Looby and Martin, 2020; Rousk et al., 2010a; Tedersoo et al.,
444 2014), but is more surprising for bacterivores, which are mainly protists in our study. Indeed,

445 studies on protist biogeography suggest that protist community composition is mainly
446 determined by climatic and topographic factors (Bates et al., 2013; Seppey et al., 2020).
447 However, most of the bacterivorous protists in our study belong to the Ciliophora and
448 Rhizaria clades that have recently been shown to be strongly affected by soil pH (Oliverio et
449 al., 2020).

450 Finally, we showed that the environment has a top-down influence on trophic network
451 composition that cascades down to microbial decomposition activity. This effect was rather
452 moderate within both habitats (Fig. 4), but our study suggests that larger long-term climate
453 changes, i.e. causing a habitat switch, would induce a radical change in decomposition
454 regulation. Moreover, our results imply that more abrupt compositional changes in the trophic
455 network, especially in consumer classes that are particularly sensitive to anthropogenic effects
456 (Xiong et al., 2021), could induce greater indirect environmental effects (O'Neill, 1994;
457 Wardle et al., 1998).

458 **5. CONCLUSIONS**

459 Our comparison of the regulation of microbial decomposition activity in forests vs. open
460 habitats demonstrates the complexity of direct and indirect environmental effects on an
461 ecosystem function. By hierarchically integrating the environment and soil trophic network,
462 we showed how top-down regulation through the soil trophic network can affect the outcome
463 of decomposition, and modulate the direct effects of the environment. Experimental studies
464 testing the trophic pathways identified here will help further understanding the biological
465 mechanisms involved in our observations. Moreover, predictive models are needed to predict
466 the cascading effects of future environmental and biodiversity changes on ecosystem
467 functioning and multifunctionality.

468 **Author statement:** CMA, TM and WT conceptualized the overall study and methodology.
469 WT, AS, CMA, TM and the ORCHAMP Consortium collected the soil data. LG, GP and AS
470 carried out the lab work for eDNA extractions, PCRs and measures of extracellular enzyme
471 activities and soil properties. CL and CMA run the bioinformatic pipelines. LZ helped with
472 the trophic assignment and bioinformatic pipelines. CMA run all statistical analyses. CMA,
473 TM and WT led the interpretation of the results. CMA drafted the initial draft of the paper
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761 **FIGURE CAPTIONS**

762 **Figure 1:** SEM of the effects of environment and composition of the soil trophic network on
763 microbial decomposition activity in forests. Arrow sizes are proportional to the associated
764 path coefficients. Paths with double arrows represent correlations. The external panels
765 represent the trophic diversity of each trophic class (grey points, left-hand y-axis) and the
766 relative proportion of each trophic group within each trophic class (colored curves, right-hand
767 y-axis) as a function of the position of the samples along the first axis of the CA (x-axis). We
768 represented only the most abundant trophic groups, and more detailed plots are provided in
769 Fig. S9. For example, for Bacteria-consumers, only the variations of Rh. (Rhizaria), Ci.
770 (Ciliophora) and Ne. (Nematoda) are represented. Other abbreviations are ii) Ac. (Acari), Co.
771 (Collembola), iii) Sa. B. (saprophytic bacteria), Che.B. (chemolitoautotrophic bacteria), Zo.
772 B. (zooparasitic bacteria), Ph.B. (phytoparasitic bacteria), Pho. B. (photoautotrophic bacteria),
773 iv) S.Sa (soil saprotrophic fungi), L.Sa (litter saprotrophic fungi), W.Sa (wood saprotrophic
774 fungi), ECM (ectomycorrhizal fungi), AMF (arbuscular mycorrhiza fungi).

775

776 **Figure 2:** SEM of the effects of environment and composition of the soil trophic network on
777 microbial decomposition activity in open-habitats. Arrow sizes are proportional to the
778 associated path coefficients. Paths with double arrows represent correlations. The external
779 panels represent the trophic diversity of each trophic class (grey points, left-hand y-axis) and
780 the relative proportion of each trophic group within each trophic class (colored curves, right-
781 hand y-axis) as a function of the position of the samples along the first axis of the CA (x-
782 axis). We represented only the most abundant trophic groups, and more detailed plots are
783 provided in Fig. S10. For example, for Bacteria-consumers, only the variations of Rh.
784 (Rhizaria), Ci. (Ciliophora) and Ne. (Nematoda) are represented. Other abbreviations are ii)
785 Ac. (Acari), Co. (Collembola), iii) Sa. B. (saprophytic bacteria), Che.B. (chemolitoautotrophic

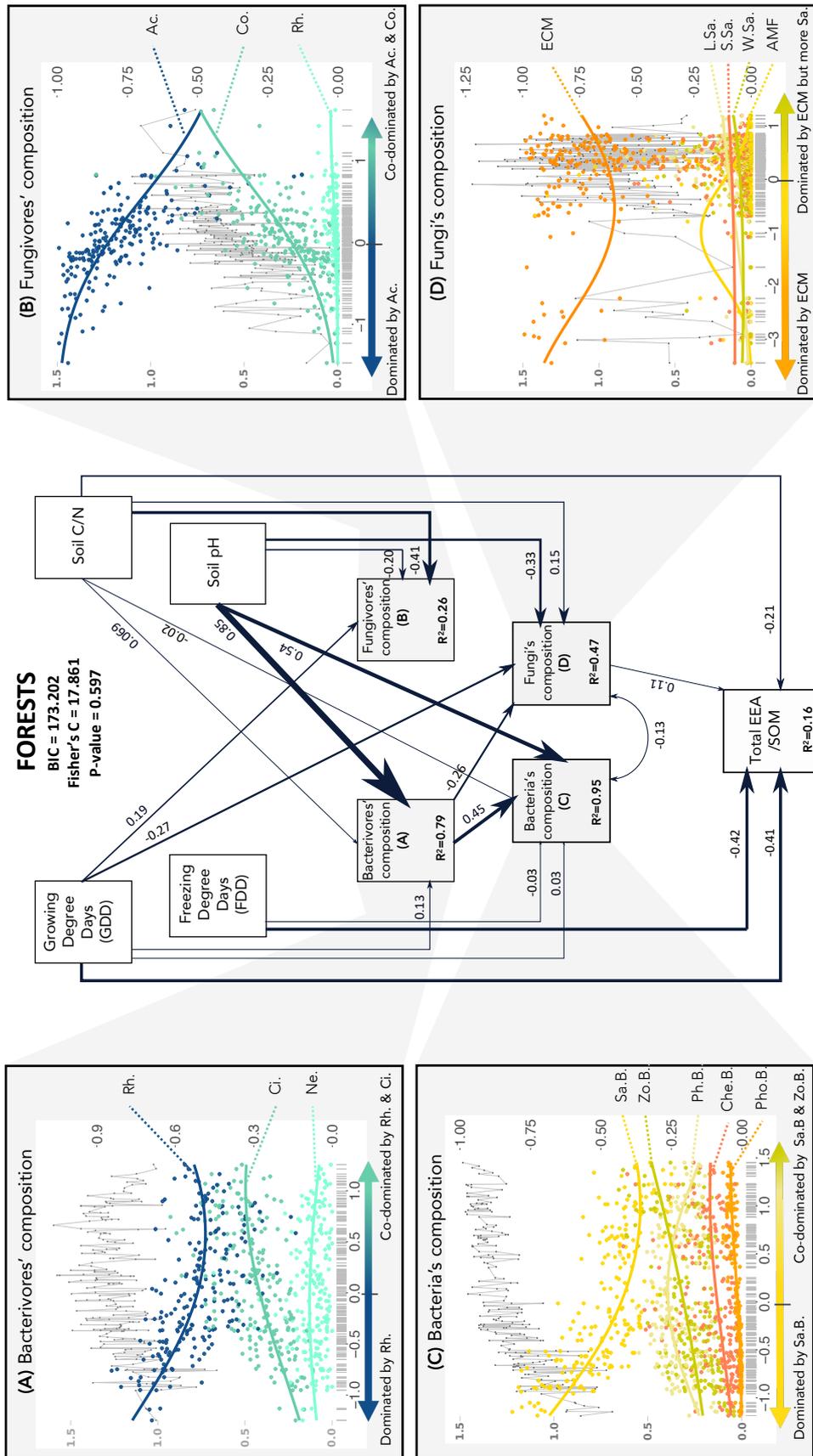
786 bacteria), Zo. B. (zooparasitic bacteria), Ph.B. (phytoparasitic bacteria), Pho. B.
787 (photoautotrophic bacteria), iv) S.Sa (soil saprotrophic fungi), L.Sa (litter saprotrophic fungi),
788 O.Sa (other saprotrophic fungi), ECM (ectomycorrhizal fungi), AMF (arbuscular mycorrhiza
789 fungi).

790

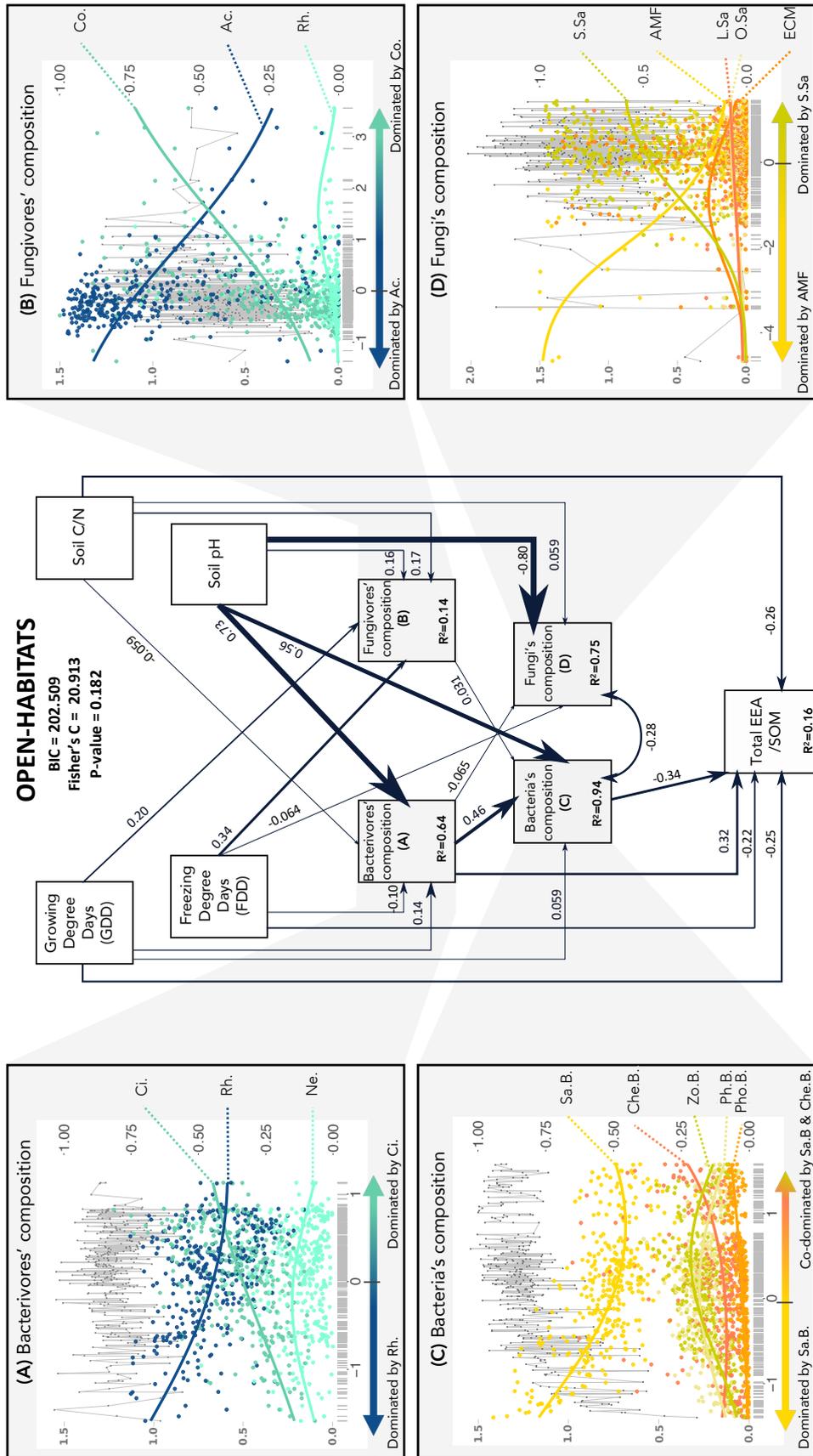
791 **Figure 3:** Comparison of direct and indirect standardized effects of soil trophic network on
792 microbial decomposition activity, extracted from the SEMs (Figs. 1 & 2). Indirect effects
793 (hatched boxes) correspond to the sum of the effects for each indirect path, where the effect
794 for each indirect path is computed as the product of the standardized path coefficients along
795 the path. The sum of the direct and indirect effect is the total effect of a variable. To meet the
796 definition of *channel*, we considered for this figure only the mediation via bacteria for
797 bacteria-channel and via fungi for fungi-channel.

798

799 **Figure 4:** Comparison of the indirect standardized effects of the environment (soil physico-
800 chemical properties and climatic variables) via consumers and primary decomposers on
801 decomposition activity, extracted from the SEMs (Figs. 1, 2). *Environmental indirect effects*
802 *via consumers* correspond to the sum of the effects of each indirect path, which includes the
803 composition of a trophic group of consumers. By contrast, *environmental indirect effects via*
804 *primary decomposers* correspond to the sum of the effects of each indirect path, which does
805 not include the composition of a trophic class of consumers. The effect of each indirect path is
806 computed as the product of the standardized path coefficients along the path.

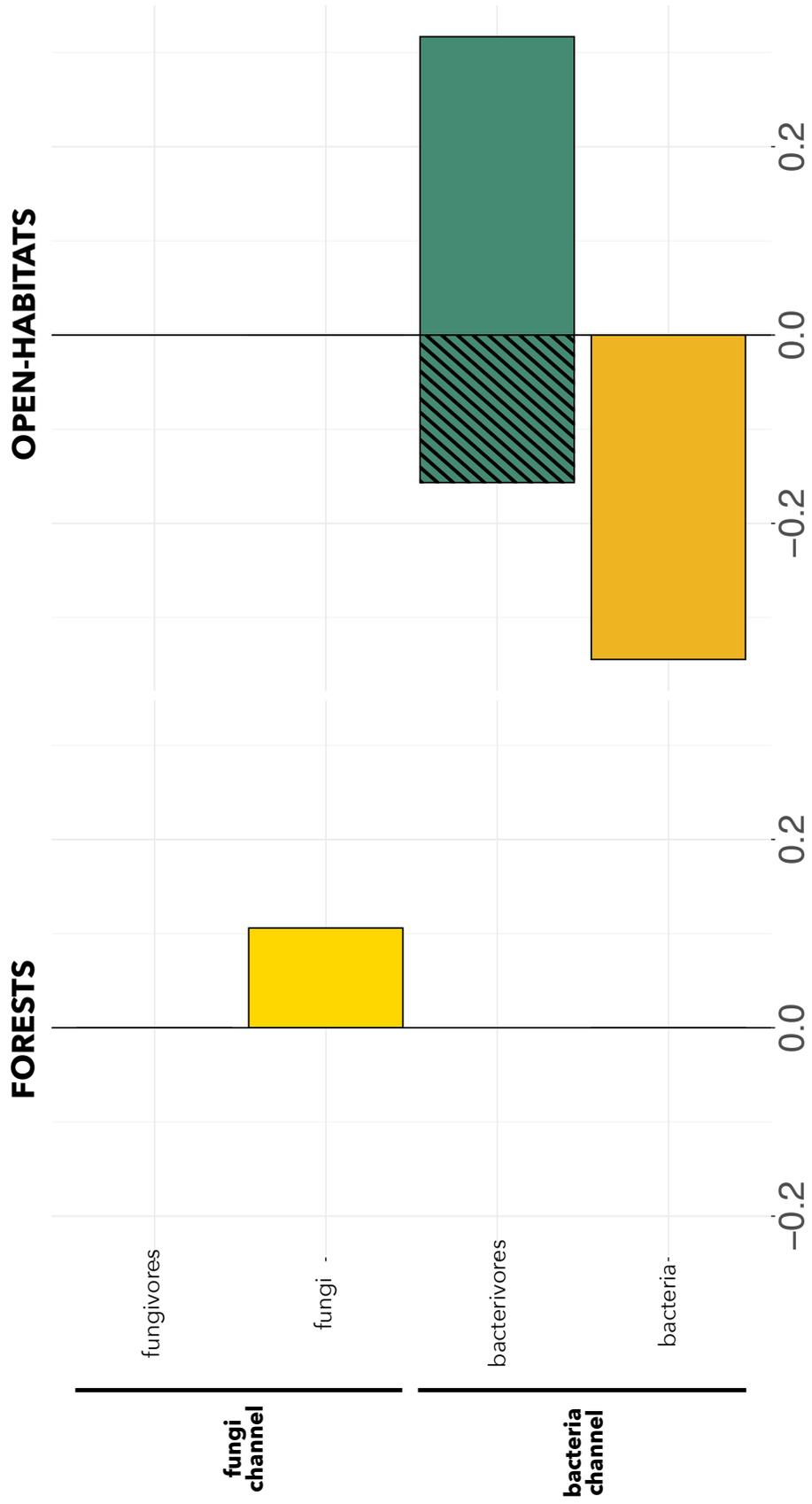


809 Figure 2:



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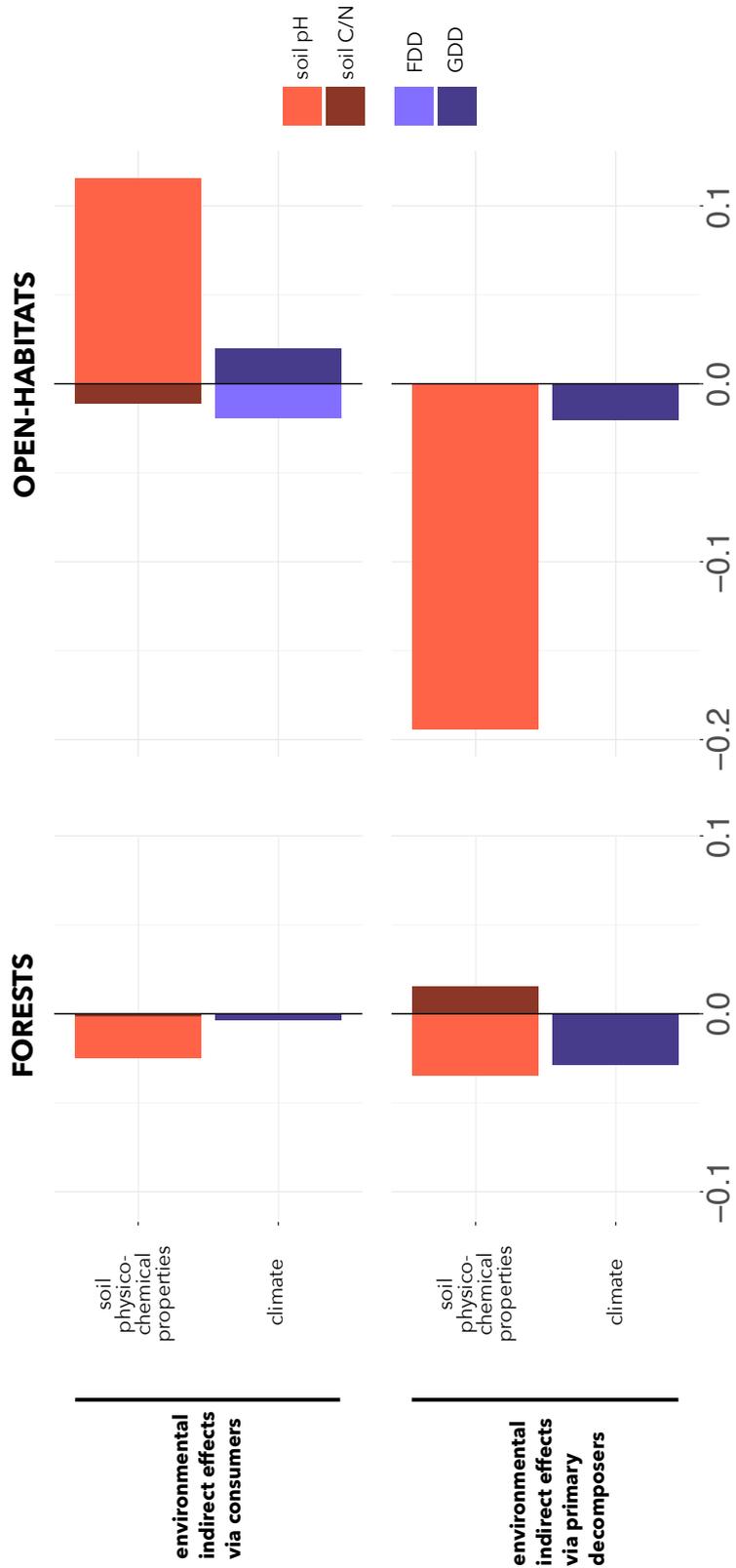
811 Figure 3:



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814 Figure 4:



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817 **SUPPLEMENTARY MATERIALS**

818 **Appendix S1: ORCHAMP: Spatio-temporal observatory of biodiversity and ecosystem func-**
819 **tioning of mountains' socio-ecosystems**

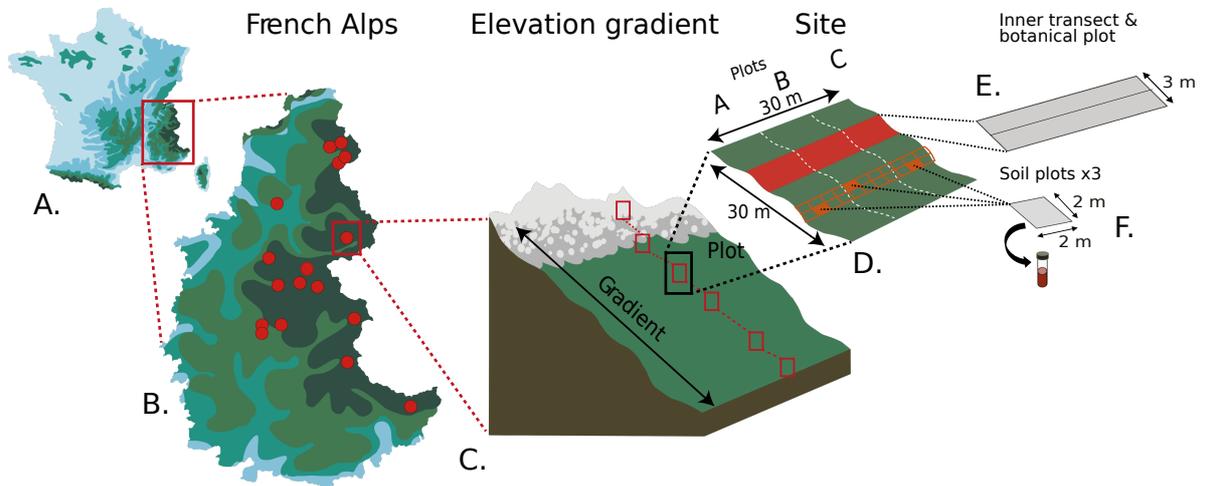
820 **1. Brief description**

821 ORCHAMP is a long-term observatory of mountain ecosystems aiming to observe, understand
822 and model biodiversity and ecosystem functioning over space and time. It relies on the active
823 involvement of local actors, managers and researchers with the objective to better safeguard
824 the contribution of biodiversity to human society.

825 ORCHAMP is built around multiple elevational gradients representative of the pedo-climatic
826 environmental space of the French Alps (Fig. S1). In this article we used 18 gradients (Figs. S1,
827 S2). Each gradient consists of 4 to 8 permanent plots distributed regularly, each with a differ-
828 ence of 200 m of altitude, from down the valley to the top, with the lowest site at 280 m and
829 the highest site at 3160 m (Fig. S2). While this work does not use temporal replicates, in OR-
830 CHAMP the gradients are resampled on average every 5 years using a rotating sampling
831 scheme. Measures include physical properties (soil temperature, physicochemical measures,
832 and pedology), biodiversity estimates (botanical surveys, multi-trophic biodiversity using soil
833 environmental DNA, tree growth, deadwood in forests), ecosystem functions (productivity,
834 enzymatic activities, soil organic matter) and human land use. Data are open-access and syn-
835 thetized following GEOBON recommendations on Essential Biodiversity Variables. Specific
836 data used in this paper are described in the main text.

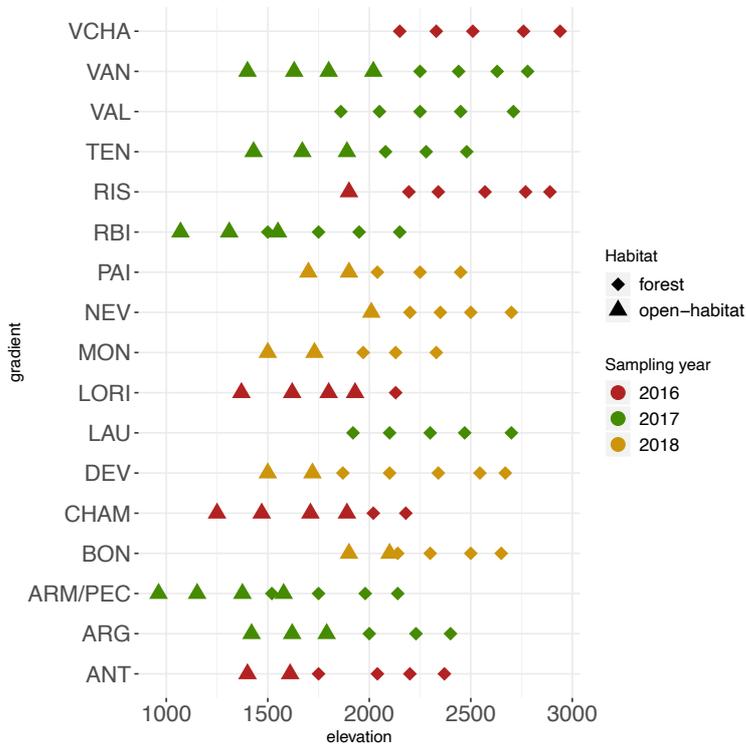
837

838 **Figure S1:** Experimental design of the ORCHAMP long-term observatory. (A) Location of the
839 observatory in the French Alps, (B) location of the 18 elevation gradients, (C) example of the
840 elevation distribution along the gradient, (D) sampling design of one site, (red area represents
841 the vegetation sampling, E), (F) represents the area where the soil sampling is done on three
842 2×2 m subplots randomly chosen for each year of sampling.

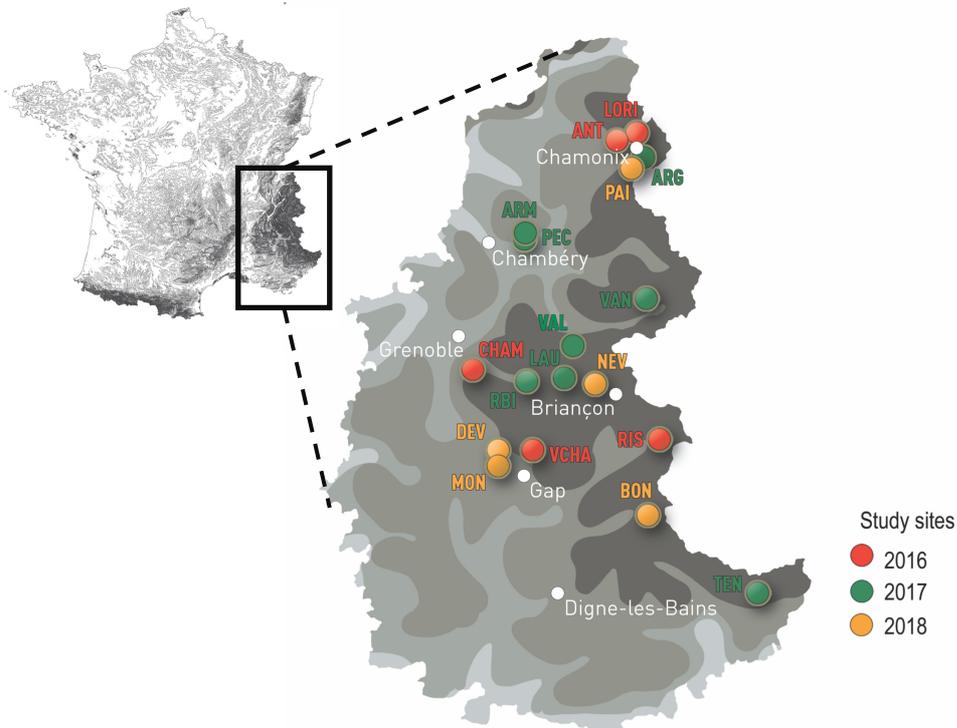


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847 **Figure S2:** Overview of the 18 gradients of ORCHAMP used in this study: Repartition of the
 848 elevations and habitat per gradient (A), location of gradients (B), names and year of sampling
 849 (A, B).



850 A.



851 B.
 852
 853

854 2. Institutions involved in ORCHAMP

855 ORCHAMP is a consortium gathering a large range of actors: national and regional park man-
856 agers, botanical conservatory experts, natural area conservatory managers, association, re-
857 searchers from universities and research institutions. Most of the actors involved in ORCHAMP
858 are also members of the LTSER Zone Atelier Alpes. The project is led by the LECA (Laboratoire
859 d'Écologie Alpine - <https://leca.osug.fr/>), located in Grenoble.

860 For additional information please visit our website: <https://orchamp.osug.fr/home> or contact
861 us: orchamp@univ-grenoble-alpes.fr

- 862 - **LECA** - Laboratoire d'Écologie Alpine; Univ. Grenoble Alpes, CNRS, Univ. Savoie Mont
863 Blanc, Laboratoire d'Ecologie Alpine, Grenoble, France
864 <https://leca.osug.fr/>
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867 <http://edytem.univ-savoie.fr/>
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869 Alpes, INRAE, UR LESSEM, Grenoble, France
870 <https://www.irstea.fr/fr/recherche/unites-de-recherche/lessem>
- 871 - **IMBE** - Institut Méditerranéen de la Biodiversité et d'Écologie marine et continentale;
872 CNRS Aix Marseille Univ., France
873 <https://www.imbe.fr/l-unite.html>
- 874 - **SAJF** - Station Alpine Joseph Fourier; Univ. Grenoble Alpes, CNRS, Grenoble, France
875 <https://www.jardinalpindulautaret.fr/>
- 876 - **CEN** - Centre d'Études de la Neige; Univ. Grenoble Alpes, Université de Toulouse, Mé-
877 téo-France, CNRS, Centre National de Recherches Météorologiques, Grenoble, France
878 <https://www.umr-cnrm.fr/spip.php?rubrique85>
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880 Rouen Normandie, Rouen, France
881 <http://ecodiv.univ-rouen.fr/fr>
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883 <http://www.geologie.ens.fr/spiplabocnrs/>
- 884 - **INRAE URFM**, UR Ecologie des Forêts Méditerranéennes; INRAE, Avignon, France
885 https://www6.paca.inra.fr/ecologie_des_forets_mediterraneennes
- 886 - **INRAE UEFM** - UE Entomologie et Forêt Méditerranéenne; INRAE, Avignon, France
887 https://www6.paca.inra.fr/entomologie_foret_med
- 888 - **CBN Alpin** - Conservatoire Botanique National Alpin
889 <http://www.cbn-alpin.fr/>
- 890 - **CBN Med** - Conservatoire Botanique National Méditerranéen de Porquerolles
891 <http://www.cbnmed.fr/src/prez.php>
- 892 - **PN des Ecrins** - Parc National des Ecrins & **RI du Lauvitel** - Réserve intégrale du Lauvitel

- 893 <http://www.ecrins-parcnational.fr/>
- 894 - **PN du Mercantour** - Parc National du Mercantour
- 895 <http://www.mercantour-parcnational.fr/fr>
- 896 - **PN de la Vanoise** - Parc National de la Vanoise
- 897 <http://www.vanoise-parcnational.fr/fr>
- 898 - **PNR du massif des Bauges** - Parc Naturel Régional du massif des Bauges
- 899 <http://www.parcdesbauges.com/fr/>
- 900 - **PNR de Chartreuse** - Parc Naturel Régional de Chartreuse
- 901 <http://www.parc-chartreuse.net/>
- 902 - **PNR du Queyras** - Parc Naturel Régional du Queyras & **RN Ristolas-Mont-Viso** - Ré-
- 903 serve Naturelle Nationale de Ristolas-Mont-Viso
- 904 <https://www.pnr-queyras.fr/>
- 905 - **ASTER** - Conservatoire d'espaces naturels de Haute-Savoie & **RN Sixt-Passy** - Réserve
- 906 Naturelle de Sixt-Passy
- 907 <http://www.cen-haute-savoie.org/>
- 908 - **CREA** - Centre de Recherches sur les Écosystèmes d'Altitude
- 909 <https://creamontblanc.org/fr>
- 910 - **Natura 2000 Clarée**
- 911 <https://inpn.mnhn.fr/site/natura2000/FR9301499>
- 912 - **Natura 2000 Dévoluy-Durbon-Charance-Champsaur**
- 913 <http://hautes-alpes.n2000.fr/devoluy>
- 914 - **SMIGIBA** - Syndicat Mixte de Gestion Intercommunautaire du Buëch et de ses affluents
- 915 <http://www.smigiba.fr/>
- 916 - **Grenoble-Alpes Métropole**
- 917 <https://www.lametro.fr/>
- 918
- 919

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- 922 - **LECA:** *Wilfried Thuiller, Amélie Saillard*, Louise Boulangeat, Manon Bounous, Irene Cal-
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- 924 Maya Gueguen, Nicolas Le Guillarme, Clément Lionnet, Camille Martinez-Almoyna, Ga-
- 925 bin Piton, Julien Renaud, Tristan Ubaldi
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- 927 net, Yoan Paillet
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- 929 - **INRAE URFM :** *Bruno Fady*, William Brunetto, Florence Courdier, Frédéric Jean, Nicolas
- 930 Mariotte
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- 933 nuel Malet
- 934 - **IMBE:** *Cécile Albert, Lenka Brousset*, Raphaël Gros, Frédéric Guibal, Frédéric Guiter,
- 935 Frédéric Médail, Eric Meineiri, Alexandre Millon, Pascal Mirleau, Pavon Daniel, Arne
- 936 Saatkamp, Brigitte Talon
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- 938 - **CEN:** *Samuel Morin*
- 939 - **Laboratoire de Géologie de l'ENS:** *Lauric Cécillon*, Laure Soucémarianadin
- 940 - **CBN Alpin:** *Bertrand Liénard, Sylvain Abdulhak*, Gilbert Billard, Luc Garraud, Thomas
- 941 Legland, Baptiste Merhan, Gilles Pache, David Paulin, Thomas Sanz, Jérémie Van Es
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- 943 - **PN des Ecrins & RI du Lauvitel:** *Richard Bonet*, Cédric Dentant, Jérôme Forêt, Damien
- 944 Combrisson
- 945 - **PN du Mercantour:** *Nathalie Siefert, Marie-France Leccia, Jérôme Mansons*, Matthieu
- 946 Kramer, Sebastien Honoré
- 947 - **PN de la Vanoise:** *Vincent Augé*, Thierry Delahaye, Franck Parchoux
- 948 - **PNR du massif des Bauges:** *Jean-François Lopez*
- 949 - **PNR de Chartreuse:** *Laure Belmont*, Jessica Bruggeman
- 950 - **PNR du Queyras & RN Ristolas-Mont-Viso:** *Anne Goussot, Alain Block*, Nicolas Tenoux
- 951 - **ASTER & RN Sixt-Passy:** *Christian Schwoehrer, Carole Birck*, Jean-José Richard Pomet
- 952 - **CREA:** *Anne Delestrade*, Irene Alvarez, Bradley Carlson, Hillary Gerardi, Colin Van Reeth
- 953 - **N 2000 Clarée:** *Laure Vuinée*
- 954 - **Natura 2000 Dévoluy-Durbon-Charance-Champsaur & SMIGIBA:** *Eric Hustache*
- 955 - **Grenoble-Alpes Métropole:** *Alexandre Mignotte*, Pierre-Eymard Biron
- 956

957 **4. ORCHAMP Funding**

958

959 Each institution involved in the consortium is co-funding the project either through in-kind
960 funding or participation to specific projects. Additional funding sources are:

961 **ANR - Agence Nationale de la Recherche:** GlobNets (ANR-16- CE02-0009), Origin-Alps (ANR-
962 16-CE93-004)

963 **ANR 'Investissement d'Avenir':** Trajectories (ANR-15-IDEX-02), Montane: (OSUG@2020:
964 ANR-10-LAB-56)

965 **AFB - Agence Française pour la Biodiversité:** Sentinelles des Alpes

966 **AURA - Région Auvergne-Rhône-Alpes:** CBNA regional convention

967 **LTSER ZAA - Zone Atelier Alpes** (CNRS, IRSTEA)

968 **Interreg Alcotra FEDER:** PITEM Biodiv'ALP

969 **Other local funding sources:** Parc National des Ecrins (PNE), Réserve intégrale du Lauvitel,
970 Parc National du Mercantour (PNM), Grenoble Alpes Métropole, Agence de l'eau Rhône-
971 Méditerranée Corse (AERMC), Electricité de France (EDF), Mairie du Dévoluy, Institut de
972 Radioastronomie Millimétrique (IRAM), Communauté de communes de la vallée de Chamonix
973 Mont-Blanc

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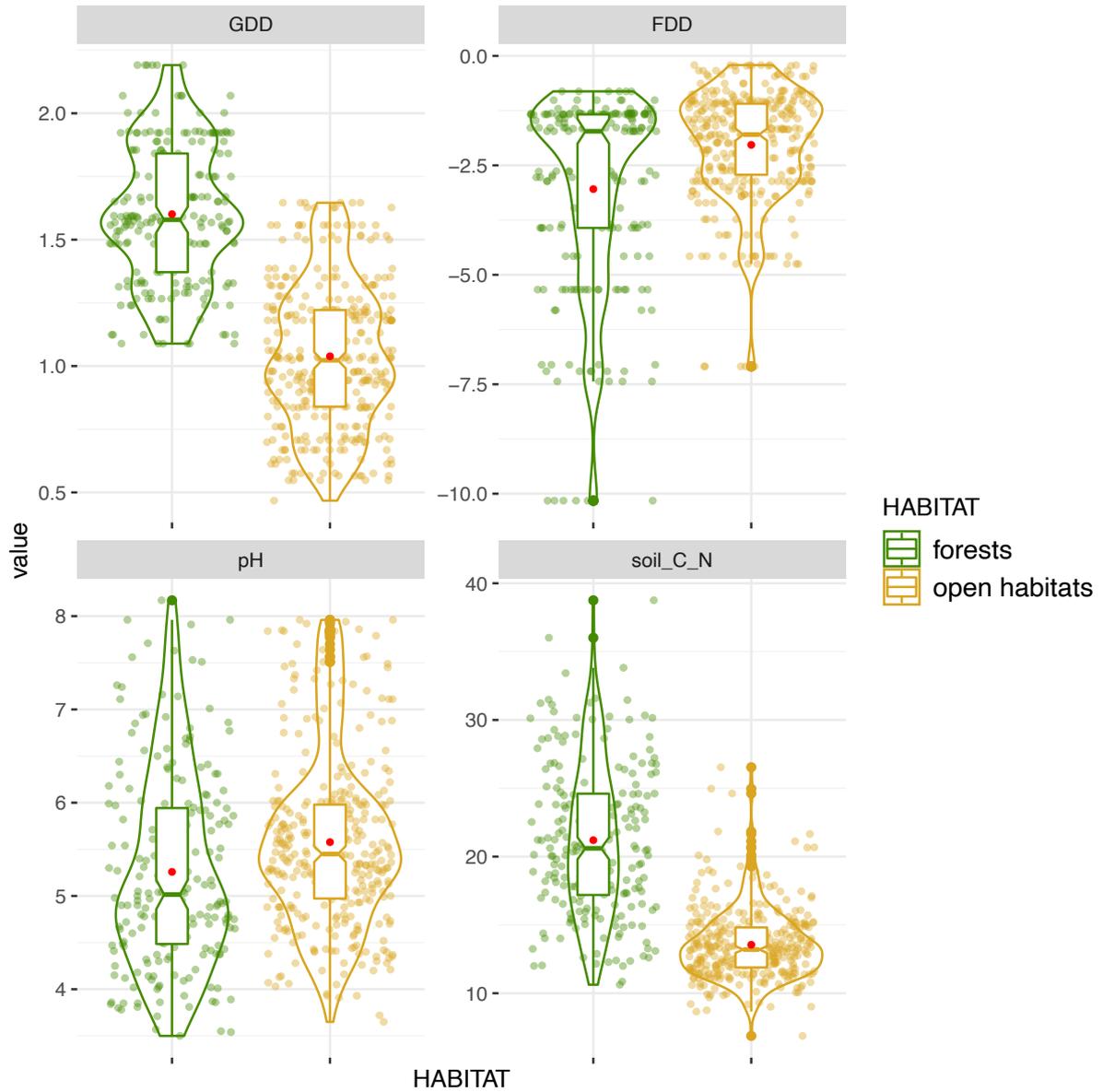
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981

982 **Appendix S2: Raw environmental and enzymatic data for forests and open habitats**

983

984 **Figure S3:** Comparisons of the used climatic variables (GDD, FDD) and soil physico-chemical
985 properties (soil C/N, soil pH) in forests and open habitats. Red points represent the mean of
986 each variable for each habitat.

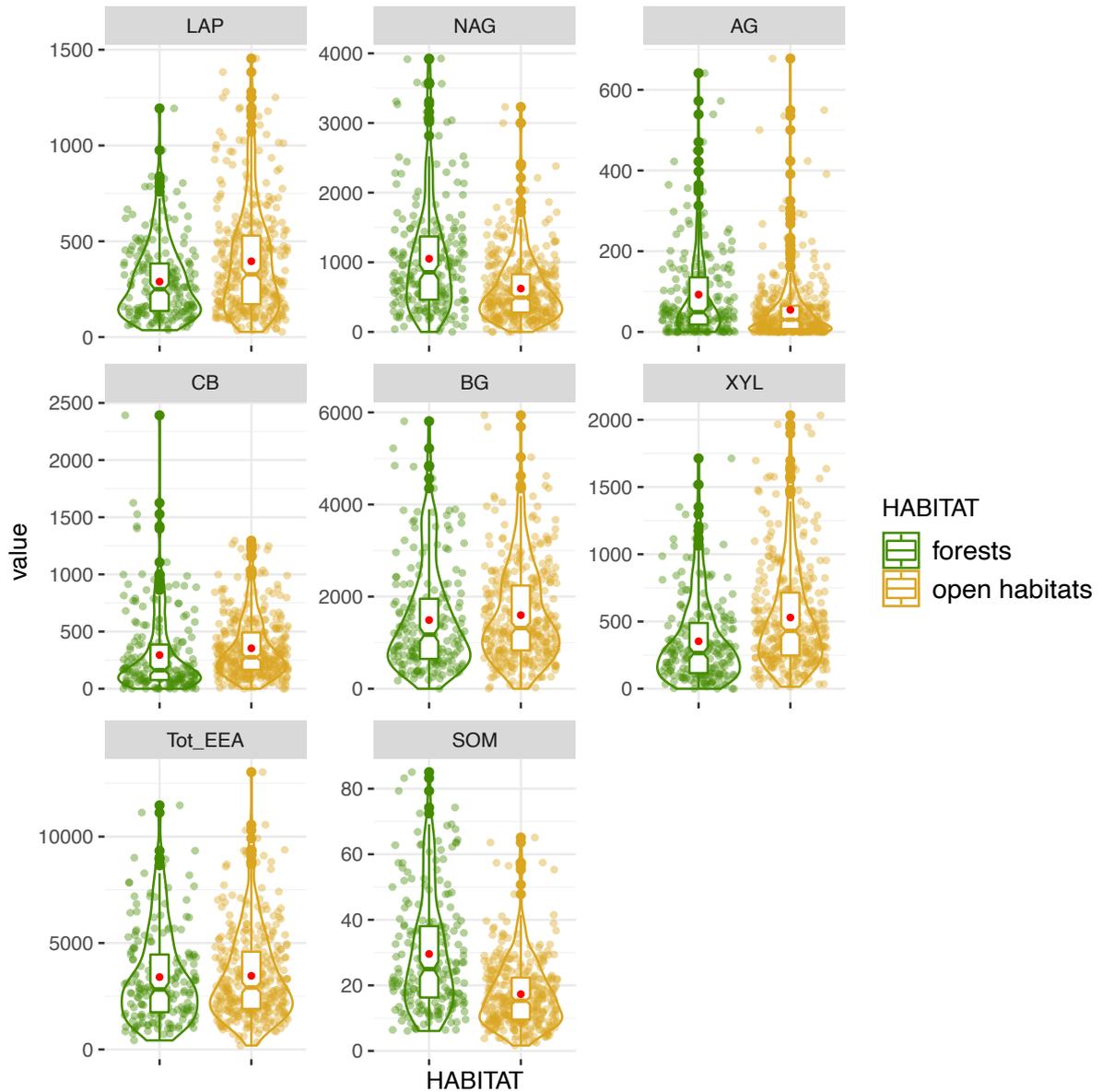


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989

990 **Figure S4:** Comparison of the original variables used to compute microbial decomposition
991 activity - six potential extracellular enzymatic activities (LAP, NAG, AG, CB, BG, XYL resulting
992 in the so called total potential extracellular enzymatic activity, Tot_EEA) and the soil organic
993 matter (SOM) - in forests and open habitats. Red points represent the mean of each variable
994 for each habitat.
995



996
997

998 **Appendix S3: Description of the soil eDNA data processing**

999

1000 **1. Soil eDNA extraction, amplification and sequencing**

1001 We conducted the soil eDNA extraction immediately in the field. In order to liberate eDNA
1002 from clay and silica particles, each sample was shaken for 15 minutes by rotation in a 15 mL
1003 saturated phosphate buffer solution (Na₂HPO₄; 0.12 M; pH ≈ 8). We then sampled 2 mL of
1004 sediment/buffer mixture and centrifuged it for 10 minutes at 10,000 g. We collected a 400 µL
1005 aliquot of supernatant and used it as starting material for eDNA extraction using the
1006 NucleoSpin® Soil extraction kit (Macherey-Nagel GmbH, Düren, Germany), following
1007 manufacturer's instructions except skipping the lysis cell step (Taberlet et al. 2012). We stored
1008 the samples in a dry environment before the elution step, which we performed back at LECA,
1009 Laboratoire d'ECologie Alpine, France. After elution, soil eDNA extracts were diluted 10 times
1010 before being used as templates for amplification. A total of 268 negative extraction controls
1011 were also performed over the three years to identify potential extraction contaminants.

1012 For eDNA amplification, we targeted Eukaryotes, Fungi and Bacteria using respectively the
1013 DNA markers Euka02 (18S rRNA), Fung02 (ITS) and Bact01 (16S rRNA) described in Taberlet et
1014 al. 2018. We added unique eight-base long tags at the 5' end of each primer so that the sample
1015 of origin of each sequencing read could be retrieved after sequencing. These tags modified
1016 from Binladen et al. 2007 and Valentini et al. 2009 differed by at least five bases. DNA
1017 amplifications were carried out in a final volume of 20 µL containing i) 2 µL of eDNA sample,
1018 ii) 10 µL of AmpliTaq Gold 360 Master Mix 2X (Applied Biosystems™, Foster City, CA, USA), iii)
1019 2 µL of primers mix at initial concentration of 5 µM each and iv) 0.16 µL of Bovine Serum
1020 Albumin. We included a total of 184 negative- and 84 positive PCR-controls over the three
1021 years to identify potential PCR-contaminants. Four PCR-replicates were amplified for each
1022 sample and control.

1023 We performed PCRs as follow: 1) samples and controls were first incubated 10 min at 95°C, 2)
1024 they underwent 40 cycles of i) 30 s at 95°C, ii) 30 s at 57°C (Bact01), 55°C (Fung02) or 45°C
1025 (Euka02) and iii) 60 s at 72°C, and 3) they went through a final elongation at 72°C for seven
1026 minutes. Then, we 4) checked the amplification success using capillary electrophoresis
1027 (QIAxcel System; Qiagen), 5) mixed PCR products in an equi-volume way (15 µl each) and 6)
1028 purified eight*100 µL-aliquots of the resulting mix using MinElute Purification kit (Qiagen
1029 GmbH, Hilden, Germany). Finally, we pooled purified products together before sequencing.

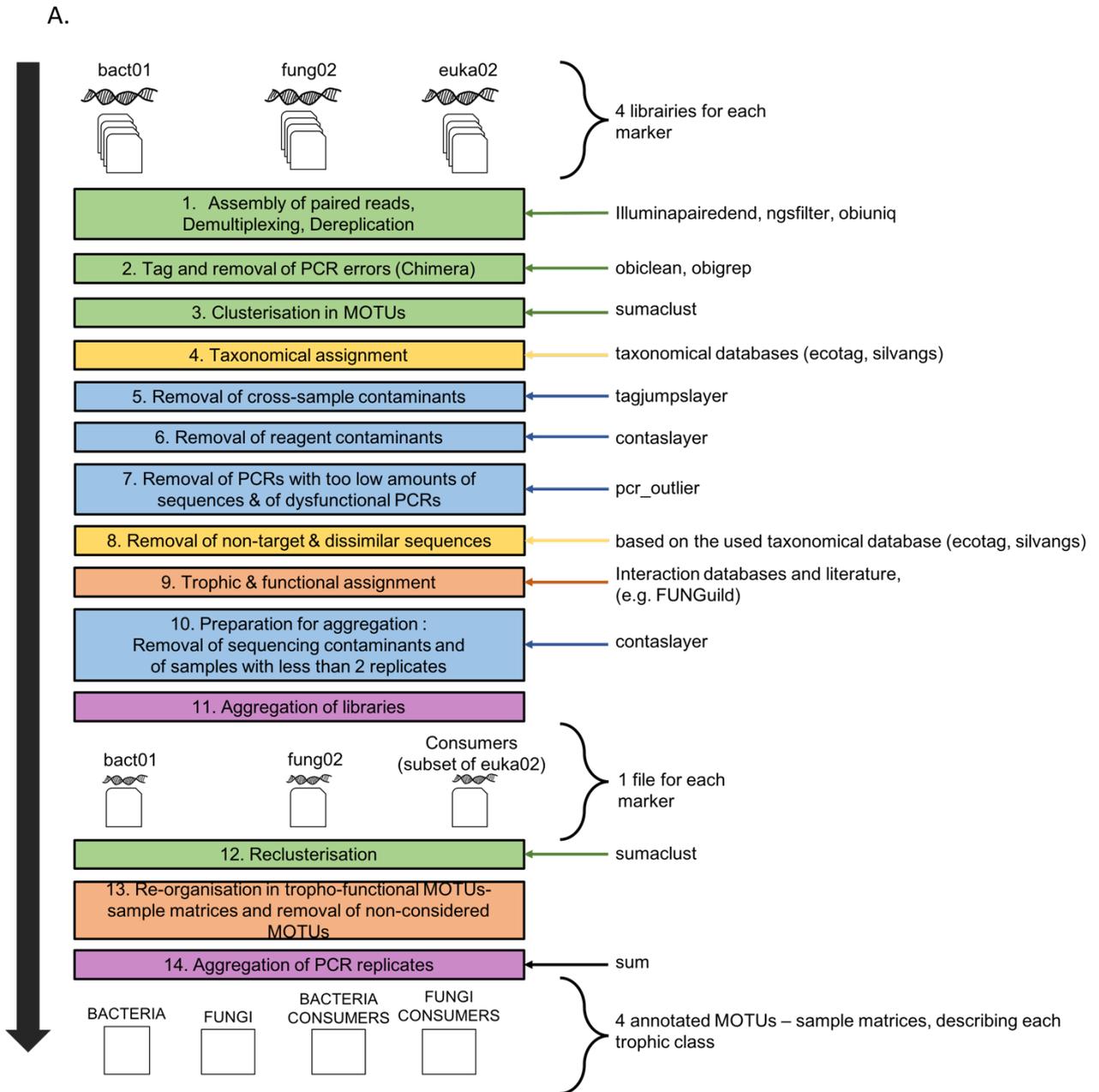
1030 Sequencing was performed by pair-end sequencing on Illumina HiSeq 2000 platform (2*125)
1031 for Euka02, and Illumina Miseq platform (2*250) for both Bact01 and Fung02) at Fasteris,
1032 Geneva, Switzerland. Data for each marker correspond to four libraries for sequencing (2016,
1033 2017 A&B, 2018). We also included 728 negative sequencing controls over the three years to
1034 retrieve false positives caused by tag-switching events during the sequencing.

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1038 **Figure S5:** Overview of the cleaning and preparation steps of metabarcoding data from
 1039 sequences to a MOTUs-sample matrix for each trophic class. Green boxes and arrows
 1040 correspond to steps done with functions belonging to the OBITools package. Blue boxes and
 1041 arrows correspond to steps done with functions belonging to the metabarR package. Yellow
 1042 and oranges boxes and arrows correspond respectively to assignment to a taxonomical path
 1043 and a trophic class and trophic group. Arrows on the right lists the function used at each step
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1048 **Table S1:** Number of reads and MOTUs (or unique sequences, steps 1 & 2) for the sample at
 1049 each cleaning or preparation step, for each marker and each library. Preparation steps and
 1050 colors correspond to the ones described in Figure S3.
 1051

Preparation step	initial marker ->	bact01		fung02		euka02	
	library / year	Nb MOTUs	Nb reads	Nb MOTUs	Nb reads	Nb MOTUs	Nb reads
1.	2016	5677215	10749030	1892336	12879880	749381	13817137
	2017 A	5821215	11526487	3148995	25539508	771441	12440817
	2017 B	5609617	10744664	3544881	25196787	698579	11539280
	2018	8562236	4443275	2153692	14613081	653709	7505885
2.	2016	343267	4306927	63874	6260060	44129	9934344
	2017 A	297169	4361944	77106	8923632	42499	8848266
	2017 B	281290	3991436	82555	11004709	40155	8380198
	2018	289477	3636825	59615	8448605	37372	5404791
3.	2016	65970	4306923	37252	6260060	15613	9922423
	2017 A	56653	4361942	36606	8917303	15388	8840773
	2017 B	55535	3991434	36830	10993612	14300	8373465
	2018	56306	3636825	20546	8432630	12892	5393325
4.	2016	65970	4306923	37252	6260060	15613	9922423
	2017 A	56653	4361942	36606	8917303	15388	8840773
	2017 B	55535	3991434	36830	10993612	14300	8373465
	2018	56306	3636825	20546	8432630	12892	5393325
5.	2016	65948	4277724	37252	6105170	15494	9169312
	2017 A	56498	4253104	36534	8745025	15286	8312455
	2017 B	55462	3966722	36759	10453765	14093	8121633
	2018	56123	3566229	20453	7810381	12809	5257314
6.	2016	65540	4151729	37245	6104984	15377	8852668
	2017 A	55087	3611820	36515	8742015	14610	8092448
	2017 B	53435	3098173	36732	10451475	13004	7496947
	2018	54302	2599510	20431	7808920	12607	3960067
7.	2016	65217	3984826	35538	6007559	15309	8688037
	2017 A	54700	3542538	35834	8711666	14240	7950499
	2017 B	53123	3052218	36514	10448195	12930	7464058
	2018	53574	2538139	20390	7762144	12582	3893344
8.	2016	63327	3976796	7263	4066180	11904	8086712
	2017 A	53513	3539099	10597	6265723	11794	7739560
	2017 B	52165	3049560	11518	7688393	10798	7288180
	2018	53474	2537752	10627	6167321	10469	3686627
9.	2016	63327	3976796	7263	4066180	2666	433512
	2017 A	53513	3539099	10597	6265723	2451	357287
	2017 B	52165	3049560	11518	7688393	2192	237341
	2018	53474	2537752	10627	6167321	2586	318699
10.	2016	63327	3976796	7262	4066179	2664	433510
	2017 A	53513	3539099	10597	6265723	2451	357287
	2017 B	52165	3049560	11515	7688384	2191	237340
	2018	53453	2537711	10624	6167313	2586	318699
11.	all libraries aggregated	175742	12610039	32384	23094281	5761	1272995
12.	all libraries	111680	12610039	20773	23094281	4587	1272995

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1053 **Table S2:** Number of extraction-, negative PCR-, positive PCR-, and sequencing controls,
 1054 Number of samples before and after data curation, Number of PCR replicates before and after
 1055 data curation for each marker and each library.

1056

library/year	Nb of extraction controls	Nb of negative PCR controls	Nb of positive PCR controls	Nb of sequencing controls	Nb of samples before data curation	Nb of samples after data curation			Nb of pcr replicates before data curation	Nb of pcr replicates after data		
						bact01	fung02	euka02		bact01	fung02	euka02
2016	40	24	0	392	174	162	166	174	696	519	544	639
2017 A	52	40	24	96	139	136	134	136	556	511	528	499
2017 B	88	44	24	96	129	127	128	128	516	483	509	494
2018	88	76	36	144	202	200	202	200	808	755	794	795

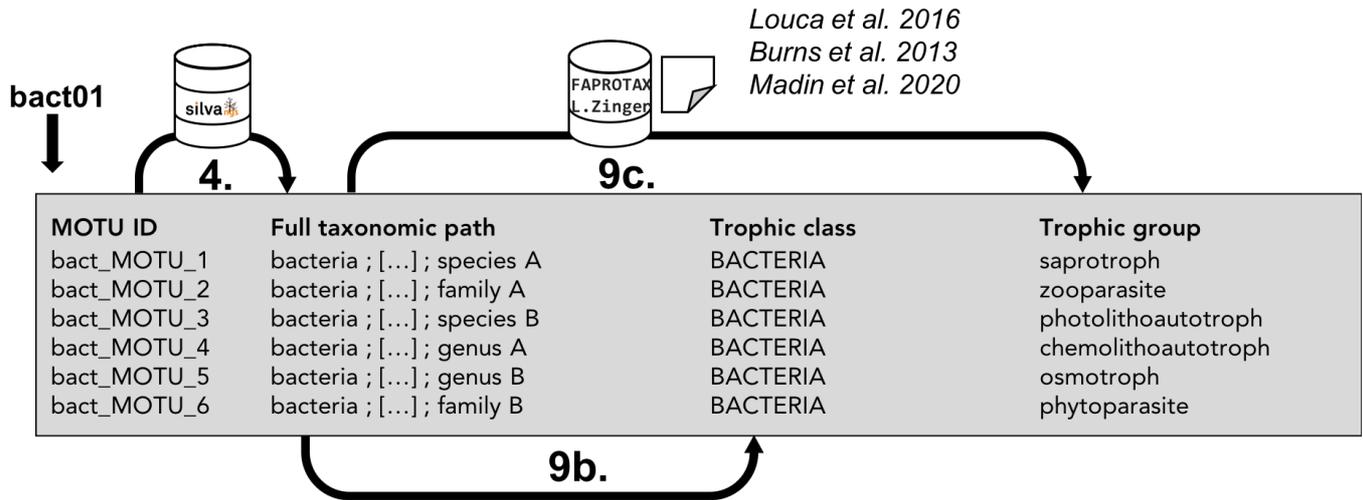
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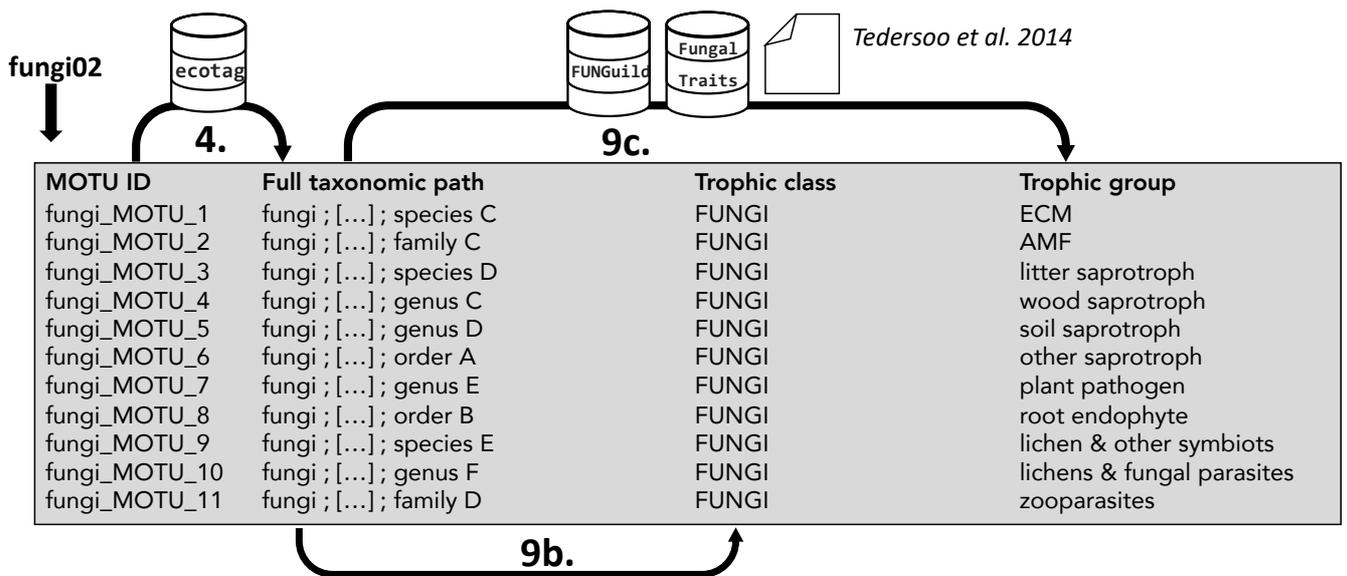
Figure S6: Details of the assignment to a taxonomical path, to a trophic class and to trophic group for the metabarcoding marker A. *bact01*, B. *fungi02*, C. *euka02*. The cylindrical schematics detail the databases used at each step. The paper schematics detail the literature used at each step. Steps are numerated according to Figure S3.

A.



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B.



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1074 **2. References for Appendix 3**

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1120 27, 277–294.

1121 **Table S3:** Characteristics of the trophic classes and trophic groups. Total number of MOTUs
 1122 and reads, average number of MOTUs and reads of trophic classes, number of MOTUs and
 1123 reads of trophic groups, also expressed as percentage of the corresponding trophic class.
 1124

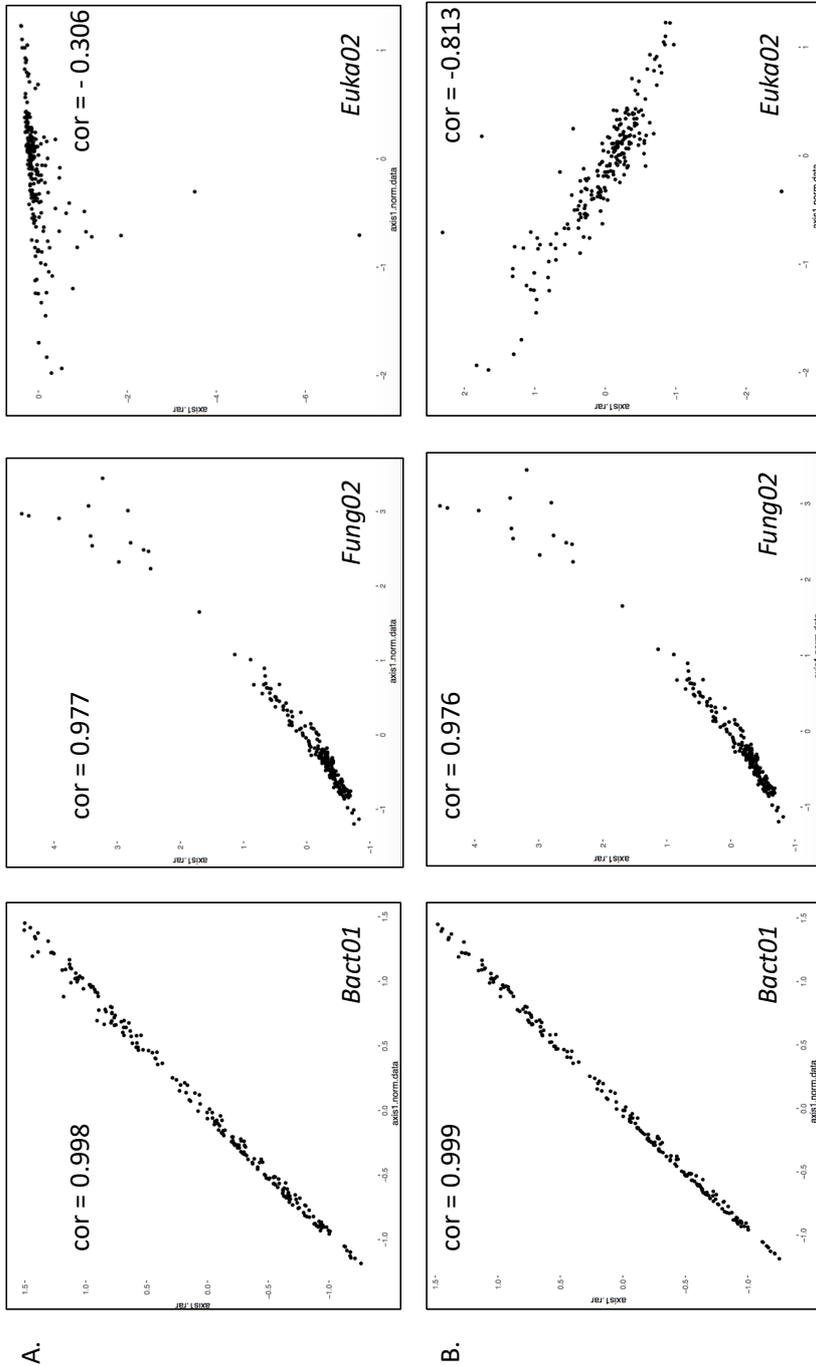
Trophic level	Trophic class	Nb motus		Nb reads		Average nb motus by sample (sd)		Average nb reads by sample (sd)		Trophic group	Nb motus (% nb motus trophic class)		Nb reads (% nb reads trophic class)	
		F	O	F	O	F	O	F	O		F	O		
primary decomposers	bacteria	73457	96783	4498164	7467886	3347.335 (1378.936)	3417.874 (1312.949)	21217.75 (13402.17)	21336.82 (14733.9)	chemolitho-autotroph	2062 (2.8)	2893 (3.0)	103656 (2.3)	183413 (2.5)
										osmotroph	139 (0.19)	215 (0.22)	2216 (0.049)	3902 (0.052)
										photolitho-autotroph	438 (0.60)	781 (0.81)	21733 (0.48)	48745 (0.65)
										phytoparasite	4255 (5.8)	4834 (5.0)	277071 (6.2)	279700 (3.7)
										saprotroph	8147 (11)	9959 (10)	575920 (13)	928379 (12)
										zooparasite	3301 (4.5)	3807 (3.9)	267092 (5.9)	300108 (4.0)
										unknown	55115 (75)	74294 (77)	3250476 (72)	5723639 (77)
	fungi	11857	13734	8934394	13400912	319.5189 (120.3817)	312.2543 (142.2961)	42143.37 (22750.61)	38288.32 (22575.02)	AMF	913 (7.7)	2016 (15)	673312 (7.5)	2715764 (20)
										ECM	3372 (28)	1223 (8.9)	5414026 (61)	1571116 (12)
										litter saprotroph	987 (8.3)	947 (6.9)	791960 (8.9)	783880 (5.8)
										soil saprotroph	1296 (11)	2498 (18)	707911 (7.9)	5194185 (39)
										wood saprotroph	759 (6.4)	700 (5.1)	431752 (4.8)	351365 (2.6)
										other saprotroph	1101 (9.3)	1626 (12)	164911 (1.8)	742784 (5.5)
										root endophyte	75 (0.63)	149 (1.1)	12371 (0.14)	99329 (0.74)
										lichens & other symbiots	87 (0.73)	327 (2.4)	12701 (0.14)	112554 (0.84)
										plant pathogen	301 (2.5)	376 (2.7)	51774 (0.58)	93432 (0.70)
										lichen & fungal parasite	90 (0.76)	113 (0.82)	12486 (0.14)	29880 (0.22)
										zooparasite	66 (0.56)	67 (0.49)	15100 (0.17)	29871 (0.22)
										unknown	2810 (24)	3692 (27)	646090 (7.2)	1676752 (12)
consumers	bacteria-consumers	2377	3181	135739	383524	133.4858 (71.2693)	153.7486 (63.38372)	640.2783 (662.5135)	1095.783 (1031.628)	Nematoda	90 (3.8)	121 (3.8)	10356 (7.6)	48393 (13)
										Ciliophora	610 (26)	797 (25)	35384 (26)	128354 (33)
										Stramenopiles	90 (3.8)	119 (3.7)	3805 (2.8)	7357 (1.9)
										Amoebozoa	291 (12)	410 (13)	4448 (3.3)	10824 (2.8)
										Dinoflagellata	4 (0.17)	2 (0.063)	18 (0.013)	28 (0.0073)
										Excavata	7 (0.29)	7 (0.22)	22 (0.016)	25 (0.0065)
										Haptophyta	20 (0.84)	24 (0.75)	280 (0.21)	851 (0.22)
										Holozoa	167 (7.0)	200 (6.3)	5007 (3.7)	10128 (2.64)
										Nuclemycea	47 (2.0)	56 (1.8)	1035 (0.76)	1419 (0.37)
	Rhizaria	1051 (44)	1445 (45)	75384 (56)	176145 (46)									
	fungi-consumers	561	676	388549	270766	31.16981 (11.43659)	24.01429 (10.28601)	1832.778 (1658.171)	773.6171 (791.7108)	Acari	194 (35)	204 (30)	313514 (81)	192510 (71)
										Collembola	192 (34)	220 (33)	68134 (18)	65567 (24)
										Nematoda	42 (7.5)	60 (8.9)	2396 (0.62)	2543 (0.94)
										Ciliophora	9 (1.6)	14 (2.1)	1170 (0.30)	3072 (1.1)
										Rhizaria	124 (22)	178 (26)	3335 (0.86)	7074 (2.6)

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1127 **Appendix S4: Sensitivity of the first axis of the CAs to sampling depth.**

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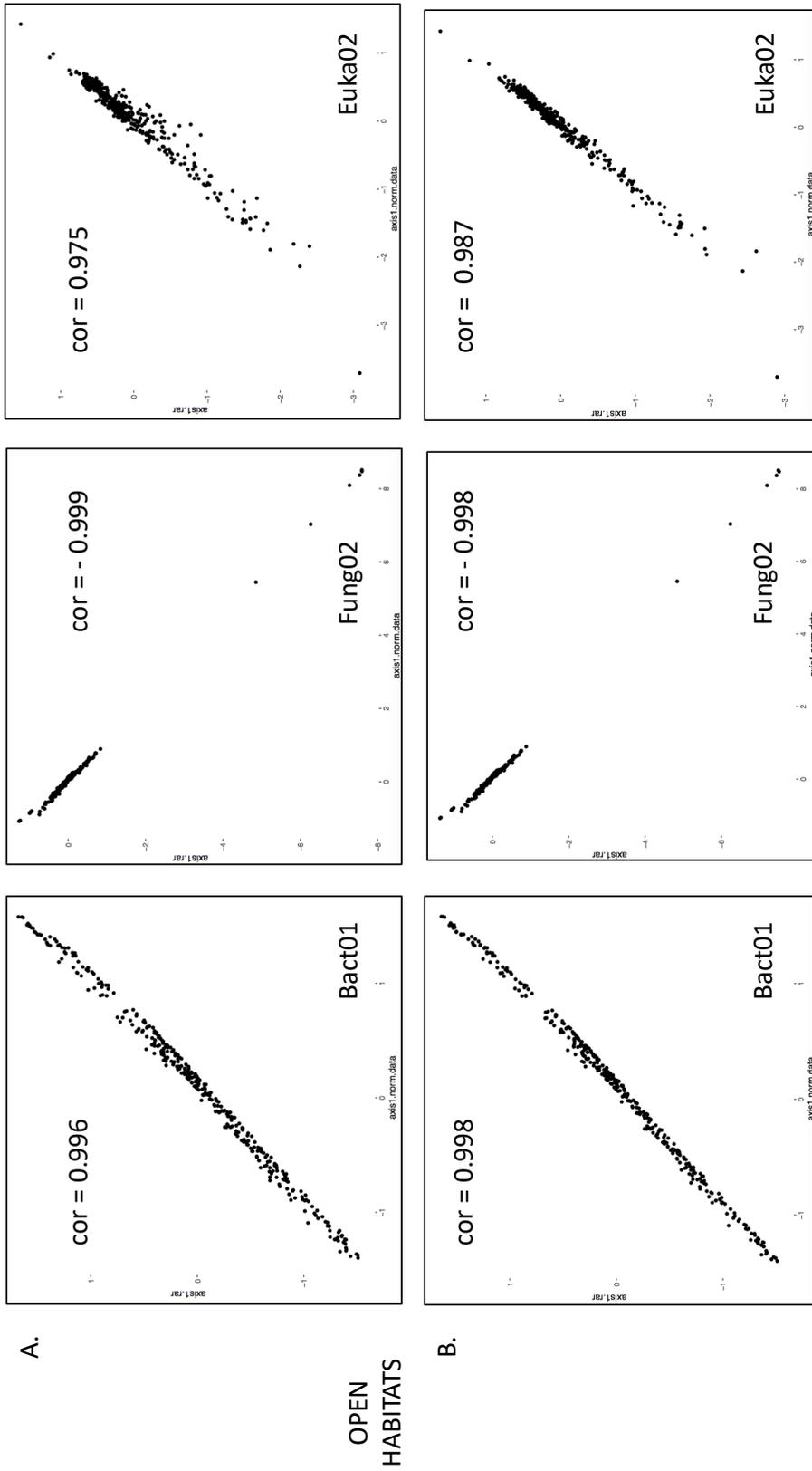
1129 **Figure S7: Forests** - Correlation between the first axes of the CAs realized on data rarefied to
1130 the number of the smallest sample (A.) or to the first quantile (25%) of the number of reads
1131 of the samples (B.) for the three markers.



FORESTS

1132

1133 **Figure S8: Open habitats** - Correlation between the first axes of the CAs realized on data
 1134 rarefied to the number of the smallest sample (A.) or to the first quantile (25%) of the number
 1135 of reads of the samples (B.) for the three markers used.



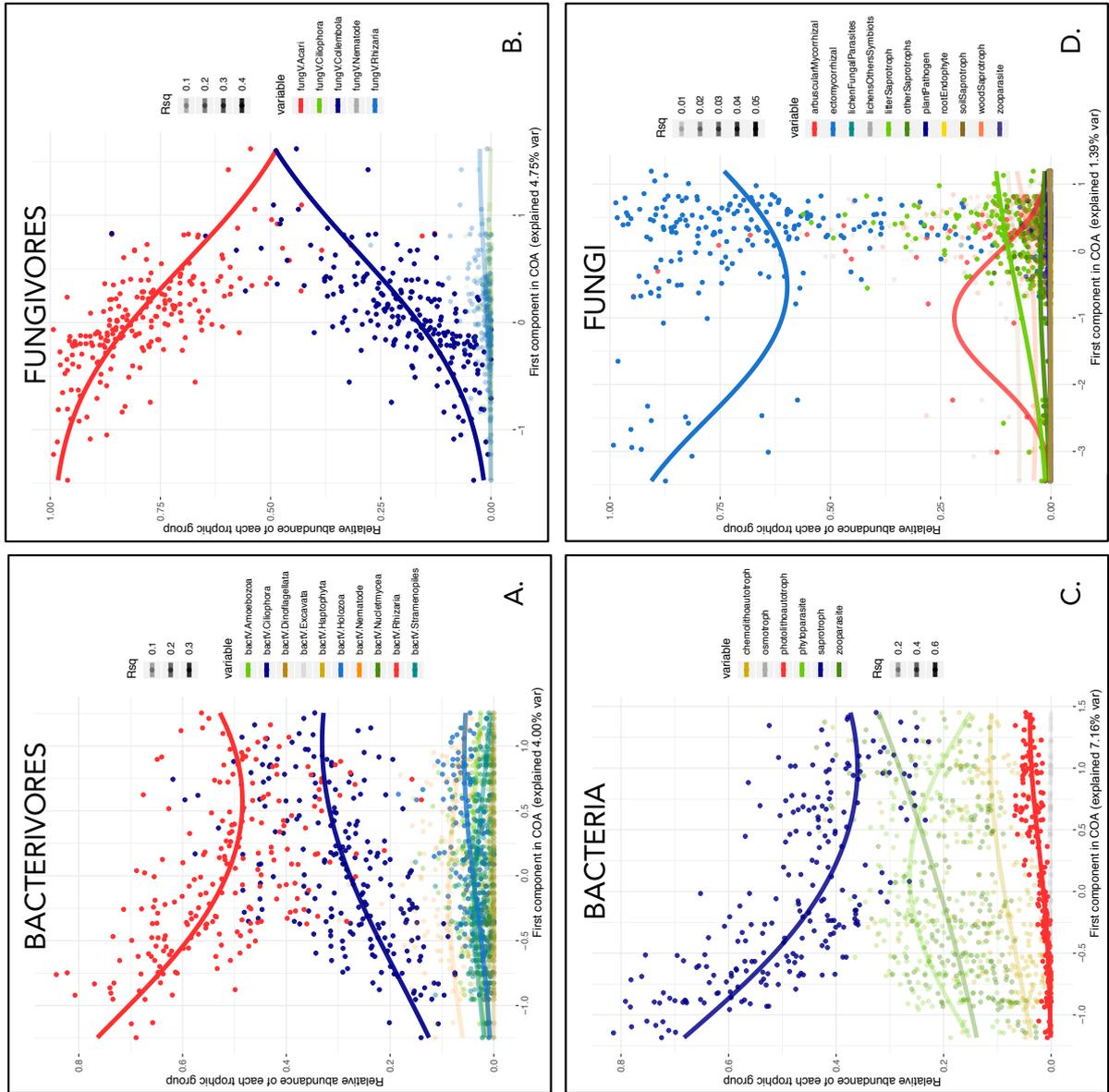
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1138 **Appendix S5: Compositional change**

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1140 **Figure S9. Compositional change between samples in forests, for A. bacterivores, B.**
 1141 **fungivores, C. bacteria, D. fungi.** This supplementary figure corresponds to the panels A, B, C
 1142 & D of the main figure 1, which were simplified for the sake of readability.

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FORESTS

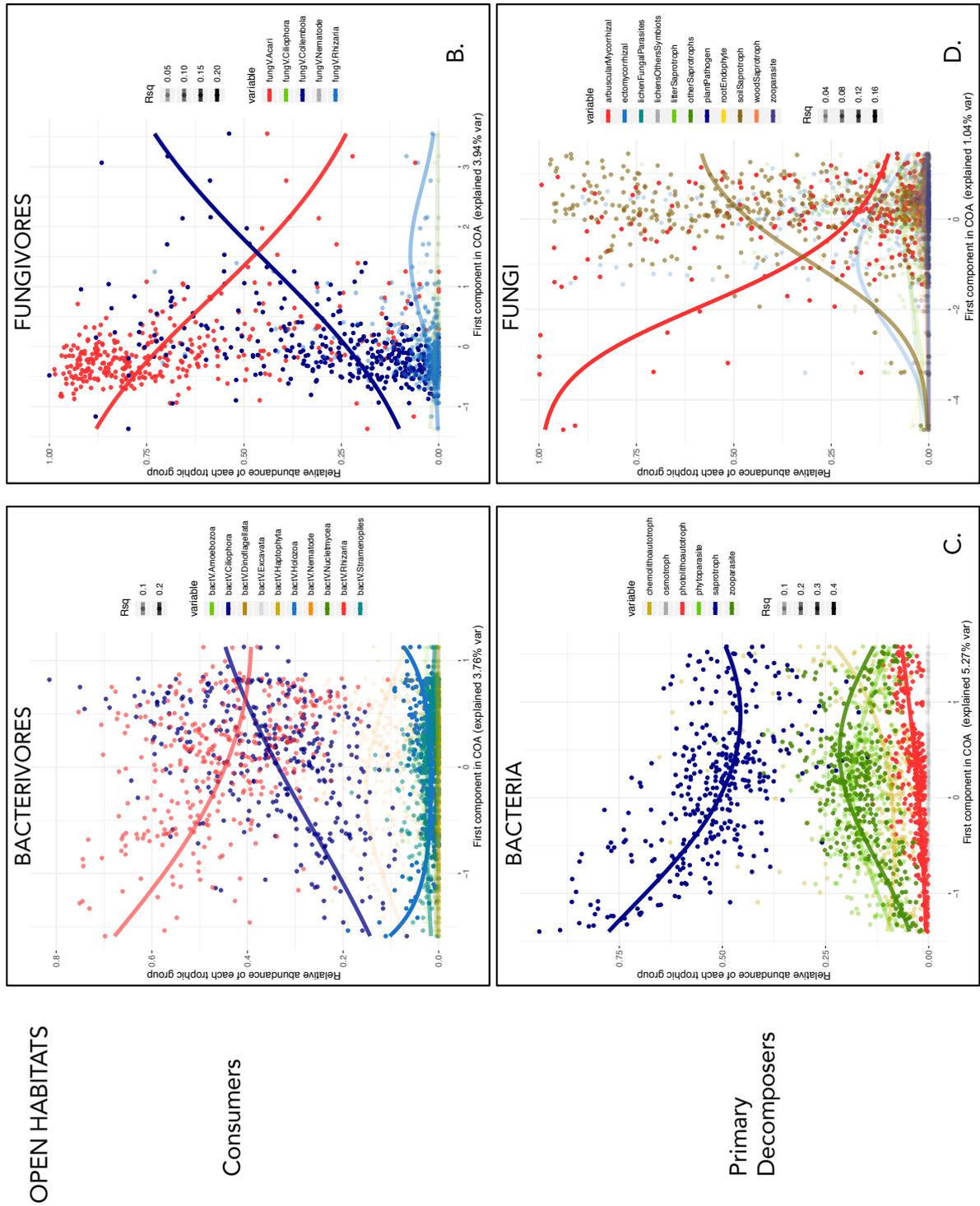
Consumers

Primary
Decomposers

1144

1145

1146 **Figure S10. Compositional change between samples in open habitats**, for A. bacterivores, B.
 1147 fungivores, C. bacteria, D. fungi. This supplementary figure corresponds to the panels A, B,
 1148 C&D of the main figure 2, which were simplified for the sake of readability.

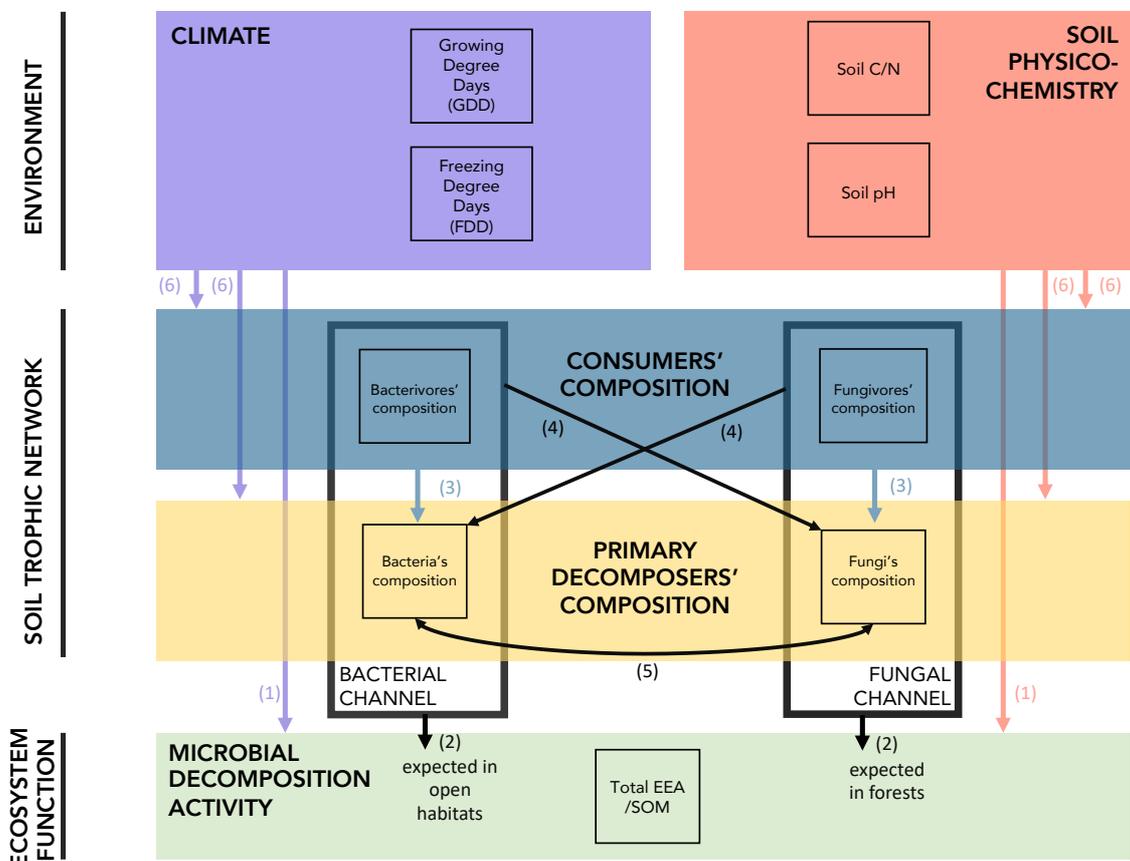


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1151 **Appendix S6: A priori SEM**

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1153 **Figure S11:** Conceptual scheme of the a priori structural equation model tested independently
 1154 in forests and open habitats. For the first question, we expected abiotic ((1), climate in purple
 1155 and soil physico-chemistry in orange, Burns *et al.* 2013; Hendriksen *et al.* 2016) and biotic ((2),
 1156 Moore *et al.* 2004; Wardle *et al.* 2004; Hättenschwiler *et al.* 2005; Thakur & Geisen 2019)
 1157 predictors to be important factors in microbial decomposition activity (in green). For the
 1158 second question, we expected the compositions of the bacterial and fungal channel to be
 1159 crucial for microbial decomposition activity in open habitats and forests, respectively ((2), in
 1160 particular hypotheses of Wardle *et al.* 2004). We expected to find evidence of trophic
 1161 regulation by consumers of primary decomposers in both habitats, having a significant top-
 1162 down effect on microbial decomposition activity ((3), consumers are in blue, primary
 1163 decomposers in yellow, Hättenschwiler *et al.* 2005; Thakur & Geisen 2019). Furthermore, this
 1164 trophic regulation could occur between the channels, as they are not completely impermeable
 1165 ((4), Geisen 2016). We set a correlation between the compositions of bacteria and fungi in the
 1166 two habitats to account for their usually strong interactions ((5), e.g. facilitation, competition,
 1167 De Boer *et al.* 2005). Finally, in considering the third question, we expected that
 1168 environmental effects on trophic class compositions would have cascading effects on
 1169 microbial decomposition activity and modulate direct environmental effects ((6 and 2),
 1170 Wardle *et al.* 1998; Wu *et al.* 2011; Tedersoo *et al.* 2014; Delgado-Baquerizo *et al.* 2018; van
 1171 den Hoogen *et al.* 2019; Oliverio *et al.* 2020; Potapov *et al.* 2020; Xiong *et al.* 2021).



1172

1173

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