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1 **Multi-trophic  $\beta$ -diversity mediates the effect of environmental**  
2 **gradients on the turnover of multiple ecosystem functions**

3

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14

15 **Keywords: biodiversity-ecosystem functioning, path analyses, multi-trophic, beta-diversity, Alpine**  
16 **systems, elevation gradient.**

17

18 **Abstract**

19 1. Much effort has been devoted to better understanding the effects of environment and  
20 biodiversity on ecosystem functioning. However, few studies have moved beyond measuring  
21 biodiversity as species richness of a single group and/or focusing on a single ecosystem function.  
22 While there is a growing recognition that along environmental gradients, the compositional turnover  
23 of multiple trophic groups influences not only productivity but multiple ecosystem functions, we do  
24 not know yet which components of multi-trophic  $\beta$ -diversity influence which ecosystem functions.

25 2. Here, we captured the biodiversity found in soils using environmental DNA to study total soil  
26 multi-trophic  $\beta$ -diversity (between all taxa regardless of their trophic group association), horizontal  $\beta$ -  
27 diversities ( $\beta$ -diversities within trophic groups) and vertical  $\beta$ -diversity ( $\beta$ -diversity across trophic  
28 groups) along a 1000-m elevational gradient in the French Alps. Using path analyses, we quantified  
29 how these  $\beta$ -diversity components mediate the effects of environmental turnover on the turnover of  
30 multiple ecosystem functions (i.e. productivity, N-cycling, N-leaching) and overall multifunctionality.

31 3. While we found a strong direct effect of soil properties on the turnover of multiple ecosystem  
32 functions, we also found an indirect effect of climate and soil properties through multi-trophic  $\beta$ -  
33 diversity. More specifically, only total multi-trophic  $\beta$ -diversity and the horizontal  $\beta$ -diversity of  
34 saprophytic fungi were strongly related to the turnover of multifunctionality and, to a lower extent,  
35 the turnover of productivity and N-cycling. Our results suggest that decomposition processes and  
36 resulting nutrient availability are key to understand how ecosystem functions change along edaphic  
37 and climatic gradients in alpine ecosystems.

38 4. Beyond alpine systems, our study stresses the paramount importance of considering the  
39 mediating role of multi-trophic diversity in environmental change impacts on different ecosystem  
40 functions and their multifunctionality.

41

## 42 INTRODUCTION

43 The idea that biodiversity enhances ecosystem functioning and acts as a buffer against  
44 environmental changes is now a consensus in ecology (Cardinale et al., 2012; D. U. Hooper et al.,  
45 2005). Indeed, diverse communities exploit a wide range of available resources (complementarity  
46 effect) and often host the best performing species (selection effect, Hines et al., 2015; Loreau et al.,  
47 2001), which ultimately leads to enhanced ecosystem functioning (Bradford et al., 2014; Hector &  
48 Bagchi, 2007). This idea mostly comes from studies focusing on diversity within single trophic levels,  
49 single ecosystem functions (mainly productivity), and often carried out under controlled conditions  
50 (Cardinale et al., 2012; Loreau, 2010). However, understanding how environmental changes across  
51 space and time will affect natural ecosystems requires to consider the multiple trophic levels in  
52 natural communities and the various ecosystem functions carried out by multi-trophic diversity  
53 (Brose & Hillebrand, 2016; Mayor et al., 2017; Soliveres et al., 2016).

54 Environmental conditions such as climate, available carbon or nitrogen vary by nature over  
55 space and time, for example along elevational gradients (Körner, 2003). They directly influence  
56 ecosystem functions such as litter decomposition, N-cycling, and primary productivity by regulating  
57 the rates of bio-chemical processes (Sveinbjörnsson, Abadie, & Butler, 1995). These environmental  
58 conditions also select specific plant and soil assemblages and there is increasing recognition that the  
59 taxonomic and functional composition of these species assemblages will then influence the  
60 ecosystem functions as well (Hautier et al., 2018; Mori, Isbell, & Seidl, 2018; van der Plas et al., 2016).  
61 It has been recently highlighted that a better process-level understanding of the roles and functions  
62 of biodiversity may be gained through the study of the turnover of ecological communities, i.e. their  
63  $\beta$ -diversity, a so far largely underexplored facet of biodiversity (Mori et al., 2018). Therefore, here we  
64 aim at deciphering direct and indirect effects of the environment by jointly considering the turnover  
65 of environmental conditions, ecosystem functions and  $\beta$ -diversity (van der Plas et al., 2016)

66 Moreover, recent studies have highlighted the importance of accounting for multi-trophic  
67 communities to fully understand the role of  $\beta$ -diversity in ecosystem functions (Hines et al., 2015;

68 Soliveres et al., 2016). Even if experimental work has identified effects at single trophic levels and for  
69 single ecosystem functions (Hines et al., 2015), these effects are likely to be more complex in natural  
70 systems. Indeed, the effects of different groups of species (same trophic level and/or similar  
71 functional characteristics, called trophic groups hereafter) can be simply additive, show synergies or  
72 go in different directions (Hines et al., 2015). For example, symbiotic fungi and herbivorous  
73 nematodes can have opposite effects on the biomass production of individual plant species  
74 (Brussaard, 1998). Therefore, teasing apart the effects of plant, symbiotic fungi and herbivorous  
75 nematodes diversity on ecosystem functioning requires a multi-trophic approach. Recently, Soliveres  
76 et al. (2016), showed that the richness variation of three trophic groups needs to be known to  
77 properly explain a single ecosystem function. In addition, depending on the amount of functional  
78 redundancy between trophic groups, their relative importance may change along environmental  
79 gradients (Setälä, Berg, & Jones, 2005). In other words, expanding the traditional focus on horizontal  
80  $\beta$ -diversity (i.e. within a single trophic group) to a vertical perspective of multi-trophic  $\beta$ -diversity (i.e.  
81 variation across trophic groups) and a total multi-trophic  $\beta$ -diversity (i.e. of all taxa regardless of their  
82 trophic group) should critically improve our understanding of the role of multi-trophic  $\beta$ -diversity on  
83 ecosystem functioning (Figure 1).

84 Finally, natural ecosystems are characterized by many interconnected ecosystem functions. It  
85 is likely that distinct ecosystem functions respond differently to various components of multi-trophic  
86  $\beta$ -diversity. A changing environmental context may also alter the links between ecosystem functions  
87 and multi-trophic  $\beta$ -diversity (Bradford et al., 2014; Setälä et al., 2005). The influence of horizontal  
88 and vertical  $\beta$ -diversities on ecosystem functioning could thus be mis-quantified when focusing on a  
89 single function, e.g. primary productivity, as a proxy for overall ecosystem functioning (Hector &  
90 Bagchi, 2007). Indeed, whereas turnover of productivity may be driven by the horizontal  $\beta$ -diversities  
91 of plants and fungi, turnover of nutrients may depend more on the horizontal  $\beta$ -diversity of bacteria  
92 (Moore et al., 2004; Wall, Bardgett, Behan-Pelletier, Herrick, Jones, Ritz, ... & van der Putten, 2012).  
93 The turnover of N-leaching, usually more related to abiotic characteristics of the ecosystem, might

94 instead be independent of multi-trophic  $\beta$ -diversity. Thus, studying horizontal and vertical  $\beta$ -diversity  
95 effects on different ecosystem functions should clarify how multifunctionality along environmental  
96 gradients is driven by different trophic groups (Delgado-Baquerizo et al., 2016).

97         Here, we study the direct and indirect effects of environmental turnover on the turnover of  
98 multiple ecosystem functions in mountain grasslands by explicitly considering the role of soil  
99 horizontal and vertical  $\beta$ -diversities (Figure 1). Along a 1000 m elevation gradient, we surveyed  
100 climate and soil properties, multi-trophic biodiversity of the most important trophic groups of the  
101 plant-soil compartment (as inferred from environmental DNA, Kress, García-Robledo, Uriarte, &  
102 Erickson, 2015; Taberlet, Coissac, Hajibabaei, & Rieseberg, 2012), and several *in-situ* ecosystem  
103 processes (i.e. primary productivity, N-leaching, N-cycling, and multifunctionality). We first tested  
104 how total multi-trophic  $\beta$ -diversity mediates the effects of environmental turnover on turnover of  
105 multiple ecosystem functions and whether these effects varied between ecosystem functions.  
106 Second, we tested the independent effects of vertical multi-trophic  $\beta$ -diversity and horizontal  $\beta$ -  
107 diversities on the spatial turnover of multiple ecosystem functions. Finally, we jointly analyzed the  
108 relative contributions of horizontal  $\beta$ -diversities of different trophic groups to the spatial turnover of  
109 multiple ecosystem functions.

110

## 111 MATERIEL AND METHODS

### 112 **Study site**

113 The study was carried out in the French Alps, along a continuous elevation gradient (1750-  
114 2725m a.s.l., Arves Massif, 45.12°N, 6,40°E) in a cow-grazed pasture. Subalpine grasslands dominate  
115 the bottom of the gradient while sparsely vegetated alpine meadows characterize higher elevations.  
116 Ten sites were sampled in summer 2012 along the same south-facing slope and they were separated  
117 by an 100m elevation difference and an average distance of 340m. Each site consisted of two  
118 10mx10m plots with homogeneous vegetation (see Chalmandrier et al., 2017, for more details).

119

### 120 **Environmental variables**

121 We considered four bioclimatic variables known to be strong drivers of community assembly in  
122 mountain systems (Körner, 2003): soil temperature, solar radiation, growing season length (GSL) and  
123 number of frost days. Growing season length and annual number of frost days were derived from  
124 Landsat 7 and 8 imageries (Carlson, Choler, Renaud, Dedieu, & Thuiller, 2015). Solar radiations were  
125 calculated with the area solar radiation tool in ArcGIS (version 10.2, 2013; Redlands, CA, USA) using a  
126 2-m LiDAR digital elevation model and the clear sky model set to a sky size of 2800 pixels (Carlson et  
127 al., 2015). Soil temperature was measured in the field.

128 To capture small scale variation, we added local topographic variation using elevation, slope, the  
129 topographic wetness index (TWI) and the topographic position index (TPI) with a 50cm resolution  
130 Digital Elevation Model derived from the airborne LiDAR data acquired the year of sampling.

131 Finally, we measured soil properties from three soil cores (10 cm depth, 5 cm diameter) taken in  
132 a 1.25m x 1.25m subplot at the center of each plot. Two soil cores were weighed, 5mm-sieved and  
133 pooled for quantifying soil moisture, soil organic matter content, pH, soil texture using standard  
134 protocols (Robertson, Coleman, Sollins, & Bledsoe, 1999), and total soil N and C content using an  
135 elemental analyzer (FlashEA1112, ThermoFisher Scientific, MA, USA). We added 100 mL of distilled  
136 water to saturate the third soil core and calculate the water-filled pore space (WFPS). The soil core

137 was then air-dried, sieved and grounded to calculate gravel weight, total porosity and apparent  
138 density (Legay et al., 2014).

139

140 We found that the first two axes of a principal component analyses run for all produced (and  
141 normalized) environmental variables (figure S1) captured respectively 48.1% and 19.4% of the  
142 environmental variability. We then split the environmental variables in two groups corresponding to  
143 the major environmental gradients of the study area: a climatic gradient and a gradient of soil  
144 properties.

#### 145 Climate

146 To measure the turnover of climate (and topography), we focused on the set of environmental  
147 variables that load strongest on the first axis of the PCA: solar radiation, soil temperature, mean and  
148 variance of GSL, number of frost days, percentage of WFPS, TPI, TWI, altitude and slope. We then  
149 computed Euclidean distances between each pair of plots for these environmental variables, and  
150 defined these pairwise distances as a measure of *climatic turnover*.

#### 151 Soil properties

152 To measure the turnover of soil properties, we focused on the set of environmental variables  
153 that load strongest on the second axis of the PCA: gravel mass, apparent density, soil porosity, soil  
154 pH, percentage of organic matter and of total N. We then computed Euclidean distances between  
155 each pair of plots for these environmental variables, and defined these pairwise distances as a  
156 measure of *soil properties turnover*.

157

#### 158 **Multi-trophic data**

#### 159 Sampling

160 To get an estimate of the diversity found in each of the sampled plot, we analyzed soils samples  
161 through DNA metabarcoding. In each plot, we collected 21 soil samples (10 cm depth, 5 cm  
162 diameter) to account for small-scale heterogeneity (ten samples on each diagonal and a



163 supplementary central one). Soil biodiversity was measured with four different DNA markers. Two  
164 universal markers, one amplifying all Eukaryotes (v6-v7 region of the 18S rRNA gene) and one  
165 amplifying all Bacteria (v5-v6 region of the 16S rRNA gene), were used to obtain a general overview  
166 of the soil multi-trophic composition of the plots. We also used two additional markers focused on  
167 fungi (Internal Transcribed Spacer 1) and vascular plants (Chloroplast trnL-P6 loop). Molecular  
168 analyses and data curation are presented in Ohlmann et al. (2018). We pooled the 21 samples per  
169 plot to obtain a single community of molecular taxonomic units (MOTUs) per plot and converted the  
170 data into presence-absences. The curated sequencing data as well as associated metadata are  
171 available on the Dryad Digital Repository under accession <https://doi.org/10.5061/dryad.5b58400>.

172

### 173 Definition of the trophic groups

174 Following Ohlmann et al. (2018), we grouped the MOTUs based on their taxonomic affiliation,  
175 shared trophic resources and main functions, such as organic matter decomposition. Hereafter, we  
176 will refer to them as *trophic groups*, while other definitions like trophic guilds or tropho-functional  
177 groups could have been given.

178 We first assigned all vascular plant MOTUs to a single trophic group of primary producers, which  
179 directly contribute to ecosystem productivity and to the quality of litter inputs to soils with potential  
180 impacts on nitrogen cycling and loss (Hooper & Vitousek, 1998). Second, we considered microbial  
181 MOTUs (i.e. bacteria and fungi) as decomposers. We distinguished bacteria from fungi since their  
182 metabolic functions do not fully overlap (De Boer, Folman, Summerbell, & Boddy, 2005). We further  
183 used the FUNguild database (Nguyen et al., 2016) distinguish symbiotic (i.e. mycorrhizal), saprophytic  
184 and pathogenic fungi. Finally, the diversity of soil micro- and mesofauna regulates the activity and  
185 abundance of soil microbes and associated nutrient recycling by shredding/grazing leaf litter or  
186 feeding directly on microbes (Crowther et al., 2015; Puleman et al., 2012). They should thus shape  
187 the multi-trophic  $\beta$ -diversity and have a determinant impact on multiple ecosystem functions. We  
188 thus extracted from the Eukaryotes-marker, all MOTUs assigned to nematodes, springtails, and

189 oribatid mites which are the most abundant belowground multicellular organisms (Wall et al. 2012).  
 190 We further distinguished bacterivore from herbivore/fungivore nematodes using the NEMguild  
 191 database (Nguyen et al., 2016), where nematode species trophic modes are defined on the basis of  
 192 the morphology of their mouth.

193

#### 194 Different components of multi-trophic $\beta$ -diversity

195 First, we computed the true turnover (Baselga, 2010) of the whole soil community (i.e. ignoring  
 196 trophic groups) as a measure of the *total multi-trophic  $\beta$ -diversity* using the Simpson dissimilarity  
 197 index between each pair of plots (Eq. 1).

$$198 \quad \beta_{kl} = \frac{\min(\|P_k\| - \|P_{k \cdot P_l}\|, \|P_l\| - \|P_{k \cdot P_l}\|)}{\|P_{k \cdot P_l}\| + \min(\|P_k\| - \|P_{k \cdot P_l}\|, \|P_l\| - \|P_{k \cdot P_l}\|)} \quad (1)$$

199 Where  $k$  and  $l$  are the focal plots (such as  $1 \leq k \leq K \wedge 1 \leq l \leq K$ ,  $K$  the total number of plots),  
 200  $P = (P_{ki})_{\substack{1 \leq k \leq K \\ 1 \leq i \leq n}}$  is the community matrix of the whole soil community ( $n$  is the total number of  
 201 MOTUs and  $P_{ki} \in \{0,1\}$  denotes the presence of the MOTU  $i$  in plot  $k$ ).  $P_k$  is the community vector of  
 202 the plot  $k$  and  $\|P_k\| = \sum_{i=1}^n P_{ki}$  denotes the MOTUs richness of the plot  $k$ .  $\|P_{k \cdot P_l}\|$  is the number of  
 203 shared MOTUs between plot  $k$  and  $l$ .

204 Second, we calculated the true turnover (Baselga, 2010) of each single trophic group as  
 205 measures of *their horizontal  $\beta$ -diversities* using the Simpson dissimilarity index between each pair of  
 206 plots (Eq. 2).

$$207 \quad \beta_{kl}^g = \frac{\min(\|P_k^g\| - \|P_{k \cdot P_l}^g\|, \|P_l^g\| - \|P_{k \cdot P_l}^g\|)}{\|P_{k \cdot P_l}^g\| + \min(\|P_k^g\| - \|P_{k \cdot P_l}^g\|, \|P_l^g\| - \|P_{k \cdot P_l}^g\|)} \quad (2)$$

208 Where  $k$  and  $l$  are the focal plots (such as  $1 \leq k \leq K \wedge 1 \leq l \leq K$ ,  $K$  the total number of plots),  $g$  is  
 209 the focal trophic group,  $P^g = (P_{ki}^g)_{\substack{1 \leq k \leq K \\ 1 \leq i \leq n_g}}$  is the community matrix of the group  $g$  ( $n_g$  is the total  
 210 number of MOTUs and  $P_{ki}^g \in \{0,1\}$  denotes the presence of the MOTU  $i$  in plot  $k$ ).  $P_k^g$  is the  
 211 community vector (of the group  $g$ ) of the plot  $k$  and  $\|P_k^g\| = \sum_{i=1}^{n_g} P_{ki}^g$  denotes the richness of the  
 212 plot  $k$  for the group  $g$ .

213

214 And finally, we calculated the richness variation across trophic groups as a measure of the  
215 *vertical  $\beta$ -diversity* using the Bray-Curtis (BC) dissimilarity index between each pair of plots (Legendre  
216 & Legendre, 1998):

$$217 \quad BC \beta_{kl} = \frac{2 \sum_{g=1}^G \min(\|P_k^g\|, \|P_l^g\|)}{\sum_{g=1}^G (\|P_k^g\| + \|P_l^g\|)} \quad (3)$$

218 Where G is the total number of trophic groups.

219

## 220 **Multifunctionality data**

### 221 Productivity

222 We measured turnover of primary productivity using two types of data. First, we measured the  
223 total green biomass of the year *in situ*, which constitutes a good proxy of the annual biomass  
224 increment. We harvested all the vegetation at the ground level on a 1mx1m plot, sorted out the  
225 current year live and recently senescent material, dried and weighed it. We used the spatial mean  
226 and variability of the Normalized Difference Vegetation Index (NDVI), a proxy of the photosynthetic  
227 activity (Yoder & Waring, 1994), as a complementary measure. For each plot, we computed spatial  
228 mean and variance of NDVI using an air-borne 15cm resolution infrared picture taken at the  
229 productivity peak in August 2012 (Yoder & Waring, 1994) for the whole elevation gradient. We then  
230 calculated their Euclidean distance for each pair of plots. *Productivity turnover* was then defined as  
231 the Euclidean distances between each pair of plots for the three measures: total green biomass,  
232 spatial mean and variance of NDVI.

233

### 234 N-Cycling

235 To estimate turnover of N-cycling, we used the same two soil cores as for soil physico-chemical  
236 measurements (see environmental data). We estimated the decomposability of organic matter by  
237 calculating the C:N ratio. Soil nutrients (nitrate ( $\text{NO}_3^-$ ), ammonium ( $\text{NH}_4^+$ ), total dissolved nitrogen

238 (TDN) and dissolved organic nitrogen (DON) were determined from soil extracts with 0.5 M K<sub>2</sub>SO<sub>4</sub>  
239 (Jones & Willett, 2006) using a photometric analyzer (Gallery Plus, Thermo Fisher Scientific, Waltham,  
240 Massachusetts, USA). We estimated the relative availability of different forms of N by calculating the  
241 ratio of total dissolved nitrogen on total nitrogen (N-TDN/N) and the ratio of dissolved organic  
242 nitrogen on mineral nitrogen (N-DON/(N-NO<sub>3</sub>+N-NH<sub>4</sub>)) because dissolved organic N, particularly  
243 amino acids, constitutes a large portion of the N budget of plants in these high latitude ecosystems  
244 (Loomis, Ruess, Sveinbjörnsson, & Kielland, 2006). Finally, potential nitrogen mineralization rates  
245 were used to estimate the ability of the ecosystem to mobilize soil organic matter and supply mineral  
246 N (Legay et al., 2016), and measured based on anaerobic incubations of fresh soil subsamples (dark, 7  
247 days, 40 °C), during which organic N was mineralized and accumulated as NH<sub>4</sub><sup>+</sup> (Waring & Bremner,  
248 1964; Wienhold, 2007). The difference between NH<sub>4</sub> contents in a given sample before (t1) and after  
249 the anaerobic incubation (t2) gave PNM = [(NH<sub>4</sub><sup>+</sup>-N)<sub>t2</sub>-(NH<sub>4</sub><sup>+</sup>-N)<sub>t1</sub>]/dw/7 days. *N-cycling turnover* was  
250 then defined as the Euclidean distance between each pair of plots for C/N, N-TDN/N, potential  
251 mineralization and N-DON/(N-NO<sub>3</sub>+N-NH<sub>4</sub>).

252

### 253 N-leaching

254 As a proxy for nitrogen losses through leaching we measured potential ammonium and nitrate  
255 leaching from the percolate. Percolated water was filtered through a Whatmann filter paper n°42  
256 (2.5µm pore size) and analyzed using a photometric analyzer to calculate potentially leached NH<sub>4</sub><sup>+</sup>-N  
257 and NO<sub>3</sub><sup>-</sup>-N (Legay et al., 2016). *N-leaching turnover* was then defined as the Euclidean distance  
258 between each pair of plots for potential ammonium and nitrate leaching.

259

### 260 Multifunctionality

261 We calculated *multifunctionality turnover* as the Euclidean distance between each pair of plots  
262 for all measured ecosystem processes. Correlations of each ecosystem function to the

263 multifunctionality turnover are presented in Appendix (Figure S2). We also run all the analyses for  
264 each ecosystem process separately.

265

## 266 **Statistical Analyses**

267 To address our first two objectives, we performed a set of path analyses using the lavaan  
268 package in R (Figure 2, R Core Team, 2018; Rosseel, 2012). All variables were first centered and  
269 normalized. First, we built four path analyses independently for each of the three single ecosystem  
270 functions and multifunctionality to determine the effects of climatic and soil properties turnover and  
271 of total multi-trophic  $\beta$ -diversity. Second, we built four path analyses independently for each of the  
272 three single ecosystem functions and multifunctionality to determine the effects of environmental  
273 turnover (turnover of climate and soil properties) and of vertical  $\beta$ -diversity. Finally, we built 36  
274 independent path analyses independently to assess the effect of each of the 9 trophic groups on  
275 each of the three single ecosystem functions and multifunctionality while including in each model the  
276 effects of the two sets of variables (climate and soil properties) for environmental turnover.

277 To address our final objective, we built an integrated path model for each ecosystem function  
278 and multifunctionality. We selected variables in a semi-exploratory way. We always included climatic  
279 and soil properties turnover to account for their direct effects on both biodiversity and ecosystem  
280 functions. In respect to multi-trophic  $\beta$ -diversity, we only included the trophic groups that had a  
281 significant horizontal effect and estimated their direct effects on turnover of multiple ecosystem  
282 functions. Since we did not have any prior expectation on their causal relationships, we did not  
283 specify any directional link between them. However, we let free covariances between each pair of  
284 trophic groups to account for the effect of their probable interactions. In turn, all our path analyses  
285 were saturated and we thus could not test the structure of the models.

286 For all above-mentioned path analyses, we tested for the significance of the effects using a  
287 parametric bootstrap procedure based on 10,000 sampling with simultaneous replacement of rows  
288 and columns to quantify confidence intervals for the parameters (Fourtune et al., 2018). This

289 approach is suitable when modelling pairwise distances where the elements of one row/column are  
290 not independent of each other (Fourtune et al., 2018). Parameters are significant when the  
291 confidence intervals do not include zero.

292

## 293 RESULTS

294 Turnover in soil properties was a consistent and strong direct predictor of multifunctionality and  
295 of the three ecosystem functions, while climatic turnover was not (Figure 3 & 4). Total multi-trophic  
296  $\beta$ -diversity was a significant predictor of productivity and multifunctionality turnover and almost as  
297 important as soil properties turnover. However, it did not explain N-cycling and N-leaching turnover  
298 (Figure 3).

299 In contrast, when using vertical  $\beta$ -diversity instead of total multi-trophic  $\beta$ -diversity, the diversity  
300 effect vanished and only soil properties turnover had a significant effect on turnover of ecosystem  
301 functions, including multifunctionality (Figure 4). In other words, the effect of total multi-trophic  $\beta$ -  
302 diversity on turnover of multiple ecosystem functions was not driven by vertical  $\beta$ -diversity.

303 Finally, focusing on the independent effects of horizontal  $\beta$ -diversities of the different trophic  
304 groups, the most important predictors of multifunctionality and productivity turnover were soil  
305 properties turnover and horizontal  $\beta$ -diversities of saprophytic fungi, followed by symbiotic fungi,  
306 herbi-fungivore nematodes, pathogenic fungi and bacteria (Figure 5, S3). For N-cycling turnover, the  
307 most important predictors were soil properties turnover and horizontal  $\beta$ -diversities of saprophytic  
308 fungi, followed by symbiotic fungi and pathogenic fungi (Figure 5, S3). No component of multi-  
309 trophic  $\beta$ -diversity was linked to N-leaching turnover (Figure 5), for which soil properties turnover  
310 was the only significant predictor (Figure S7). For the non-aggregated ecosystem processes, different  
311 subsets of trophic groups were the best predictors, but the general trends remained (Figure S7).

312  
313 The integrated path models that considered several trophic groups together, but were built  
314 independently for each ecosystem function and multifunctionality, suggested how the pieces of the  
315 puzzle can be put together (Figure 6). Consistent with the results above, soil properties were of  
316 primary importance for all considered ecosystem functions and multifunctionality directly, whereas  
317 climate was not (Figure 6, Figure S4 & S5). Similar figures emerged when considering each ecosystem  
318 process independently (Figure S7).

319 Climatic turnover and soil properties turnover influenced horizontal  $\beta$ -diversities of most of the  
320 trophic groups (Figure S6). Pathogenic fungi (Figure 6, Figure S4 & S5, Table S1) and, to a lower  
321 extent, saprophytic fungi (Table S1) were directly affected by climate. Bacteria and, to a lesser  
322 extent, herbi-fungivorous nematodes and saprophytic fungi were directly affected by soil properties  
323 (Figure 6, Figure S4 & S5, Table S1).

324 Importantly, all trophic groups were interlinked and were thus involved in the indirect effects of  
325 climate and soil properties on multiple ecosystem functions. Pathogenic fungi were strongly linked to  
326 symbiotic and saprophytic fungi (Figure 6, Figure S4 & S5). Bacteria were linked especially to  
327 saprophytic fungi (Figure 6, Figure S4) and to a lesser extent to symbiotic fungi (Table S1).

328 Finally, the only significant biotic predictor for the turnover of multifunctionality was the  
329 horizontal  $\beta$ -diversity of saprophytic fungi (Figure 6). Additionally, horizontal  $\beta$ -diversity of herbi-  
330 fungivorous nematodes showed a strong effect even if not significant (Table S1). Results for  
331 productivity turnover showed comparable trends but with weaker effects (Figure S4). The combined  
332 horizontal  $\beta$ -diversities did not explain N-cycling turnover (Figure S5). N-leaching turnover was not  
333 considered here since it was not positively linked to any of the multi-trophic  $\beta$ -diversity components  
334 in the previous path analyses. When we considered the non-aggregated ecosystem processes in the  
335 same way, different trophic groups, also mostly fungi, had a significant effect on different ecosystem  
336 processes: saprotroph fungi on dissolved N:total N, symbiotic fungi on soil C:N, pathogenic on  
337 dissolved organic N:dissolved inorganic N and fungi-herbivorous nematodes on total green biomass  
338 (Figure S7.C, S7.D).

339

340



341 **DISCUSSION**

342 Brose & Hillebrand (2016) recently called for a shift from traditional biodiversity and  
343 ecosystem functioning experiments under controlled conditions to natural systems with (i) multi-  
344 trophic communities, (ii) varying environmental conditions, and (iii) larger spatial scales. Here, we  
345 tackled this challenge by using multi-trophic  $\beta$ -diversity measures to investigate how they mediate  
346 the influence of environmental turnover on the turnover of multiple ecosystem functions.

347 In our study along an elevation gradient in the French Alps, we found that environmental  
348 turnover influenced ecosystem functioning turnover both directly and indirectly via biodiversity  
349 turnover. Surprisingly, only the turnover of soil but not climatic properties contributed significantly to  
350 the direct pathway. Due to varying limitations in soil organic matter and water availability,  
351 decomposition rates and nutrient retention times changed across the gradient, with direct  
352 consequences on N-cycling, productivity and N-leaching (Gavazov, 2010; Louca et al., 2018). In  
353 contrast to our findings, a large body of literature on size reduction of alpine plants with increasing  
354 elevation led us expect that differences in temperature-related variables (e.g. Growing Season  
355 Length, number of frost days and solar radiations) captured in our climatic turnover variable (PCA  
356 axis 1, Figure S1) would drive at least productivity turnover (Choler, 2005; Körner, 2003; Schöb,  
357 Kammer, Choler, & Veit, 2009; Sundqvist, Sanders, & Wardle, 2013). However, a few recent studies  
358 that also included the indirect effect of climate through biodiversity support our results. Together  
359 this suggests that under natural conditions the direct effect of climate on ecosystem functioning can  
360 be overridden and/or compensated by complex cascading effects from microorganisms to plants. For  
361 example, Crowther et al. (2015) showed that turnover of ecosystem functions can be bottom-up  
362 regulated by the climatic conditions in harsh environments but top-down regulated through  
363 consumption of the microbes by the soil fauna, when environmental constraints are less extreme.  
364 Also, at the global scale, Delgado-Baquerizo et al. (2016) reported only a negligible effect of  
365 temperature on multifunctionality, while the effect of microbial community diversity was always  
366 strong and positive. Our results also demonstrated that on top of its direct response to soil

367 properties, turnover of multiple ecosystem functions depends on soil and climatic turnovers through  
368 their effects on the  $\beta$ -diversities of several trophic groups (Figure S6).

369 In order to untangle these cascading effects, we contrasted the effects of several multi-trophic  $\alpha$ -  
370 and  $\beta$ -diversity aspects on multiple ecosystem functions. Unlike total  $\beta$ -diversity (Figure 3), total  $\alpha$ -  
371 diversity (Figure S8) appeared to be a weak predictor of ecosystem functioning, suggesting that a  
372 number of species perform similar functions in soil communities, i.e. they are functionally redundant.  
373 Also, vertical  $\beta$ -diversity did not cause turnover of ecosystem functions (Figure 4), indicating that  
374 whatever their richness, trophic groups cluster particularly functionally redundant species (Louca et  
375 al., 2018; Setälä et al., 2005). Nevertheless, intra-group functional redundancy level may depend on  
376 the studied trophic group. For example, Mori et al. (2015) argue that changes in the composition of  
377 fungal communities can modify ecosystem functioning by altering which ecosystem functions are  
378 preferentially provided, while Louca et al. (2018) showed that bacterial taxa have similar broad  
379 metabolic potential, leading most ecosystem functions to be barely dependent on the taxonomic  
380 composition of bacterial communities. Likewise, in our study, the relationship between  $\alpha$ -diversity  
381 and ecosystem functions was linear and positive only for a small selection of trophic groups and  
382 ecosystem functions (Figure S8). Together, these results suggest that a few of our trophic groups  
383 contain functionally complementary species, pivotal for ecosystem functioning.

384 To avoid an overestimation of the direct effect of these key trophic groups on ecosystem functioning  
385 (Ohlmann et al., 2018), the horizontal  $\beta$ -diversities of their interaction partners partaking in the  
386 studied ecosystem functions should not be omitted (Brose & Hillebrand, 2016; Hines et al., 2015;  
387 Thompson et al., 2012). As such, we found that most trophic groups influenced ecosystem functions  
388 when considered alone (figure 5, figure S6). However, when the horizontal  $\beta$ -diversities of their  
389 interaction partners were added, only the saprophytic fungi  $\beta$ -diversity was significantly linked to the  
390 turnover of multifunctionality, and to a lesser extent to productivity and N-cycling (figure 6, figure S4,  
391 figure S5, Table S1). Saprophytic fungi are critical in the decomposition process because they produce  
392 exo-enzymes processing complex organic compounds (Baptist et al., 2008; Moore et al., 2004; Wall

393 et al. 2012). The resulting simpler compounds, scarce in alpine environments, become available for  
394 plant and microbial absorption (Moore et al., 2004; Wall et al., 2012). Changes in saprophytic fungi  
395 communities should thus alter nutrient availability, which impacts productivity, N-cycling and  
396 multifunctionality (Mori et al., 2016; Valencia et al., 2018). Nevertheless, also the other trophic  
397 groups  $\beta$ -diversities indirectly drove ecosystem functions turnover through their strong links to the  
398 saprophytic fungi  $\beta$ -diversity. In line with a growing number of studies, this suggests that species links  
399 in soil food webs could be pivotal for ecosystem functioning and that they need to be accounted for  
400 in addition to just the  $\beta$ -diversity of species within (horizontal) and across (vertical) trophic groups  
401 (Ohlmann et al., 2019; Setälä et al., 2005; Thompson et al., 2012). In particular, we found that  
402 specific regulators of fungi (e.g. herbi-fungivorous nematodes, figure 6, S4) and competitors (e.g.  
403 bacteria and other fungal trophic groups, De Boer et al., 2005; Nazir, Warmink, Boersma, & Van Elsas,  
404 2010) tend to have an indirect influence on multiple ecosystem functions through their influence on  
405 the compositional turnover of saprophytic fungi. In turn, climatic variables and ecosystem functions  
406 are not linked by a single indirect pathway but by multiple indirect pathways with saprophytic fungi  
407 as a corner stone. This result is in line with several other studies (Mori et al., 2016; Setälä et al., 2005;  
408 Valencia et al., 2018).

409 Our results on both an integrated measure of multifunctionality and more specific measures  
410 of three important functions of alpine ecosystems (i.e. productivity, N-cycling, N-leaching, Sundqvist  
411 et al., 2013) are also consistent with several studies arguing that major biogeochemical pathways are  
412 regulated by a reduced number of energy pathways, broadly supported by some key trophic groups  
413 and sometimes strongly driven by some limiting environmental conditions (Louca et al., 2018). At the  
414 highest scale of aggregation of multiple ecosystem functions, saprophytic fungi being keystones of  
415 multifunctionality suggests that, due to the strong nitrogen limitations in alpine ecosystems (Loomis  
416 et al., 2006; Robson, Lavorel, Clement, & Roux, 2007; Sundqvist et al., 2013; Sveinbjörnsson et al.,  
417 1995), decomposition is acting as a bottle neck for other ecosystem functions (Setälä et al., 2005;  
418 Wardle, 2002). Indeed, ammonium and nitrate produced by decomposers can be leached out,

419 adsorbed on soil particles, denitrified, volatilized, or assimilated by plants and bacteria. The balance  
420 between these processes mainly depends on abiotic soil conditions which control water and solute  
421 transfers, and on the nitrogen demand of plant and microorganisms (Robson et al., 2007) especially  
422 during the productivity peak when plant N-uptake is the highest (Legay et al., 2016). Therefore,  
423 weaker effects of each trophic group horizontal  $\beta$ -diversity on the turnover of productivity and N-  
424 cycling could be explained by a functional complementary effect between trophic groups of fungi and  
425 their specific biotic regulators, and feedbacks between trophic groups and soil. Adding other, and so  
426 far, a bit less studied pathways (e.g. P-cycling, Leff et al., 2015), may have uncovered additional direct  
427 and indirect links of environmental turnover and functioning turnover via  $\beta$ -diversities.

428

429 To conclude, looking at multiple ecosystem functions showed an important mediating role of multi-  
430 trophic  $\beta$ -diversity. Our finding particularly supports the paramount importance of decomposers,  
431 especially saprophytic fungi, and of their interaction partners, in nitrogen limited alpine systems. In  
432 this sense, our study supports recent calls to explicitly integrate known interactions between trophic  
433 groups (Thompson et al., 2012) and for temporal monitoring of the ecosystems (Brose & Hillebrand,  
434 2016), two missing steps towards a better understanding of functional complementarity and  
435 selection effects of diversity and of their role in multiple ecosystem functions (Hines et al., 2015) and  
436 their trade-offs in natural systems.

437 **Author Contributions statement:**

438 CMA, TM and WT conceptualized the overall study and methodology. LC, JCC, TM, WT and LZ  
439 collected the data. LZ run the bioinformatic pipelines. MO built the trophic groups and CMA run all  
440 statistical analyses. CMA led the interpretation of the results and the writing with contributions of all  
441 authors.

442

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448

449 **Data accessibility statement:**

450 Data will be provided after acceptance.

451

452

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619

## Figure Captions

620 **Figure 1:** Environmental turnover (box 1) affects turnover of multiple ecosystem functions (box 3)  
621 directly and indirectly through multi-trophic  $\beta$ -diversity (box 2) along a 1000m elevation gradient  
622 (box 4). In our example (turnover between plots A, B and C, box 2 and 4) total multi-trophic  $\beta$ -  
623 diversity is high between A and B but low between A and C ; horizontal  $\beta$ -diversity is high between  
624 plots A and B for mites and springtails and between A and C for plants but low between B and C for  
625 springtails (community C is nested in B); vertical  $\beta$ -diversity (variation of MOTUs richness across the  
626 groups) is high between B and C but low between A and C.

627 **Figure 2:** Structure of the tested path models.

628

629 **Figure 3:** Total multi-trophic  $\beta$ -diversity mediates the effect of environmental turnover on the  
630 turnover of multiple ecosystem functions. Only direct standardized effects are represented. Direct  
631 standardized effect of total multi-trophic  $\beta$ -diversity is highlighted with a grey area. Significant and  
632 non-significant standardized effects are represented with black and grey points and their associated  
633 confidence intervals, respectively. Direct standardized effects of climatic and soil turnover on the  
634 vertical  $\beta$ -diversity are represented in appendix (Figure S6).

635

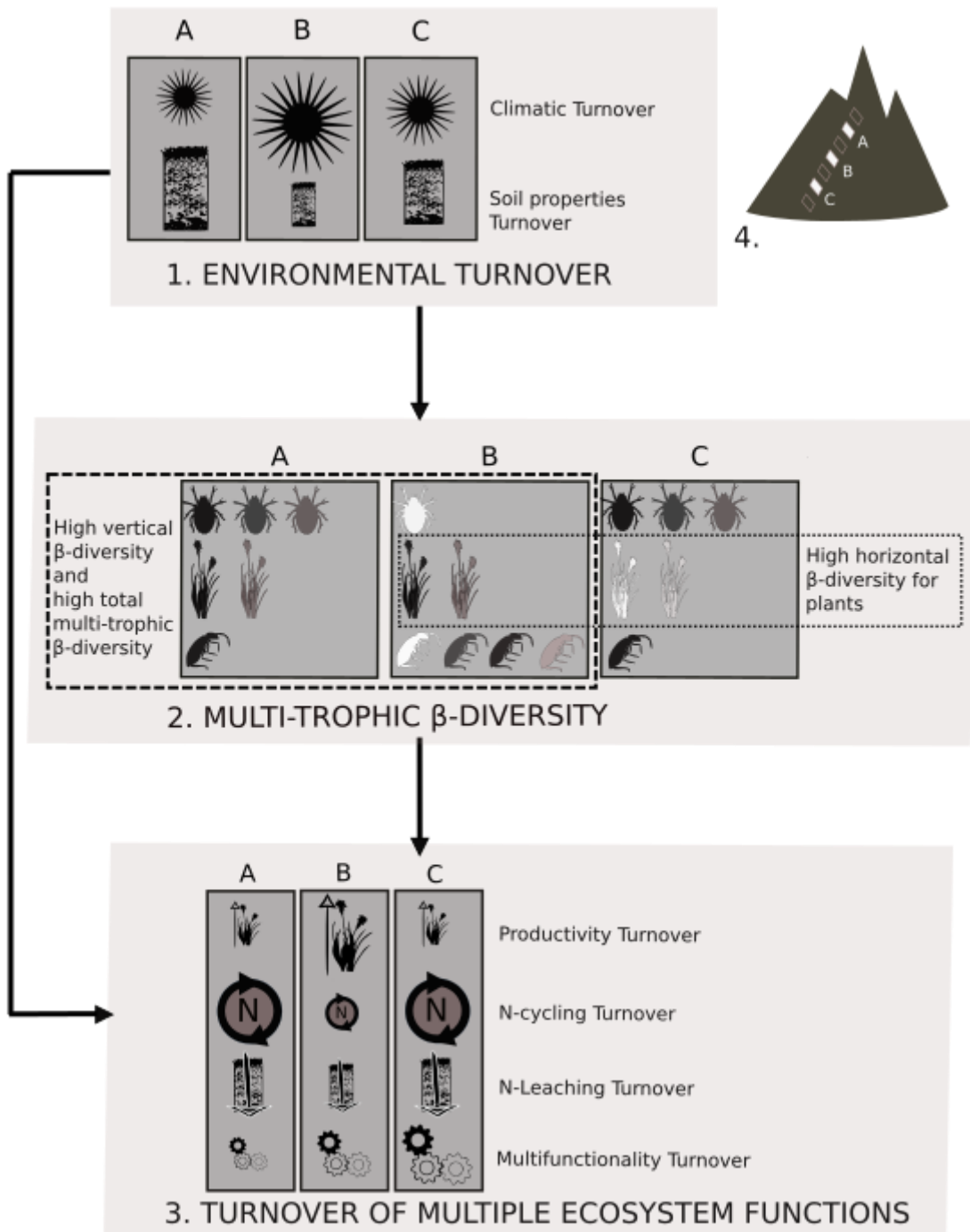
636 **Figure 4:** Vertical  $\beta$ -diversity does not mediate the environmental turnover effect on the turnover of  
637 multiple ecosystem functions. Only direct standardized effects are represented. Direct standardized  
638 effect of vertical  $\beta$ -diversity is highlighted with a grey area. Significant and non-significant  
639 standardized effects are represented with black and grey points and their associated confidence  
640 intervals, respectively. Direct standardized effects of climatic and soil turnover on the vertical  $\beta$ -  
641 diversity are in figure S6.

642 **Figure 5:** Horizontal  $\beta$ -diversities of several trophic groups mediate the environmental turnover  
643 effect on the turnover of multiple ecosystem functions. Only direct standardized effects are

644 represented. Significant and non-significant standardized effects are represented with black and grey  
645 points and intervals, respectively. Direct standardized effects of climatic and soil turnover on the  
646 horizontal  $\beta$ -diversities and on the multiple ecosystem functions are in figure S5 & S6.

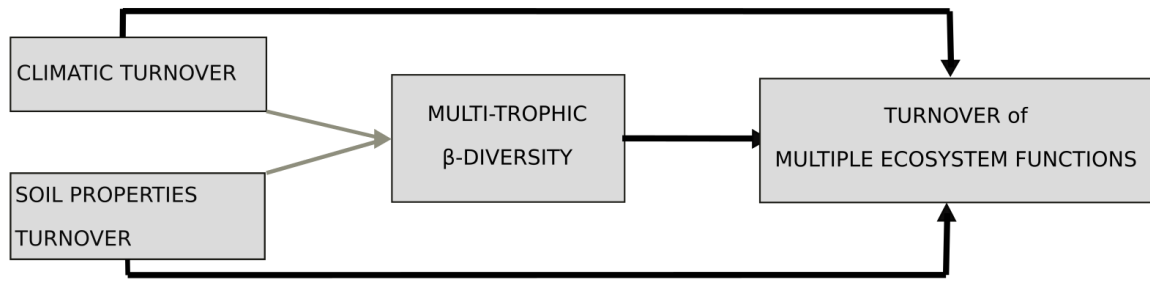
647 **Figure 6:** Integrated path model highlighting the direct and indirect effects of climate and soil  
648 turnover on turnover of ecosystem multifunctionality. The size of the arrows is proportional to the  
649 size of the associated standardized path coefficients (only for significant paths). Dotted grey lines  
650 represent non-significant paths. Paths with double arrows represent correlations.

Figure 1



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Figure 2



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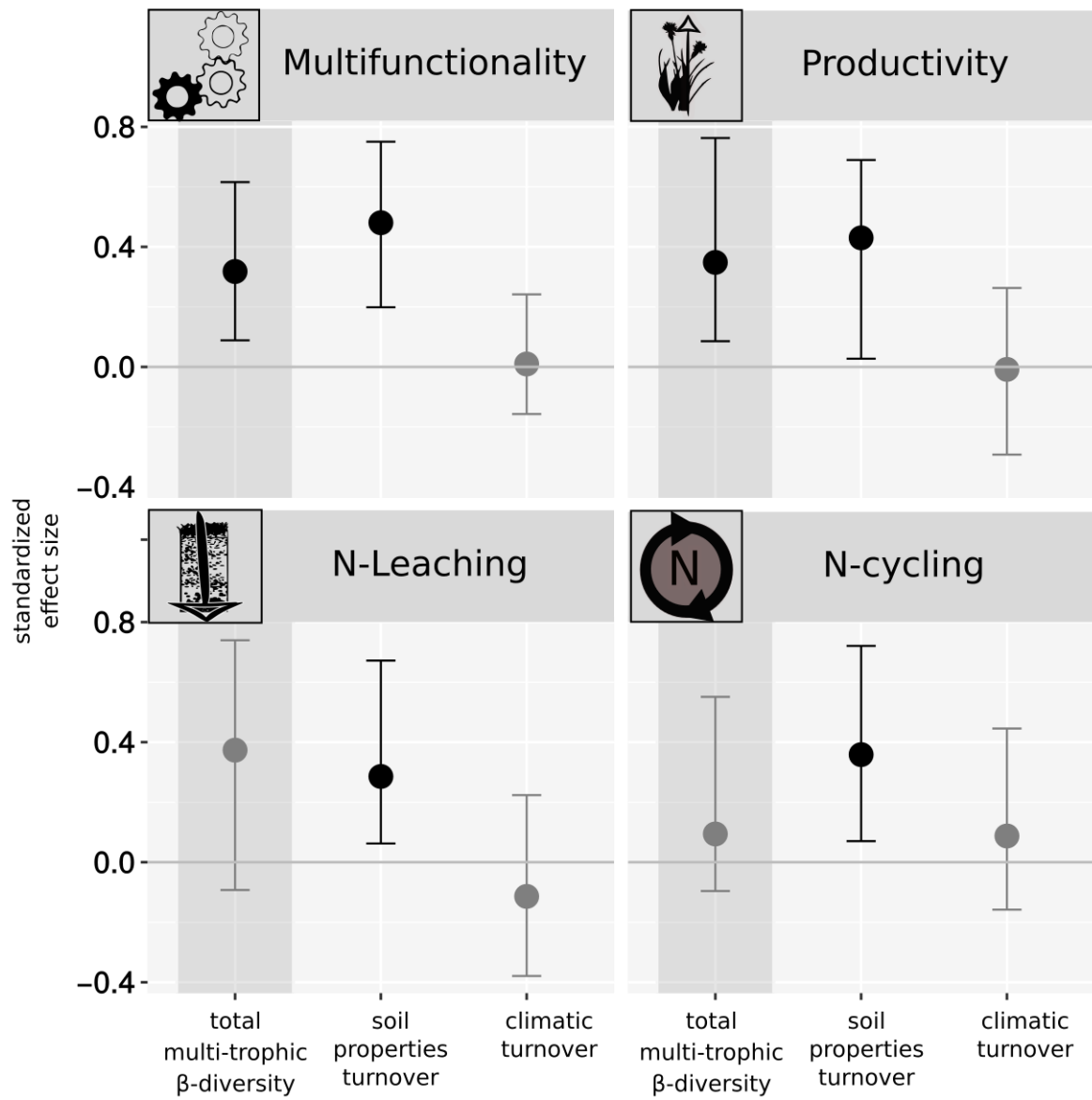
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Figure 3



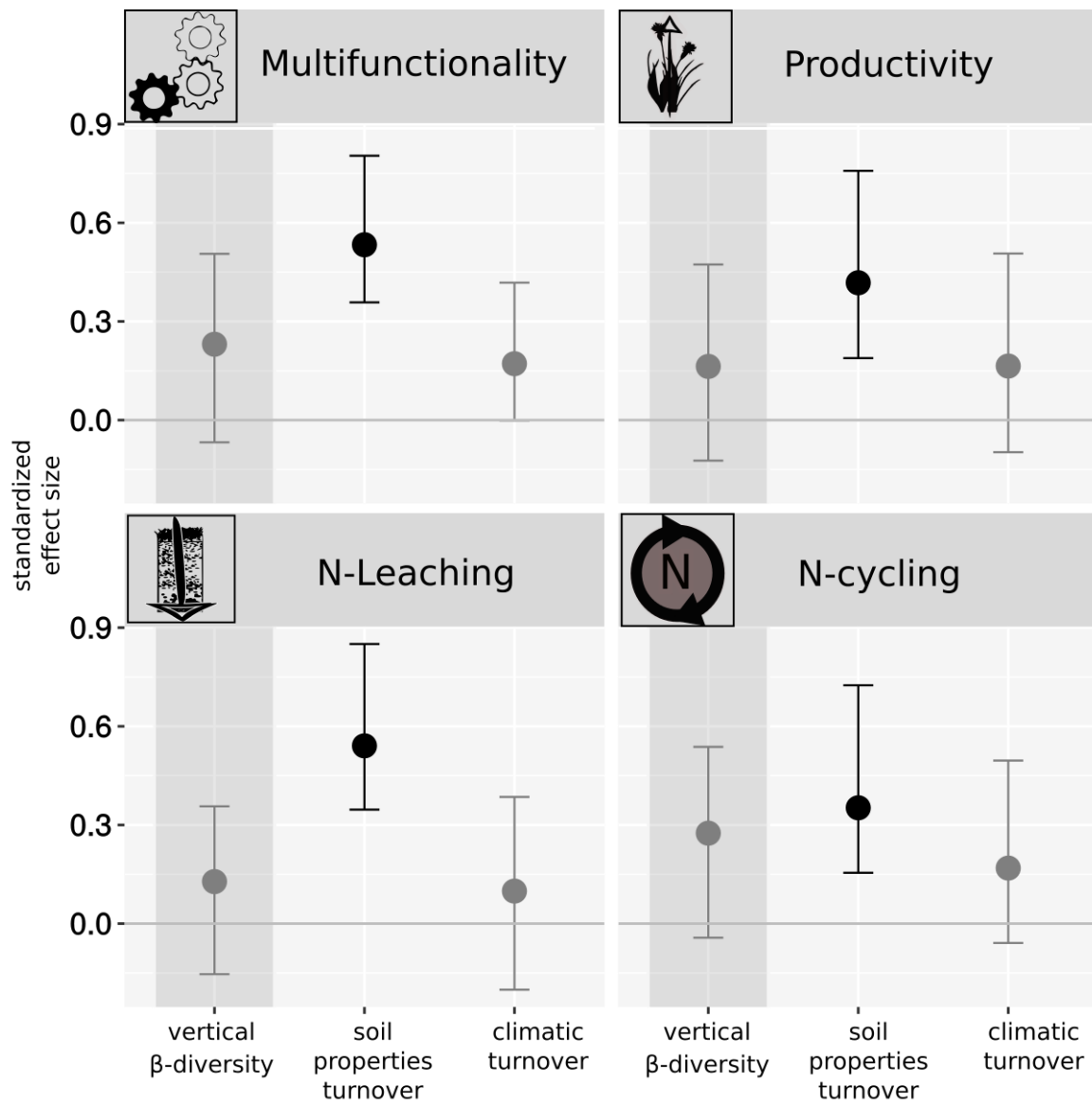
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Figure 4

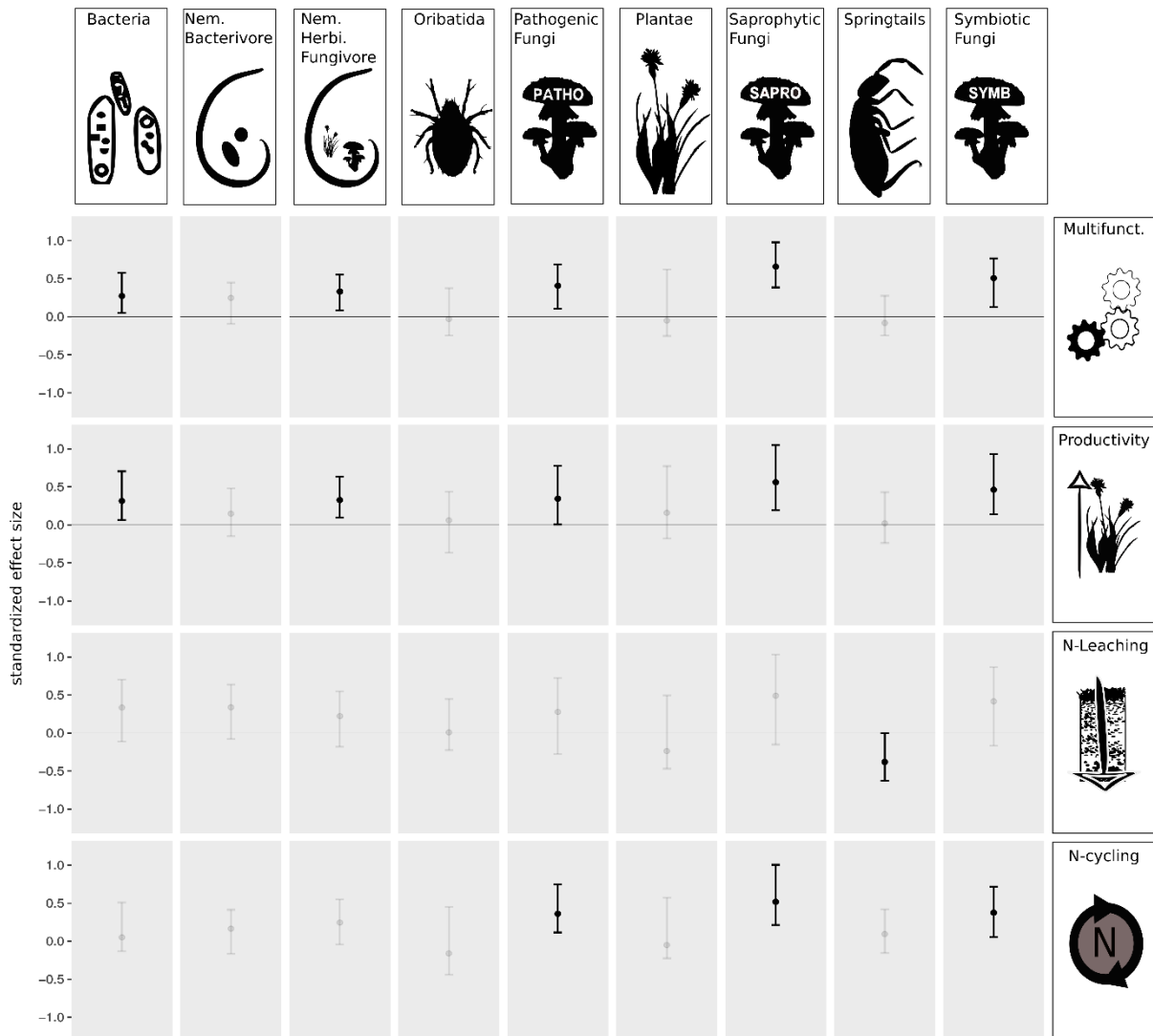


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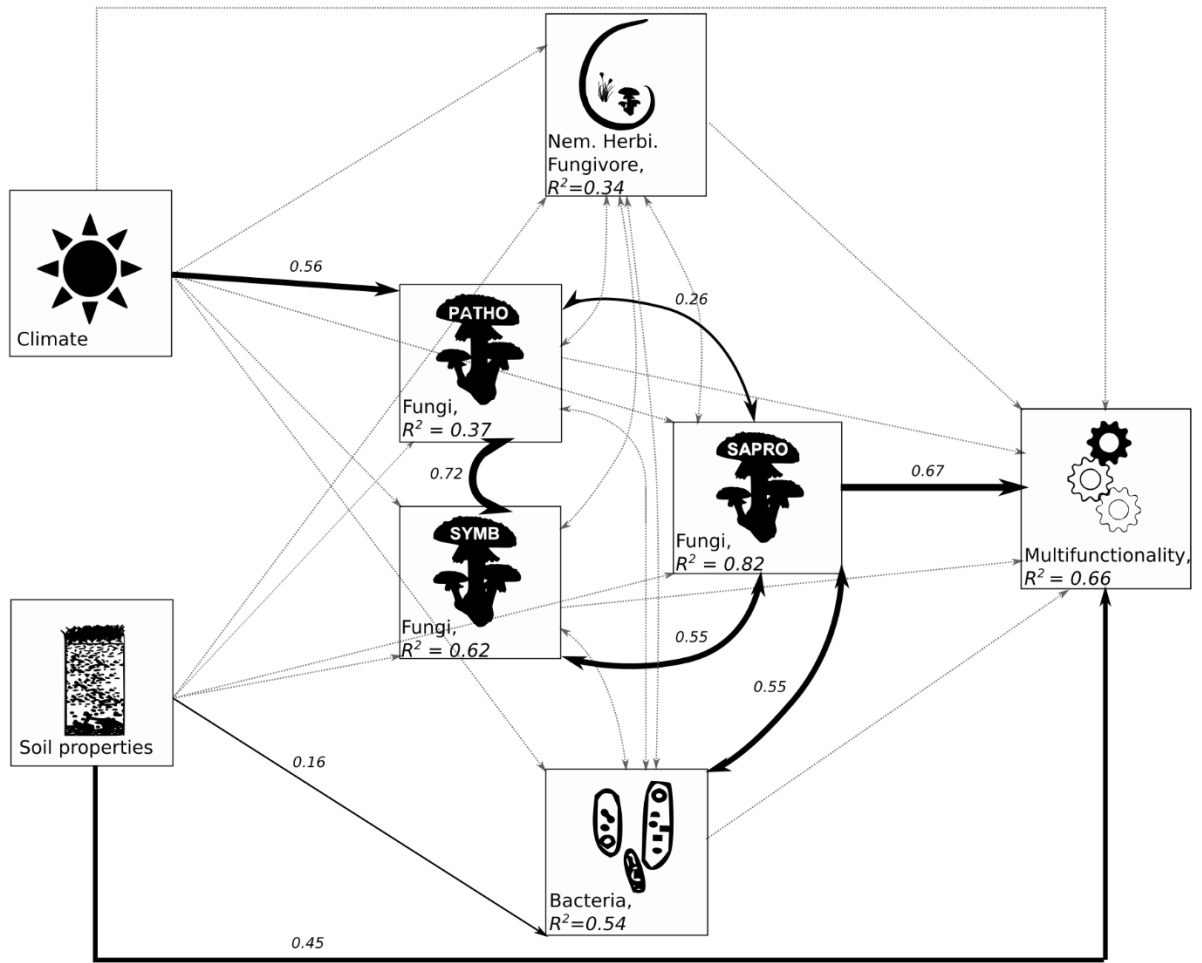
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Figure 5



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Figure 6



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