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## Food web structure and energy flux dynamics, but not taxonomic richness, influence microbial ecosystem functions in a Sphagnum-dominated peatland

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### ► To cite this version:

Vincent E.J. Jassey, Owen Petchey, Philippe Binet, Alexandre Buttler, Geneviève Chiapusio, et al.. Food web structure and energy flux dynamics, but not taxonomic richness, influence microbial ecosystem functions in a Sphagnum-dominated peatland. *European Journal of Soil Biology*, 2023, 118, pp.103532. 10.1016/j.ejsobi.2023.103532 . insu-04182721

**HAL Id: insu-04182721**

**<https://insu.hal.science/insu-04182721>**

Submitted on 10 Oct 2023

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1 **Food web structure and energy flux dynamics, but not taxonomic richness, influence**  
2 **microbial ecosystem functions in a *Sphagnum*-dominated peatland**

3  
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23  
24 **Authorship:** VEJJ conceived the study in close consultation with JMB and OLP. DG and FLD obtained the  
25 field permit for sampling. VEJJ, PB, AB, GC, FD, DG, EADM and FLD did the sampling. VEJJ performed  
26 the microscopic analyses with the help of DG and EADM. AB performed the vegetation survey. PB and FD  
27 performed the enzymatic and decomposition analyses, respectively. VEJJ and JMB developed the food web  
28 modelling framework with the help of OLP. VEJJ performed numerical analyses and wrote the first draft of  
29 the manuscript. All authors reviewed and contributed to the final form of the manuscript.

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37  
38 **Running title** (45 characters): Microbial food web-ecosystem functions linkages

39 **Highlights**

- 40 • Soil microbial food webs determine soil biodiversity and ecosystem functioning
- 41 • What aspect of microbial food web underpin ecosystem functions is unclear
- 42 • Biomass and energy flux dynamics, but not taxonomic richness, influence peatland ecosystem
- 43 functions
- 44 • The inclusion of microbial food web properties in biogeochemical models is fundamental

45 **Abstract**

46 Soil microbial communities are vital for multiple ecosystem processes and services. In particular, soil  
47 microbial food webs are key determinants of soil biodiversity, functioning and stability. Unclear,  
48 however, is how structural features of food webs, such as species richness and turnover, biomass and  
49 energy transfer across trophic levels, influence the provisioning and stability of ecosystem  
50 functioning. Here, we explore the relationships between different facets of microbial food web  
51 structure (e.g. species richness, connectance, biomass and energy fluxes across trophic levels) and  
52 ecosystem functions (i.e. decomposition and microbial enzyme activity) across different habitats and  
53 depths in a peatland. We show that no aspect of taxonomic richness directly explained variation in  
54 ecosystem functions. Instead, we find that trophic interactions between basal species and primary  
55 consumers, and especially increasing connectance, biomass and energy flux transiting from  
56 decomposers and phototrophs to algivores, bacterivores and fungivores, enhance ecosystem functions  
57 in the peatland. These findings demonstrate that focusing on taxonomic diversity without explicit  
58 inclusion of food web structure and energy flows therein gives an incomplete and uninformative  
59 comprehension of relationships between biodiversity and ecosystem functioning, at least in peatlands.  
60 Our findings further suggest that the inclusion of soil microbial food webs in large-scale  
61 biogeochemical models is of fundamental importance to provide the necessary guidance for managing  
62 and mitigating the effects of environmental change.

63

64 **Keywords**

65 Biodiversity-ecosystem functioning, ecosystem function variation, energy channels, food web  
66 modelling, microbiome, soil functioning, phototrophs, decomposition, predation

67

## 68 1. Introduction

69 The current erosion of biodiversity raises concerns regarding the provisioning and stability of  
70 ecosystem functioning. A large body of experimental studies showed the positive, but saturating,  
71 effect of increasing biodiversity on ecosystem functioning across different groups of organisms,  
72 trophic levels, and ecosystems [1–6]. These findings provided fundamental knowledge in  
73 understanding the link between diversity and ecosystem services and offered novel insights for  
74 predicting the consequences of global biodiversity loss on ecosystems [7,8]. However, studies  
75 examining the effect of biodiversity on ecosystem functioning are often limited in terms of the  
76 diversity tested. For example, many studies only involved levels of species richness far lower than in  
77 natural conditions— especially in soils [9]— and/or examined biodiversity effects only within a single  
78 trophic level [6]. These limitations constrain the practical importance of any revealed relationship  
79 between diversity and ecosystem functioning because real systems are often very diverse and have  
80 multiple trophic levels [6,10,11].

81 Recently, ecologists began to remove this limitation by exploring the effect of biodiversity on  
82 ecosystem functioning in multitrophic systems [4,12,13], sometimes highlighting hidden  
83 relationships between biodiversity and ecosystem functioning [10]. Although these studies have  
84 provided fundamental advances about how the structure of complex ecological systems modulates  
85 ecosystem functioning [14,15], they are often based on unrealistically simplified food chains or food-  
86 web configurations [10,16] but see [17,18]. Furthermore, a number of these studies typically  
87 investigated trophic structures with qualitative feeding relationships assessed in terms of network  
88 connectance and nestedness [19,20], ignoring important aspects of food web structure such as  
89 biomass distribution across trophic levels, omnivory, intraguild predation, and fluxes of energy along  
90 trophic links.

91 Such structural features of food webs have long been demonstrated to have large impacts on  
92 food-web stability [21,22], but their effect on the provisioning and stability of ecosystem functioning  
93 is still poorly understood [15,21,23,24]. Yet changes in trophic structure facets can influence  
94 ecosystem functioning [23,25]. For example, previous work showed that ecosystem functions such  
95 as productivity decrease when consumer diversity increases and/or when the diversity of basal species  
96 decreases [10,15]. Other studies suggested that shifts in the biomass of basal species and/or predators  
97 can destabilize connected ecosystem functions such as primary production or carbon mineralization  
98 through top-down or bottom-up effects [26–28]. Further, energy fluxes across trophic levels which  
99 express energy consumption by different trophic groups [29] can have feedback effects on basal  
100 consumers and the ecosystem processes they drive such as C, N, and P mineralization rates [28,30–  
101 32]. What trophic structure facet best predict rates of ecosystem functioning is however poorly

102 known, and many links between structural features of food webs and ecosystem functions still remain  
103 to be tested.

104 Despite an increasing focus on understanding whether and how structural features of food  
105 webs can determine ecosystem functioning, very little concentration emerged on soil systems. The  
106 largest body of evidence comes from modelled and experimental studies focusing on aquatic systems,  
107 plants, and animals [33,34], often leaving aside soil microbiomes (but see [5,30,31]. This imbalance  
108 is concerning given that soils are among the most diverse ecosystems on the planet with millions of  
109 species of bacteria, archaea, fungi, protists, and metazoan occupying various trophic levels in soil  
110 food webs [35–37]. Although relatively rare, observational evidence shows that soil microbial  
111 diversity can determine numerous ecosystem functions [12,38]. However, data are relatively scarce  
112 for the relationship between multitrophic soil communities, including bacteria, fungi, protists, and  
113 metazoan, and ecosystem functions [5]. Moreover, information about what soil microbial trophic  
114 features determine ecosystem functions is also lacking. A rigorous assessment of the role of  
115 qualitative and quantitative structural features of soil microbial food web in regulating ecosystem  
116 functions is urgently needed to better understand the consequences of soil biodiversity losses for the  
117 maintenance of ecosystem functioning and services that are critical for global ecosystem  
118 sustainability.

119 Here, we used an observational field study to identify what structural features of the microbial  
120 food web (e.g. richness, connectance, biomass, and energy fluxes across trophic levels) underpin  
121 ecosystem functioning. We conducted a soil microbiome analysis across twelve natural peatland plots  
122 equally divided between a dry and a wet area (see details in section 2.1). In each plot, we analysed  
123 soil microbiome (including bacteria, fungi, protists, and metazoans) at three different depths as  
124 decreasing light availability and increasing peat moisture are likely influencing microbial  
125 communities and hence food web structures and properties [39,40]. We chose such a multi-spatial  
126 approach to simulate changes in microbial richness, diversity, and biomass [39,41], and so the food  
127 web structure. Using a machine learning approach to uncover microbial food webs from species lists  
128 and traits [42], we obtained plot-and depth-scale food webs (12 plots x 3 depths = 36 food webs in  
129 total). We also obtained data for two main ecosystem functions that are influenced by soil  
130 microorganisms and that correspond to key components of peatland ecosystem services— organic  
131 matter decomposition and soil enzyme activity. We aimed at answering two questions: 1) How do  
132 structural features of microbial food web vary along a depth profile and between wet and dry areas?  
133 2) What structural feature of the microbial food web relates to ecosystem functions best?

134

135

## 136 2. Materials and methods

### 137 2.1 Study site and sampling

138 The research was conducted in an undisturbed *Sphagnum*-dominated peatland; Le Forbonnet peatland  
139 (Jura Mountains, north-eastern France (46°49'35''N, 6°10'20''E). Cold winters (on average -1.4 °C)  
140 and mild summers (on average 14.6 °C) characterized the site. The annual mean temperature  
141 measured at the site over the last fifteen years was 6.5 °C and the annual precipitation was 1200 mm  
142 (<https://data-snot.cnrs.fr/data-access/>). The site is characterized by two dominant and adjacent areas.  
143 The first area (hereafter “WET”) was a transitional *Sphagnum*-dominated poor fen, relatively flat,  
144 homogeneous, and wet (Fig. S1). This area was characterized by a moss cover dominated by  
145 *Sphagnum fallax*, and to a lesser extent by vascular plants such as *Eriophorum vaginatum*, *Vaccinium*  
146 *oxycoccus*, and *Andromeda polifolia*. The second sampling area (hereafter “DRY”) was a *Sphagnum*  
147 bog directly adjacent to the poor fen area. Patterns of hummocks with *S. magellanicum*, *V. oxycoccus*,  
148 *E. vaginatum* and *Calluna vulgaris*, and hollows with *S. fallax*, *Carex rostrata* and *A. polifolia*  
149 characterized the DRY area. The terms “WET” and “DRY” are used to denote the existence of  
150 hydrological, microtopographic, and vegetation gradients driven by the decrease of the water table  
151 depth, the increasing microtopography, and the increase of plant diversity and abundance of vascular  
152 plants between WET and DRY microhabitats [43] (Fig. S1). Commonly found in *Sphagnum*-  
153 dominated peatlands, these two areas are representative of peatlands both in terms of  
154 microtopography, water table depth, and vegetation [44].

155 In WET and DRY areas, we selected six homogeneous and independent plots (50 x 50 cm; twelve  
156 plots in total; see section 2.7) based on their microtopography, water table depth and vegetation cover  
157 (Fig. S1). On June 26<sup>th</sup> 2008, samples of *Sphagnum fallax* were collected in each plot. The minimum  
158 distance between the two closest plots was 7m and the maximal distance was 37 m. *S. fallax* shoots  
159 were collected in each plot around 10 permanent markers for microbial and function analyses (see  
160 below). The goal of this sampling design was to obtain a composite sample from each plot and avoid  
161 any bias due to micro-spatial heterogeneity [41].

162

### 163 2.2 Microbial abundances and biomasses

164 *S. fallax* shoots were separated immediately in the field into three depths: 0-3 cm (living segments)  
165 and 3-6 cm (early decaying segments) and 6-9 cm (dead segments) from the capitulum. Then, the  
166 samples were fixed in 20 mL glutaraldehyde (2% final concentration) and stored at 4°C in the dark.  
167 Microorganisms were extracted from *Sphagnum* mosses following [39]. Briefly, each sample was

168 shaken for 1 min, followed by pressing the mosses by hand to extract liquid. This first filtrate was  
169 kept in a capped tube. Subsequently 20 ml of glutaraldehyde (2%) was added to the mosses, shaken  
170 for 1 min, and pressed again. This second filtrate was left for 8 hours at 4°C to sediment, after which  
171 time the supernatant was added to the mosses while the bottom was added to the first filtrate. The  
172 process of shaking, pressing, and sedimentation was repeated six times, each time using the  
173 supernatant from the previous sedimentation. At each iteration, the sediment was added to the initial  
174 solution to obtain a final sample of 40 ml. The remaining fraction of *Sphagnum* was dried at 80 °C  
175 for 48h and weighed to express microbial density and biomass in grams of dry mass (DM) of  
176 *Sphagnum*. The bacterial abundance was quantified by flow cytometry (bacterial counts) and  
177 epifluorescence microscopy (bacterial size). For the estimations, 1 ml sub-samples were filtered using  
178 a mesh (pores size: 10  $\mu\text{m}$ ). The resulting filtrates were stained with SYBR Green ( $0.1 \times$  final  
179 concentration), incubated in the dark for 15 min, and run on a flow cytometer (FACScalibur,  
180 Novocyte) at a low speed with a count rate not exceeding 5,000 events.s<sup>-1</sup>. Epifluorescence  
181 microscopy was used to determine the size of bacteria: 1 ml sub-samples were stained with DAPI  
182 (4,6- diamino- 2- phenylindole; 3  $\mu\text{g ml}^{-1}$  final concentration), incubated in the dark for 15 min,  
183 filtered on 0.2  $\mu\text{m}$  black membrane filters, and examined by fluorescence microscopy at 1,000 $\times$   
184 magnification. Bacteria sizes were determined automatically using the ImageJ software. The  
185 abundance of fungi, phototrophs (microalgae and cyanobacteria), primary consumers (flagellates,  
186 ciliates, rotifers, and nematodes), and top-predators (testate amoebae), as well as their identification  
187 to species-level when possible, was carried out using a 3- ml subsample and inverted microscopy  
188 ( $\times 400$ , Utermöhl method). For fungi, the number and length of hyphae and spores were quantified.  
189 We chose that approach because our aim was to estimate fungal biomass, for which estimation using  
190 molecular methods is currently limited [45]. The abundance of each species (or group) was then  
191 converted into biovolume ( $\mu\text{m}^3$ ), calculated based on geometrical shapes using dimensions measured  
192 under the microscope (length or diameter; width, and height) [46]. Biovolumes were then converted  
193 to biomass ( $\mu\text{g C}$ ) using conversion factors as given in [46]. The abundance data were then expressed  
194 into carbon biomass, in micrograms of C per gram of *Sphagnum* dry mass ( $\mu\text{g C/g DM}$ ).

195

### 196 2.3 Ecosystem functions

197 Total phenoloxidase activity was quantified as a proxy of soil enzyme activity in each plot and depth.  
198 We chose this enzyme as a proxy because of its crucial role in peatland C cycling [47,48]. Following  
199 Jassey et al. (2011a), phenoloxidases were extracted from 3g of fresh *Sphagnum* shoots in 50 mL  
200 extraction solution containing 0.1 M CaCl<sub>2</sub>, 0.05% Tween 80 and 20g of polyvinylpyrrolidone.  
201 The samples were shaken at room temperature for 1h on a reciprocal shaker (120 rpm), centrifuged



202 at 10,000g for 10 min and filtered through 1.2  $\mu\text{m}$  Whatman GF/D filters, and concentrated for 24h  
203 in dialysis tubes (10 kDa molecular mass cut-off) covered with polyethylene glycol until a final  
204 volume of 1/10 of the initial volume. Enzymatic activities were measured in microplates with L-  
205 DOPA (10mM) as substrate. The plates were incubated at 23°C for 24h, and L-DOPA oxidation rates  
206 were measured every hour using a spectrophotometer at 460 nm. For each plot, a control with boiled  
207 enzyme extraction (2h at 90°C) was used. Enzyme activities were calculated by subtracting the mean  
208 absorbance of controls from the mean absorbance of enzyme extracts. Phenoloxidase activities were  
209 expressed in enzymatic units (U) defined as 1 nmol of substrate oxidized per hour per gram dry mass.

210 As a proxy of the organic matter decomposition rate, micro-morphological analyses were  
211 performed using light microscopy to quantify the percentage of well-preserved plant tissues in the  
212 peat [50]. Bulk peat samples were taken at the same depth as microbial biomass and mounted as  
213 smear slides and examined at 20 and 50x magnifications. The plant surfaces covered by primary  
214 organic micro-remains were quantified with a reticulated eyepiece on a total of 3000-5000 items per  
215 sample.

216

#### 217 2.4 Inferring microbial food webs and food web metrics

218 Microbial feeding interactions were inferred using a trait-matching and taxonomic approach and  
219 following the workflow developed by [42]. Using a database comprising 27,060 microbial feeding  
220 links for 164 taxa and 34 predictors including six taxonomic variables (Species, Genus, Family,  
221 Order, Phylum, and Kingdom) and eleven traits (Organism type, Nourishment, Feeding group,  
222 Morphology, Lifestyle, Locomotion, Movement, Feeding strategy, Body length, Body width, and  
223 Biovolume), we trained a Boosted-regression tree model to predict microbial feeding links in each  
224 plot and depth from microbial species lists. The food webs are resolved at the species level, except  
225 for bacteria and fungi which remained at their generic group level. The boosted-regression tree  
226 algorithm was chosen among five other machine-learning algorithms because it was the most accurate  
227 and robust for predicting microbial feeding interactions (see [42] for details). Following food web  
228 inferences, we pruned the binary food webs based on the abundance of the prey and consumers and  
229 link strength calculations (see details in [42]).

230 To characterize how various nodes and connections between nodes are arranged in each food  
231 webs, we calculated seven unweighted food web metrics, including the number of species (S),  
232 connectance (C), generality (G), vulnerability (V), shortest path length (SPL), short-weighted trophic  
233 level (TL), the degree of omnivory (OI), averaged food chain length (FCL), and the proportion of  
234 basal (Ba), intermediate (Int) and top species (Pred), as well as vulnerability SD and generality SD  
235 [51,52]. These metrics were chosen because they relate to the vertical (trophic level, omnivory) and

236 the horizontal (generality, vulnerability) dimensions of the food webs and to their complexity (species  
237 richness, connectance). In addition, we calculated weighted metrics to account for the magnitude of  
238 feeding interactions, i.e. link strength, namely the average strength of links (st), the average strength  
239 distribution among links (ps), the weighted shortest path length (dist\_w), the transitivity (trans), the  
240 average strength of each node's connection (neigh), the modularity (mod), the sum of link weights  
241 (flow), the global efficiency (eff), the node-weighted generality (nwG) and vulnerability (nwV), and  
242 node-weighted trophic level (nwT). Node-weighted generality and vulnerability are the biomass-  
243 weighted averages of prey per predator and of predators per prey, respectively, whilst the node-  
244 weighted trophic level is the average of the trophic level weighted by the biomass. More details on  
245 these metrics can be found in [42,51,52].

246

## 247 2.5 Calculation of energy flux in food webs

248 The flux of energy in food webs was estimated by calculating metabolic rates from the body mass,  
249 assimilation efficiencies, and energy transfer between trophic levels [29,53] and using the *fluxweb* R  
250 package [53]. In short, this approach assumes system equilibrium, which implies that each species'  
251 losses due to predation or physiological processes are balanced by the metabolized energy it gains  
252 from consumption. It considers allometric scaling laws to quantify individual metabolic rates that are  
253 dependent on body mass, which together with losses to predation and assimilation efficiencies are  
254 used to quantify incoming fluxes (due to consumption) and outgoing fluxes (due to predation) for  
255 each species. Individual metabolic rates (I [J/year]) were calculated using the equation:

$$256 \quad X_i = (X_0 \times M_i^a) \times B_i$$

257 where  $X_i$  is the metabolic loss of species  $i$ ,  $X_0$  is the organism-specific normalization constant (-0.29),  
258  $M_i$  the body mass of species  $i$  ( $\mu\text{gC}$ ),  $a$  is the allometric scaling constant ( $a = -0.25$ ), and  $B_i$  is the  
259 biomass of species  $i$  ( $\mu\text{gC/g dw}$ ). Because  $X_0$  and  $a$  are virtually unknown for most microorganisms,  
260 we used the same for all species as suggested by Gauzens et al., (2019). Assimilation efficiencies  
261 which express the proportion of eaten biomass that can be used for biomass production plus  
262 metabolism were estimated from the literature [53–58]: microalgae and cyanobacteria = 0.545, testate  
263 amoebae = 0.405, flagellates = 0.200, rotifers = 0.750, nematodes = 0.820, ciliates = 0.650, bacteria  
264 = 0.430, fungi = 0.190. The biomass of each taxon was in  $\mu\text{g}$  per gram of dried *Sphagnum*. As such,  
265 the units of the calculated energy flux are micro-joules per gram of dried *Sphagnum* per second.  
266 Please note that the calculated fluxes are a modelled proxy for energy flow in the food webs, and are  
267 used to compare the different conditions (vegetation cover, depth). Feeding habit analyses for each

268 taxon in each condition would be required to quantify the absolute flow of energy through each food  
269 web.

270

## 271 2.6 Vegetation and environmental parameters

272 We performed vegetation surveys by the point-intercept method [59]. Briefly, we used a 50 x 50 cm  
273 Plexiglas frame placed above a permanently marked quadrat by means of four adjustable poles. A  
274 ruler with 20 holes was moved along 20 different positions to obtain 400 measuring points. A metal  
275 pin with a 1 mm diameter tip was lowered through each hole in the ruler and each contact of the pin  
276 with green living vegetation was recorded by species until the pin reached the moss substrate. Moss  
277 and vascular plant species abundances were expressed as a percentage of the mean number of hits  
278 (%). Water chemistry was analysed in pore water samples taken in each plot at the three depths (0-3,  
279 3-6, and 6-9 cm) using a syringe and piezometers. pH was measured in the field using a pH-meter  
280 whilst total dissolved nitrogen (DN) and dissolved organic carbon (DOC) were determined with a  
281 SHIMADZU SSM-5000A total C, and N analyser (Shimadzu Schweiz, Reinach, Switzerland).  
282 Ammonium (NH<sub>4</sub><sup>+</sup>), nitrate (NO<sub>3</sub><sup>-</sup>), and total phosphorus were analysed colorimetrically using a  
283 continuous flow analyser (FLOWSYS; Systea, Roma) after filtering the bog water at 0.45 μm. Depth  
284 to water level was measured in each plot in a deep piezometer (>1 m depth). All these analyses were  
285 performed on the same day as microbial sampling.

286

## 287 2.7 Statistical analyses

288 To characterize the main differences in food web structures between habitats and depths, we  
289 performed a multivariate principal component analysis (PCA) on all food web metrics. Analysis of  
290 similarities (ANOSIM) was used to test statistically whether there are significant differences between  
291 microhabitats and/or depths. We further calculated the network dissimilarity by measuring the  $\beta$ -  
292 diversity of species interactions (WN) and their decomposed components S (dissimilarity in species  
293 composition of food webs), ST (dissimilarity of interactions due to species turnover), and OS  
294 (dissimilarity of interactions between shared species in the food webs) using the *betalink* R package  
295 [60]. We finally used analysis of variance to test the individual response of food web properties,  
296 biomass across trophic levels and energy fluxes to habitat and depth. Assumptions on normality and  
297 homogeneity of variances were verified using diagnostic plots. Pairwise differences between the  
298 algorithms were tested with the Tukey posthoc test. Multivariate distance matrix regressions  
299 (MDMR) were used to identify the environmental predictors (vegetation properties, water chemical  
300 variables, and water table depth) of microbial biomass distribution across trophic levels, food web

301 qualitative and quantitative properties, and energy fluxes across trophic levels at the different depths  
302 and between WET and DRY areas. Finally, we assessed the effect of distance on species and food  
303 web compositions with Mantel tests (999 permutations) using the Spearman correlation coefficient  
304 between dissimilarities of species (Bray-Curtis distance) and food webs (WN index) and the Euclidian  
305 distance matrix based on sample coordinates. The resulting mantel correlograms showed that  
306 microbial communities and microbial food webs were slightly spatially correlated at an Euclidean  
307 distance of one (Mantel correlation = 0.25), and beyond that distance they were not spatially  
308 autocorrelated (Fig. S2). These results thus validate the choice of having rather distant plots (typically  
309 much greater than 7m apart) since they could then be treated as statistically independent.

310 To identify what structural feature of microbial food webs predicted ecosystem functions best,  
311 we used generalized linear models (GLMs). Assumptions on normality and homogeneity of variances  
312 were verified using diagnostic plots. Then, to evaluate the effect of environmental changes on the  
313 linkages between structural features of microbial food webs and ecosystem functions, we fitted a  
314 piecewise structural equation model [61]; a suitable tool to evaluate direct and indirect effects in  
315 ecological systems [62]. Specifically, the model tested whether environmental change (vegetation  
316 properties, water chemistry, microtopography and WTD), microbial richness and their interactions  
317 directly influenced ecosystem functions (averaged standardized values of each function) or indirectly  
318 through their respective effects on food web properties (PCA axis of qualitative and quantitative  
319 metrics), biomass across trophic levels and energy flow across trophic levels. The model was created  
320 using GLMs and pruned using Akaike Information Criteria corrected for small sample size (AICc)  
321 until we reached a simple and robust model to test direct and indirect effects.

322 All computations and statistical analyses were performed in *R* [63] using custom-written codes  
323 and available R packages. Several of the food web metrics including the food web graph were  
324 performed using the *igraph* package [64].

325

### 326 **3. Results**

#### 327 3.1 Food web dissimilarity and metrics

328 The microbial food webs showed substantial variability over *Sphagnum* segments and across habitats  
329 in terms of species composition (Fig. 1a, b) and biomass distribution among trophic levels (Fig. 2;  
330 Fig. S3, S4). Network dissimilarity analyses revealed that microbial food webs strongly diverged with  
331 depth ( $WN > 0.3$ ) as a result of dissimilarity in species composition of food webs ( $S \sim 0.2$  overall,  
332 Fig. 1a) and in feeding interactions due to species turnover ( $ST \sim 0.3$  overall, Fig. 1a) rather than of  
333 dissimilarity of feeding interactions between shared species in the food webs ( $OS$  values  $< 0.1$ ; Fig.  
334 1a). Food web divergences along *Sphagnum* segments translated in changes of food web metrics, as  
335 shown by the PCA analysis capturing the relationships and associations of food web metrics along

336 *Sphagnum* segments and habitats (Fig. 1c, d). For example, unweighted and weighted connectance  
337 and generality increased between living and decaying/dead *Sphagnum* segments, as well as the size  
338 of food chains and the importance of omnivores and intermediate consumers (Fig. 1d, Table 1). On  
339 the opposite, living segments were characterized by unweighted and weighted short food chains (SPL  
340 and dist\_w) and by a higher proportion of basal and top-predator species (Fig. 1d, Table 1).

341 Besides the depth effect, microbial food webs strongly diverged across habitats (WN > 0.4; Fig.  
342 1b). Here again, they diverged because of dissimilarity in species composition (S ~ 0.2 overall, Fig.  
343 1b) and in feeding interactions due to species turnover (ST ~0.4 overall, Fig. 1b) rather than of  
344 dissimilarity of feeding interactions between shared species in the food webs (OS values < 0.1; Fig.  
345 1b). Despite food web dissimilarity across habitats, we found that food web metrics only slightly  
346 varied across habitats (Fig. 1c, d, Table 1). While food web metrics in living and bottom *Sphagnum*  
347 segments were similar, we found that transitivity, FCL efficiency, and the proportion of intermediate  
348 consumers and omnivores slightly decreased between WET and DRY habitats, although these  
349 tendencies were only marginally significant ( $P \sim 0.1$ ).

350 Weighted metrics only slightly contributed to food web properties divergences among *Sphagnum*  
351 segments and/or across habitats (Fig. 1c). However, the biomass distribution across trophic levels  
352 strongly varied with depth and habitats (ANOVA,  $F_{2,113} = 11.1$ ,  $P < 0.001$ ; Fig. 2). Regardless of  
353 habitat and depth, the microbial biomass was mostly distributed among basal species (trophic level =  
354 1) and primary consumers (i.e., bacterivores, fungivores and algivores, trophic level = 2), and in a  
355 lesser extent among top-predators (trophic level = 2.2; ANOVA,  $F_{3,113} = 213.6$ ,  $P < 0.001$ ; Fig. 2).  
356 We further found that the microbial biomass across trophic levels increased with depth (ANOVA,  
357  $F_{2,113} = 33.2$ ,  $P < 0.001$ ), whilst it was overall higher in DRY than in WET habitat, respectively  
358 (ANOVA,  $F_{1,113} = 42.9$ ,  $P < 0.001$ ; Fig. 2). In particular, we found that the biomass of decomposers  
359 (ANOVA,  $F_{2,30} = 105.6$ ,  $P < 0.001$ ), primary consumers (ANOVA,  $F_{2,30} = 12.6$ ,  $P < 0.01$ ) and top-  
360 predators (ANOVA,  $F_{2,30} = 11.2$ ,  $P = 0.002$ ) increased with depth in both habitats, while the biomass  
361 of phototrophs decreased (ANOVA,  $F_{2,30} = 19.8$ ,  $P < 0.001$ ; Fig. S3). Also, the biomass of  
362 phototrophs (ANOVA,  $F_{1,30} = 12.1$ ,  $P = 0.001$ ) and top-predators (ANOVA,  $F_{1,30} = 3.6$ ,  $P = 0.06$ )  
363 were higher in DRY than in WET (Fig. S3).

364 Relating species turnover and biomass change to environmental parameters, we found that  
365 vegetation properties (composition, richness, and diversity) were the most important drivers of  
366 species turnover, biomass shifts across trophic levels, and food web properties (Table S1). To a lesser  
367 extent, total phosphorous and pH were also significantly linked to species turnover and biomass shifts  
368 across trophic levels, respectively, whilst microtopography and conductivity were significantly  
369 related to food web properties (Table S1).

### 370 3.2 Energy fluxes across trophic levels

371 Total energy flux transiting in microbial food webs significantly varied along *Sphagnum* segments  
372 and across habitats (ANOVA,  $F_{2,30} = 4.5$ ,  $P = 0.019$ ; Fig. 3). On average, it increased from  $19.7 \pm 4.6$   
373  $\text{mJ g}^{-1} \text{sec}^{-1}$  to  $61.4 \pm 26.2 \text{ mJ g}^{-1} \text{sec}^{-1}$  between living and dead *Sphagnum* segments, respectively  
374 (ANOVA,  $F_{2,30} = 30.6$ ,  $P < 0.001$ ). Total energy flux also increased from  $27.1 \pm 14.2 \text{ mJ g}^{-1} \text{sec}^{-1}$  to  
375  $49.3 \pm 28.9 \text{ mJ g}^{-1} \text{sec}^{-1}$  between WET and in DRY (ANOVA,  $F_{1,30} = 25.2$ ,  $P < 0.001$ ), respectively  
376 across all segments. Total energy flux was primarily driven by a high energy demand from  
377 bacterivores/fungivores, and in second place by algivores, whereas the energy fluxes transiting  
378 through mixotrophs and predators were low (Fig. 3b). Bacterivory/fungivory increased with depth in  
379 both habitats (ANOVA,  $F_{1,30} = 6.1$ ,  $P < 0.01$ ; Fig. 3). It was also 1.5 times higher in DRY ( $36.6 \pm$   
380  $25.1 \text{ mJ g}^{-1} \text{sec}^{-1}$ ) than in WET ( $21.2 \pm 13.5 \text{ mJ g}^{-1} \text{sec}^{-1}$ ; ANOVA,  $F_{2,30} = 5.3$ ,  $P = 0.03$ ), regardless  
381 of the depth considered (ANOVA, depth x habitat  $F_{2,30} = 1.8$ ,  $P = 0.18$ ; Fig. 3a, b). Algivory increased  
382 with depth in both habitats (ANOVA,  $F_{2,30} = 5.2$ ,  $P = 0.02$ ), as well as between habitats (WET =  $5.52$   
383  $\pm 5.93 \text{ mJ g}^{-1} \text{sec}^{-1}$ ; DRY =  $12.4 \pm 24.8 \text{ mJ g}^{-1} \text{sec}^{-1}$ ) but this tendency was not significant (ANOVA,  
384  $F_{2,30} = 1.8$ ,  $P = 0.18$ ). The energy transiting through mixotrophs and predators did not vary across  
385 habitats but increased with depth (mixotrophy: ANOVA,  $F_{2,30} = 2.4$ ,  $P = 0.10$ ; predation: ANOVA,  
386  $F_{2,30} = 6.1$ ,  $P < 0.01$ ; Fig. 3).

387 Relating energy fluxes to environmental parameters, we found that vegetation composition and  
388 diversity were the most important environmental variables driving energy fluxes through food webs  
389 (Table S1). Water phenols were also related to energy fluxes in the food webs but to a lesser extent  
390 (Table S1).

391

### 392 3.3 Linkages between structural features of microbial food webs and ecosystem functions

393 Species diversity across trophic levels, species turnover (index S), and network dissimilarity indices  
394 (OS, ST, and WN) were not related to ecosystem functions (Fig. 4a, b;  $P > 0.05$ ). Food web metrics  
395 were poorly connected to ecosystem functions as well. Only the first PCA axis was significantly  
396 related to the microbial activity (measured as phenoloxidase activity;  $P < 0.05$ ; Fig. 4c). In particular,  
397 high connectance, proportion of intermediate consumers, effectiveness, transitivity, and food chain  
398 length were found to promote soil enzyme activity, while high fraction of top predators and weighted  
399 shortest path length were found to reduce soil enzyme activity (Fig. S4). Similarly, total biomass  
400 across trophic levels was poorly linked to ecosystem functions. Only the biomass of intermediate  
401 consumers was significantly linked to microbial activity ( $P < 0.05$ ; Fig. 4d). On the opposite, total  
402 energy flux transiting in the food webs was significantly correlated to the decomposition state of the

403 peat (ANOVA,  $F_{2,30} = 6.2$ ,  $P < 0.02$ ) and soil enzyme activity (ANOVA,  $F_{1,22} = 13.9$ ,  $P < 0.01$ ; Fig.  
404 4). In particular, the decomposition state was significantly related to the energy transiting through  
405 algivores (effect size = -0.95,  $P = 0.05$ ) and predators (effect size = -0.89,  $P = 0.06$ ), whereas soil  
406 enzyme activity was significantly related to the energy flux transiting through bacterivores/fungivores  
407 (effect size = 1.15,  $P = 0.03$ ) and algivores (effect size = 0.94,  $P = 0.05$ ).

408 Structural equation modeling explained 63% of the variance of ecosystem functions (Fig. 5).  
409 We found indirect effects of species richness and environmental conditions on ecosystem functions  
410 mediated by an increase of basal species biomass and changes in food web properties (food web  
411 metrics PCA axis), respectively. Increasing vegetation cover (path = 0.36) and total phosphorous in  
412 pore water (path = 0.56) both had positive effects on the biomass of basal species in the food web,  
413 while the shift in microtopography was an important driver of species richness in the food web (path  
414 = -0.74). Increasing biomass of basal species further promoted energy flow through the food web,  
415 which in turn promoted ecosystem functions (Fig. 5). Microbial richness had no significant effect on  
416 energy flow through the food web nor on ecosystem functions. Finally, our model also showed a  
417 direct effect of increasing vegetation cover on ecosystem functions (path = -0.54; Fig. 5).

418

#### 419 **4. Discussion**

420 Understanding the effects of taxonomic diversity and trophic structure on ecosystem functions is a  
421 key question in the ecology of ecosystem services [21]. Here, we explore the relationships between  
422 microbial food web structure and ecosystem functioning across different habitats and depths in a  
423 peatland. Linking qualitative and quantitative food web metrics to ecosystem functioning, we further  
424 our understanding of how structural features of microbial food web determine key peatland functions  
425 such as decomposition and soil enzyme activity. Our analyses reveal that no aspect of taxonomic  
426 richness directly explained variation in ecosystem functions, whereas aspects of food web structure  
427 and energy fluxes did. This demonstrates that, at least in the complex microbial food webs in  
428 peatlands, focusing on taxonomic diversity without explicit inclusion of food web structure and  
429 energy flows therein will give an incomplete and likely quite uninformative view of relationships  
430 between biodiversity and ecosystem functioning. This finding supports conceptual predictions that  
431 biomass and energy flux dynamics in ecological networks underpin multitrophic biodiversity-  
432 ecosystem functioning relationships [29,33]. This result also agrees with findings from grassland  
433 studies demonstrating the importance of consumption rates in determining soil N mineralization [30].  
434 Moreover, our results clearly show that the integration of a trophic perspective into microbial  
435 communities is key for understanding ecosystem functions [29,65].

436 By analysing microbial communities at different depths and across an environmental gradient,  
437 we found that changes in microtopography and to lesser extent nutrient availability in pore water were  
438 important but rather indirect determinants of structural features of microbial food webs through their  
439 direct effect on species richness and biomass. Microtopography is a complex ecological variable that  
440 underpins microvariations in soil moisture, temperature, micro- and mesoporosity, and water  
441 chemistry, and which ultimately influence microscale microbial richness and biomass [41,66]. Shifts  
442 in microbial richness and biomass further indirectly influence microbial food web structure and  
443 functioning (Fig. 5). With depth, the microbial community composition and biomass of species  
444 shifted, and so did the food webs (Figs. 2, 5). Notably, the phototrophic biomass decreased. Such a  
445 result was expected as phototrophs are by definition sensitive to light availability (Davies et al., 2013;  
446 Hamard et al., 2021b; Jassey et al., 2022), which decreases with peat-depth. Phototrophic gross  
447 primary production usually decreases under low light availability, thus reducing phototrophic  
448 biomass [68,70]. While one would have expected a decrease in the importance of phototrophs in the  
449 food web structure with depth, we found the exact opposite with an increase in the energy flux  
450 transiting from phototrophs to algivores (Fig. 3). This was unexpected and can be explained by the  
451 remarkable plasticity of the phototrophic photosynthetic machinery under low light. Previous findings  
452 showed an increase of messenger RNAs involved in phosphorylation under decreasing light [70],  
453 allowing phototrophs to persist. Phosphorylation occurs in all kinds of phototrophs when conditions  
454 cannot support growth [71], and thus provides energy to phototrophs when photosynthesis is not  
455 possible [72]. We, therefore, suggest that phototrophs increasingly supported higher trophic levels  
456 under low light through an increase of phosphorylation in their cells, as showed in biofilms [70]. The  
457 ingestion of bacteria by some algae to overcome the lack of light and meet their energetic needs may  
458 further explain why phototrophs increasingly support higher trophic levels with depth [73]. Anyway,  
459 these findings confirm the importance of phototrophs in peatland C cycling [74], and underline the  
460 importance of considering phototrophs in soil food webs for ecosystem functioning [75,76].

461 Besides phototrophs, we found that bacterial and fungal biomass increased with depth and  
462 with vascular plant cover. These patterns have been already shown in peatlands [40,49,77] and most  
463 probably result from an increase in resource availability, such as vascular plant root exudates [78],  
464 that fuels decomposers [79]. We found that the increase in bacterial and fungal biomass supported  
465 higher trophic levels, as shown by the increase in energy transiting from decomposers to  
466 bacterivores/fungivores (Fig. 3, 5). This indicates an increase in bacterial and fungal consumption by  
467 bacterivores and fungivores (mostly protists, nematodes, and rotifers) [29]. Such an increase in  
468 bacterivory and fungivory contributed significantly to peatland functions, especially enzyme activity  
469 (Figs. 4, 5). This finding agrees with previous studies showing that predatory-prey interactions within  
470 the microbiome influence soil C cycling such as decomposition, respiration, and enzyme activity



471 [40,80–82]. Mechanistically, bacterivores and fungivores might increase decomposition and enzyme  
472 activity via specific trophic interactions that change and/or promote microbial functioning. For  
473 example, wastes from bacterivores and fungivores, such as undigested food particles and labile  
474 carbon, are usually easily degradable and hence favorable for bacterial re-growth [80]. Also,  
475 bacterivores and fungivores may preferentially feed on senescent bacteria, thus maintaining young  
476 bacteria with higher metabolic activity [83]. Together with our results on algivory, these findings  
477 reveal how changes in abiotic conditions have not only direct effects on trophic groups that are  
478 directly associated with these changing conditions but also indirect effects on other trophic levels  
479 through linkages across food webs, which ultimately modifies ecosystem functions.

480 We found that species richness across trophic levels, as well as species and network turnover,  
481 were poor predictors of ecosystem functions (Fig. 4). It contrasts most recent findings on multitrophic  
482 systems, suggesting that increasing microbial richness/diversity promotes ecosystem functioning  
483 [5,38]. The choice of ecosystem functions tested here might explain such a finding. However, our  
484 finding is consistent with recent results on multi-trophic aquatic food webs showing that there is no  
485 clear pattern between ecosystem function variability and species richness across different types of  
486 empirical food webs [15]. This suggests that more diverse microbial communities do not necessarily  
487 exhibit higher ecosystem function than less diverse ones. It also suggests that species richness of a  
488 specific trophic level does not necessarily influence the associated specific ecosystem function (e.g.  
489 between basal species (TL = 1) and decomposition/soil enzyme activity). Further, we show that  
490 trophic interactions rather than richness across trophic levels are better predictors of ecosystem  
491 functions, which is in line with findings from a grassland experiment [10]. Moreover, our results  
492 partially confirm previous findings in terrestrial systems suggesting that metrics like connectance,  
493 modularity, and hubs provide insights into the structure and functioning of ecosystems [20]. We found  
494 that connectance (i.e. the number of feeding links), transitivity, efficiency, and the proportion of  
495 intermediate consumers (i.e. bacterivores, fungivores, and algivores) were positively correlated with  
496 soil enzyme activity, while the proportion of top predators and shortest path length (i.e. length of food  
497 chains) were negatively correlated. It suggests that highly connected food webs with high connections  
498 among basal and intermediate consumers promote ecosystem functions such as microbial activity,  
499 supporting our findings on the energy flux dynamic in the food webs. This result is also in line with  
500 previous experiments demonstrating the importance of primary consumers in mediating ecosystem  
501 process rates [84,85].

502 By embracing the trophic structure of ecological networks, our analyses provide novel insights  
503 into patterns of variation in ecosystem function in multitrophic systems. We find that trophic  
504 interactions between basal species and primary consumers, and especially increasing connectance,

505 biomass, and energy flux transiting from decomposers and phototrophs to algivores, bacterivores, and  
506 fungivores, enhance ecosystem functions. In other words, increasing the strength of interactions (e.g.  
507 consumption) along microbial trophic levels promotes carbon loss from peatland. We caution that the  
508 observed multitrophic-ecosystem function relationship highlighted here is strictly correlative, and  
509 that future experimental studies are needed to test this specific microbial mechanism in ecosystem  
510 functioning. Nevertheless, our findings are supported by recent multitrophic model simulations  
511 predicting changes in ecosystem functions following changes in consumer biomass and energy fluxes  
512 [23], thus providing confidence in the microbial mechanism found here. Moreover, if such food web  
513 structure-ecosystem function relationships can be confirmed for a wider range of peatlands, such  
514 structural features of microbial food webs may prove key to explaining variation in global carbon  
515 cycling. Climate change has the potential to stimulate bacterial biomass [26,40], while reducing top-  
516 down control of top microbial predators on intermediate consumers [26,86,87]. These possible  
517 climate-induced changes in microbial food webs may trigger a rise in the trophic interactions between  
518 basal species and bacterivores, thus promoting soil enzyme activity and decomposition rates. Only  
519 by pursuing our understanding of microbial food web structures and their associated functions can  
520 we identify general patterns and mechanisms that determine ecological functions and provide the  
521 necessary guidance for managing and mitigating the effects of environmental change.

522

## 523 **Acknowledgments**

524 This work has been supported by the MIXOPEAT (Grant No. ANR-17-CE01-0007 to VEJJ) and  
525 PEATWARM (ANR-07-VUL-010 to FLD, DG, and AB) projects, both funded by the French  
526 National Research Agency. JMB was kindly supported by the Dutch Science Foundation (grant  
527 no. ENW-M OCENW.M20.339) during the writing stages of this paper. The authors warmly thank  
528 the managers of the Regional Natural Reserve of Frasné-Bouverans for allowing access to the site  
529 and the SNO Tourbières (<https://www.sno-tourbieres.cnrs.fr/>) for providing access to environmental  
530 data. We kindly thank Romain Frelat for his help in plotting food webs and for sharing his R scripts.

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533 **References**

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845 **Table 1.** Food web metrics at the three depths and in the two microhabitats. Abbreviations are given  
846 in the method. Letters indicate significant differences between depths and microhabitats ( $P < 0.05$ ,  
847 GLMs).

848

## 849 **Figure captions**

850 **Figure 1:** Characterization of the divergence between microbial food webs with depth and/or habitats.  
851 (a, b) Network beta-diversity indices of the pairwise comparison between the food webs along  
852 *Sphagnum* segments (a) and habitat among the same depth (b). OS = dissimilarity of interactions  
853 between shared species in the food webs, S = dissimilarity in species composition of food webs, ST  
854 = dissimilarity of interactions due to species turnover, WN =  $\beta$ -diversity of species interactions. (c,  
855 d) Principal component analysis (PCA) biplot of food web metrics summarising the depth and habitat  
856 variability in the food web structure. Transparent coloured areas define the convex hull of the depth  
857 and habitat clusters grouping plots with similar food web properties. The arrow colours of the metrics  
858 represent different approaches: qualitative metrics (blue), node-weighted metrics (orange) and link-  
859 weighted metrics (red). The insert on (d) shows the percentage contribution of each food web metric  
860 to PC1 and PC2. Abbreviations of food web metrics are given in section 2.4.

861 **Figure 2:** Microbial biomass distribution across trophic levels of each food web. Barplots of the total  
862 biomass spread across trophic levels at each depth and across habitats. Shown are the mean  $\pm$  SD.  
863 Letters indicate significant differences among habitats and depths (ANOVA).

864 **Figure 3:** Energy fluxes in food webs ( $\mu\text{J/g/sec}$ ). Boxplots of the energy flux transiting in the entire  
865 food webs (total) and into each trophic function, *i.e.*, bacterivory/fungivory, algivory, mixotrophy  
866 and predation, respectively, at each depth and across habitats. Shown are the median and the 25%  
867 and 75% interquartile range. Letters indicate significant differences among *Sphagnum* segments  
868 (ANOVA,  $P < 0.05$ ), whereas asterisks indicate a global habitat effect (ANOVA,  $P < 0.05$ ).

869 **Figure 4:** Linkages between food web complexities and ecosystem functions. Relationships between  
870 ecosystem functions (decomposition and microbial activity) and diversity across trophic levels (a),  
871 food web dissimilarity components (b), biomass across trophic levels, (d) and energy fluxes across  
872 functional groups are shown (e). Responses represent standardised effect sizes of GLM models  $\pm$  SD,  
873 with points situated above or below zero (dotted line) indicating an increase or decrease of the  
874 function to the increasing value of food web complexity taken into account. Responses with error  
875 bars not intersecting zero (red) are significant ( $P < 0.05$ ), and non-significant responses are black.

876 **Figure 5:** Structural equation model (SEM) of environmental and species richness effects on the  
877 linkages between microbial food web structural features and ecosystem functioning. Solid black  
878 arrows are significant paths ( $P < 0.05$ , piecewise SEM) while dashed arrows are non-significant paths  
879 ( $P > 0.05$ , piecewise SEM).  $R^2$ s of the component are given in the boxes of endogenous variables.  
880 SEM global goodness-of-fit are Fisher's  $C = 34.2$ ,  $P = 0.08$ ,  $Df = 24$ ,  $AIC = 80.7$ . TL 1 = trophic  
881 level 1, *i.e.* basal species. Food web properties are the first PCA axis from Fig. 1c, d. Decomposition  
882 was used as a proxy for Ecosystem functions in this model.

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887 **Supplementary figures**

888 **Figure S1:** Characterization of the WET and DRY areas. (a) Depth to Water Table (DWT, in meters)  
889 in the WET and DRY area over 2009. DWT has been measured continuously using sensors for Water  
890 Level measurements (Campbell scientific®) installed in piezometers in each area. (b-d)  
891 microtopography (m), plant diversity, and plant community composition in each area. Asterisks  
892 indicate significant differences between the WET and DRY areas (ANOVAs).

893 **Figure S2:** Effect of distance on the beta-diversity of the microbial communities and associated food  
894 webs. The Mantel correlogram for microbial species assemblages is based on Bray-Curtis  
895 dissimilarities compared to the Euclidean spatial distances and the Spearman correlation coefficient.  
896 The Mantel correlogram for microbial food webs is based on the network-dissimilarity index (WN,  
897 see section 2.7) compared to the Euclidean distances and the Spearman correlation coefficient.  
898 Positive and significant correlations were detected between 0 and 7 m, no correlations at distances  
899 between 7 and 37 m were found.

900 **Figure S3:** The food web metawebs across habitats and *Sphagnum* segments. Node colours  
901 correspond to a taxon's main functional grouping and node size to the biomass of the respective node.  
902 R = node richness, C = connectance, N = nestedness.

903 **Figure S4:** Biomass of each functional group in function of depth and habitat. Shown are the mean  
904  $\pm$  SD. Letters indicate significant differences among depths (ANOVA). L = living segments, Dec =  
905 decaying segments; D = dead segments.

906 **Figure S5:** Correlation coefficient between food web metrics and microbial activity, measured as  
907 phenoloxidase activity. Bars in black are significant at  $P < 0.05$ , whilst white bars are non-significant.  
908 Abbreviations are given in the method.

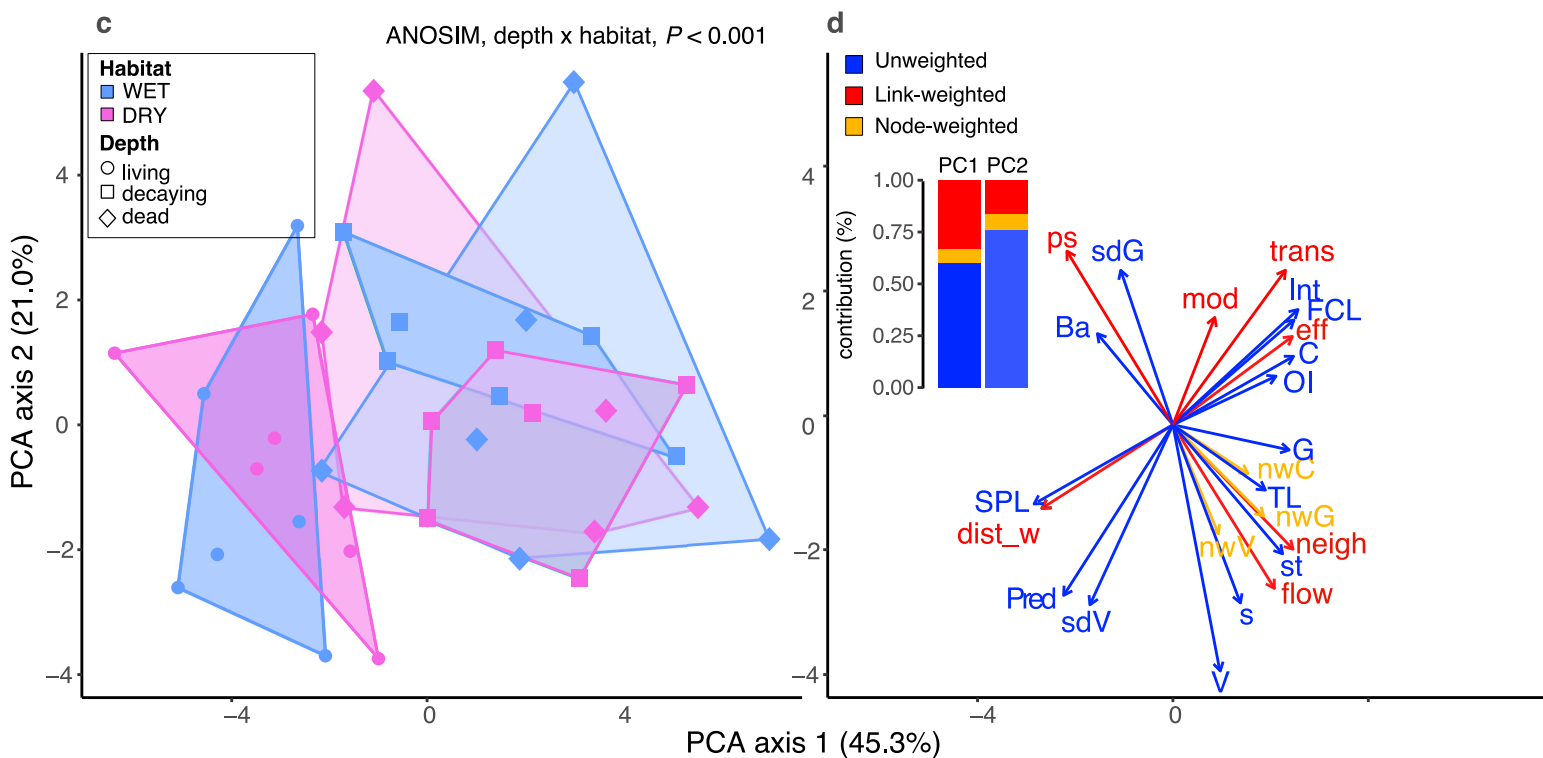
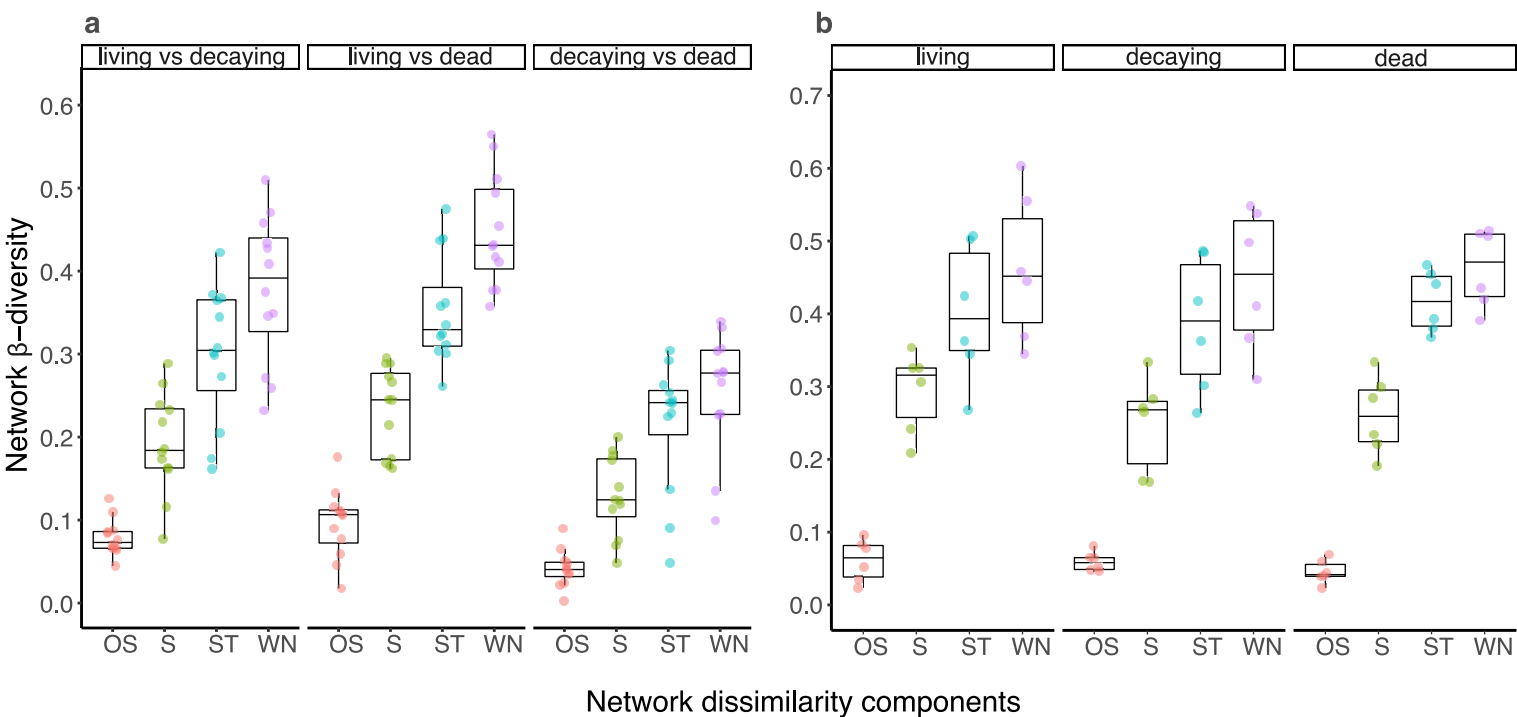
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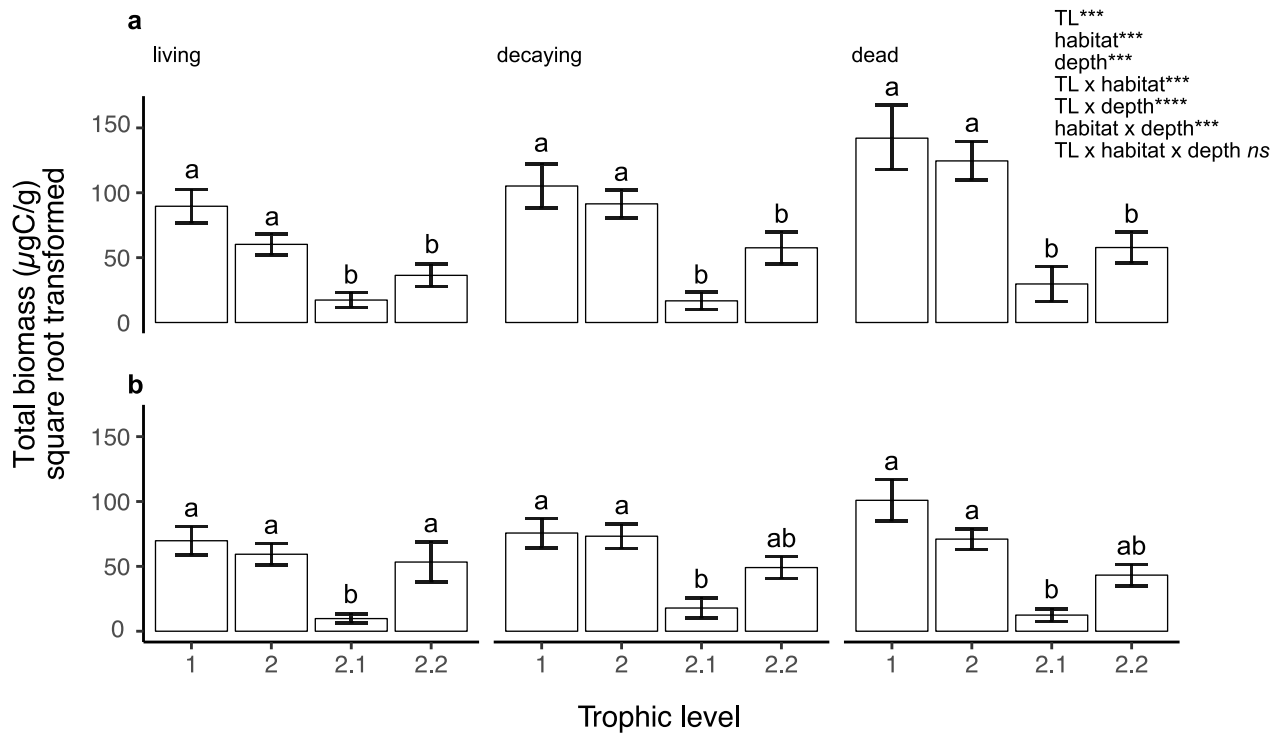
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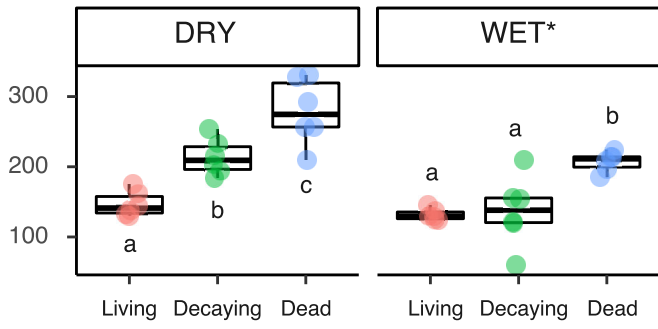
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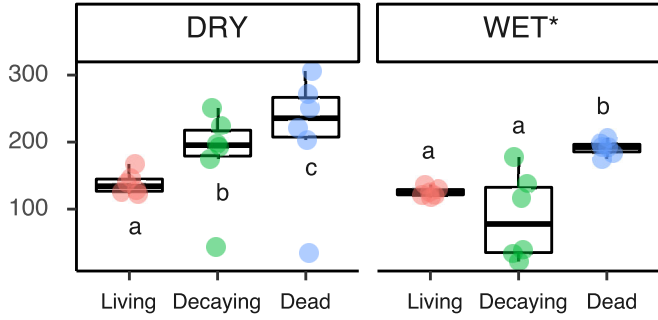




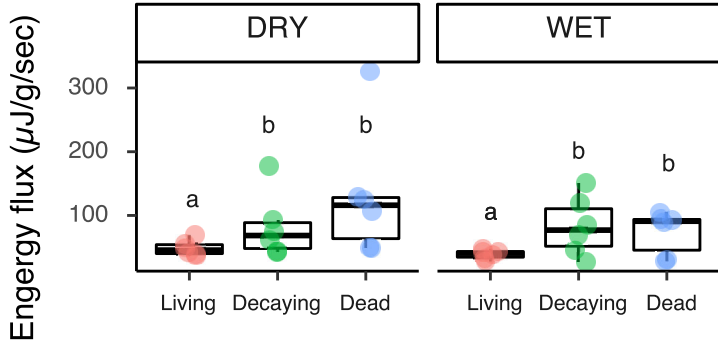
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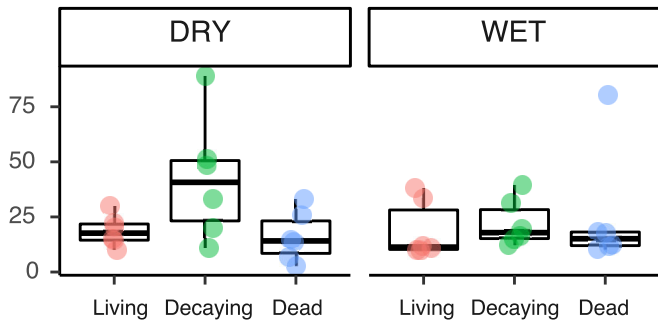
### Bacterivores/fungivores



### Algivores



### Mixotrophs



### Predators

