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## A meta-analysis of peatland microbial diversity and function responses to climate change

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1           **A meta-analysis of peatland microbial diversity and function**  
2                                   **responses to climate change**

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4  
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14

15 **Abstract**

16 Climate change threatens the capacity of peatlands to continue storing carbon (C)  
17 belowground. Microorganisms are crucial in regulating the peatland C sink function, but  
18 how climate change affects the richness, biomass and functions of peatland  
19 microbiomes still remains uncertain. Here, we conducted a global meta-analysis of the  
20 response of peatland bacterial, fungal and micro-eukaryote communities to climate  
21 change by synthesizing data from 120 climate change experiments. We show that  
22 climate drivers such as warming, drought and warming-induced vegetation shift strongly  
23 affect microbial diversity, community composition, trophic structure and functions. Using  
24 meta-analytic structural equation modelling, we developed a causal understanding  
25 among the different strands of microbial properties. We found that climate drivers  
26 influenced microbial metabolic rates, such as CO<sub>2</sub> fixation and respiration, methane  
27 production and oxidation, directly through physiological effects, and indirectly, through  
28 microbial species turnover and shifts in the trophic structure of microbial communities.  
29 In particular, we found that the response of microbial CO<sub>2</sub> fixation increased for each  
30 degree in air temperature gained, while the response of microbial CO<sub>2</sub> respiration  
31 tended to decline. When extrapolated at the global peatland scale using the CMIP6  
32 model under the SSP5-8.5 scenario, our findings suggest that the increasingly positive  
33 response of microbial CO<sub>2</sub> fixation to temperature anomalies in northern latitudes might  
34 compensate to some extent for the possible loss of C from microbial CO<sub>2</sub> respiration,  
35 possibly allowing peatlands to remain C sinks on long-term. Our findings have crucial  
36 implications for advancing our understanding of carbon-climate feedback from  
37 peatlands in a warming world.

38

39 **Keywords:** Warming, drought, vegetation shift, microbial biomass, community composition, soil  
40 carbon cycle, carbon fixation

## 41 **1. Introduction**

42 Northern latitudes are expected to experience climate change greater than the global  
43 average (Smith et al., 2019; IPCC, 2023). Such a more intense climate change is likely  
44 to deteriorate major ecosystem functions and services provided by northern  
45 ecosystems, such as peatlands. This includes climate regulation, recreational services,  
46 and provision for foods and goods (Solomon et al., 2007; Frank et al., 2015; Gallego-  
47 Sala et al., 2018; Malinauskaite et al., 2019; Swindles et al., 2019; Harris et al., 2022;  
48 IPCC, 2023). Because peatlands' response to climate change may exert positive  
49 climatic feedback, further exacerbating human-induced warming (Dise, 2009; Qiu et al.,  
50 2020, 2021), understanding and predicting the response of biotic parameters that  
51 underpin peatlands' functioning is of high priority.

52 Peatlands store massive amounts of C belowground, a stock estimated between  
53 500 and 1,000 GtC (Nichols and Peteet, 2019; Yu et al., 2021), and hence, exert a net  
54 cooling effect on the global climate by removing CO<sub>2</sub> from the atmosphere. Recent  
55 modelling approaches predict that undisturbed peatlands could be persistent C sinks in  
56 the future (Qiu et al., 2020). Thus, maintaining peatland functioning can be seen as a  
57 simple and inexpensive natural-based contribution to mitigate climate change (Qiu et  
58 al., 2020; Strack et al., 2022). However, while modelling approaches are valuable tools  
59 to predict the fate of peatland global C pool in the future, they also suffer from major  
60 flaws such as the under-representation of microbial processes involved in C cycling  
61 even though they represent key functions such as decomposition and respiration (Wang  
62 et al., 2017; Qiu et al., 2018). Consolidating existing peat models with additional  
63 microbial parameters is, therefore, necessary to improve our estimation of peatland C's

64 response to climate change and reduce the uncertainties in model simulations that are  
65 caused by the lack of available data. These models are crucial because they can be  
66 used to decide the fate of peatlands (restoration or conservation) and they can help  
67 predict the effects of such decisions on the peatland C cycle and therefore on the global  
68 C cycle (Bonn et al., 2016; Loisel et al., 2020).

69 Identifying key microbial parameters that underpin the C response of peatlands  
70 to climate change is an urgent but challenging need. Peatland microbial communities  
71 are highly diverse (Andersen et al., 2013), assembled in complex trophic networks  
72 (Jassey et al., 2023), and support many biogeochemical functions related to the C cycle  
73 (Laiho, 2006; Bardgett et al., 2008; Andersen et al., 2013; Artz, 2013). For instance,  
74 microorganisms mediate critical C fluxes, like CH<sub>4</sub> oxidation into CO<sub>2</sub> (Raghoebarsing et  
75 al., 2005; Kip et al., 2010), CH<sub>4</sub> emissions (Juottonen, 2020; Juottonen et al., 2022) and  
76 CO<sub>2</sub> emissions (Dorrepaal et al., 2009; Hoppo et al., 2020). Recent studies further  
77 showed the importance of microbial CO<sub>2</sub> fixation in peatlands, which could approximate  
78 c. 10% of peatlands CO<sub>2</sub> uptake (Hamard et al., 2021). In addition to being diverse in  
79 their functions, peatland microbial communities also showed contrasting responses to  
80 climate change, making predictions difficult. For instance, experimental drought and  
81 warming have been shown to decrease microbial diversity (Delarue et al., 2015; Song et  
82 al., 2021; Carrell et al., 2022), increase bacterial, archaeal and fungal biomass (Delarue  
83 et al., 2015; Mpamah et al., 2017; Cao et al., 2018; Jiang et al., 2020; Song et al., 2021)  
84 and reduce the abundance of microbial consumers (Jassey et al., 2013, 2016;  
85 Lamentowicz et al., 2013; Basińska et al., 2020). These structural shifts often threaten  
86 the peatland C balance by increasing microbial metabolisms such as respiration,

87 methanogenesis and decomposition (Dorrepaal et al., 2009; McCalley et al., 2014;  
88 Gavazov et al., 2018; Jassej et al., 2018; Reczuga et al., 2018; Hopple et al., 2020).  
89 However, negative or neutral responses of microbial communities to climate drivers  
90 have also been reported in numerous studies (Peltoniemi et al., 2015; Defrenne et al.,  
91 2021; Lamit et al., 2021; Xue et al., 2021), raising uncertainty on the role of microbes in  
92 determining the fate of peat C.

93         The inconsistent responses of peatland microbial communities to climate change  
94 components could be tightly linked with climate change magnitude and duration (Jassej  
95 et al., 2015, 2018; Hollister et al., 2023), suggesting that sometimes the amplitude of the  
96 disturbance ensures that climate-induced changes on biological attributes remain close  
97 to a tipping point (Briske et al., 2006). Alternatively, the inconsistency among studies in  
98 microbial responses to climate change may also result from the experimental approach  
99 used. These inferences often rely on three major approaches, namely field experiments,  
100 laboratory manipulative experiments and space-for-time substitutions. These  
101 methodological constraints may lead to different results, as data are not generated the  
102 same way, and thus limit our ability to properly quantify the impacts of climate change  
103 on peatland microbial communities. Overall, studies making a synthesis of information  
104 regarding the response of peatland microbial communities and C dynamics sensitivity to  
105 climate change remain scarce. Yet, by looking at this response we can make an initial  
106 estimate and extrapolate the effects of climate change on microbial attributes at a global  
107 scale. This could help to better identify which microbial parameters are key for  
108 understanding and predicting peatland responses to climate change.

109 To summarise climate change effects on peatland microbial communities and  
110 functions, and hone forecast for particular climate change scenarios, we synthesized  
111 microbial responses from 120 experimental studies published in the last decades (1970-  
112 2023). We screened for changes from a few weeks to several years of experimental  
113 climate change (warming, drought, precipitation shift and vegetation shift) conducted in  
114 16 different countries (Figure 1, Table S1). In particular, we aimed to quantify the  
115 responses and sensitivities of key microbial attributes, including richness, alpha- and  
116 beta-diversity, abundance, biomass and functions (respiration, CO<sub>2</sub> and CH<sub>4</sub> oxidation  
117 and production, enzyme activities) to climate change drivers and develop causal  
118 understanding among these attributes. To achieve this goal, we addressed the following  
119 questions: (1) what are the impacts of climate change drivers on peatlands' microbial  
120 attributes? (2) do climate drivers affect microbial functions directly through physiological  
121 responses or indirectly through changes in microbial diversity and trophic structure? and  
122 (3) what can we learn from models built on the data obtained and extrapolation of future  
123 changes in peatland C fluxes?

124



## 125 **2. Materials and methods**

### 126 **2.1 Literature survey**

127 We searched for studies that tested the effect of climate change drivers on microbial  
128 properties. Data from multifactor experiments which factorially performed both multiple  
129 single-factor treatments and their combination were also included and treated either as  
130 single-factor or multiple-factor effects, respectively. Peer-reviewed publications were  
131 collected by searching databases such as Web of Science (all databases), Google  
132 Scholar, PubMed and the professional network ResearchGate for the period 1 January  
133 1970 – 31 March 2023. Climate change drivers considered were: temperature increase  
134 (TI), winter warming (WW), drought (DR, including precipitation shifts), warming-induced  
135 vegetation shift (VS) and their possible combinations (Table 1). TI and WW were not  
136 pooled because some studies were a mix of warming during winter, snow removal and  
137 snow addition. We used the following keywords for the title and abstract searches:  
138 ‘peatland’ AND ‘microorganisms’ OR ‘microbes’ OR ‘bacteria’ OR ‘nematodes’ OR  
139 ‘fungi’ OR ‘virus’ OR ‘protists’ AND ‘richness’ OR ‘abundance’ OR ‘biomass’ OR  
140 ‘function’ AND ‘warming’ OR ‘drought’ OR ‘precipitation shift’ OR ‘water-table shift’ OR  
141 ‘vegetation change’. Personal unpublished (or from under-review studies) data were  
142 also included in the database. This literature search resulted in 170 peer-reviewed  
143 studies published for the period 1970-2023.

144 Following this literature search, we selected publications by reading each title and  
145 abstract and made sure that they reported climate change effects on microbial  
146 properties. Publications that reported significant or non-significant effects of climate

147 change on microbial properties were then carefully screened by reading the methods  
148 and results sections to identify which of them met the following inclusion criteria:

- 149 - Experiments or observations were conducted in peatlands, including bogs, fens  
150 or palsa mires (Table S1). Because of the paucity of studies, tropical peatlands  
151 were not included in this synthesis. The latitude cutoff was 30°N;
- 152 - Studies reported manipulative experiments conducted *in situ* or in the laboratory  
153 and had both control and experimental groups. Each treatment group had  
154 several replicates. Natural gradients used as space-for-time design were  
155 included as well as regression-based experimental designs. Studies conducted in  
156 the field included natural gradient, transplantation and all manipulation directly  
157 implemented on the field (open top chamber, irradiation, plant removal,  
158 protection against the rain, snow removal/addition, peat removal/addition,  
159 drainage), other studies including incubation in the laboratory, microcosms and  
160 mesocosms were classified as laboratory experiments;
- 161 - The studies should include data on at least one microbial attribute related to  
162 either diversity, biomass, community structure or function. Because of a lack of  
163 data on viruses, they were not included in our analysis;
- 164 - The studies should include experimental and control sample size and p-values  
165 (or correlation coefficients) in the main text, the figures or the supplementary  
166 information.

167 Based on the above criteria, a total of 120 studies (Table S1) were selected from the  
168 170 initial studies. The global distribution of the peatlands' experimental sites is shown

169 in Figure 1. Facing the paucity of multiple-factor experiments with similar combinations  
170 and microbial attributes, only single-factor effects were used.

171

## 172 **2.2 Data collection**

173 For each selected publication, basic information including publication year, climate  
174 drivers, site location (fieldwork location or sampling location for laboratory experiments),  
175 peatland type (fen, bog, mire and other), experimental type (field or laboratory  
176 experiment), sample sizes, methods used for quantifying microbial properties, the  
177 manipulation magnitudes of climate drivers, the group of microorganisms (bacteria,  
178 archaea, fungi, micro-eukaryotes and total) and the duration of the experimentation  
179 were extracted from the methods. We also attributed a functional group to each group of  
180 microorganisms (photoautotrophs, consumers, decomposers, archaea, bacteria, fungi  
181 and total; Table S2). Microbial consumers were further subdivided into testate  
182 amoebae, ciliates, rotifers, flagellates, and nematodes. We defined a consumer as a  
183 microorganism feeding on any kind of living microorganisms (bacteria, fungi, protists,  
184 and/or metazoan). Mixotrophic microalgae were not included in consumers as poorly  
185 known in peatlands.

186 Then, the p-values related to the responses of each microbial attribute were  
187 retrieved from the text or figures. This included microbial richness (Chao1, OTUs, ASVs  
188 or species counts), alpha-diversity (Shannon and Simpson), beta-diversity (response of  
189 community structure following Hellinger transformation, Bray-Curtis dissimilarity,  
190 Jaccard, Gower or UniFrac distances and modification of denaturing gradient gel  
191 electrophoresis (DGGE) matrices), abundance (qPCR, microscopy, sequencing and  
192 terminal restriction fragment length polymorphism (TRFLP)) and the biomass

193 (microscopy-based, phospholipids-derived fatty acids (PFLA)). Finally, the responses of  
194 microbially-driven functions were also recorded and included enzyme activities (alpha  
195 and beta-glucosidase, chitinase, aminopeptidases, phosphatase, phenol-oxidases,  
196 invertase, urease, peroxidase, glycosidase, hydrolase), CO<sub>2</sub> respiration and fixation,  
197 CH<sub>4</sub> production and oxidation and N<sub>2</sub> fixation. All details can be found in Supplementary  
198 Tables S2 and S3. In total, 1,069 p-values (or correlation coefficient) were extracted  
199 from the 120 selected studies; among them, 24.4% were related to richness/alpha-  
200 diversity/community structure, 37.9% to abundance/biomass and 37.7% to functions.

201

### 202 **2.3 Calculation of the standardized mean differences**

203 We used the standardized mean difference (SMD, unbiased estimator Hedges' *g*) as an  
204 effect size metric to estimate the magnitude and sensitivity of responses of each  
205 variable (Durlak, 2009). Hedges' *g* is a unit-free metric modified from Cohen's *d*  
206 estimator (Hedges and Olkin, 1985). Cohen's *d* estimates the difference between two  
207 population means (treatment and control) scaled by the pooled standard deviation of the  
208 data (Cohen, 2013). Hedges' *g* is useful in the ecological meta-analysis because it  
209 provides a statistical bias correction to Cohen's *d* to treat small samples size (Hedges  
210 and Olkin, 1985). This metric allows a quantitative assessment of patterns when  
211 methodology varies among studies (Elmendorf et al., 2012; Koricheva et al., 2013).  
212 Effect sizes were calculated in *R* (R Core Team, 2022) with the package '*compute.es*'  
213 (Re ACD, 2013) using p-values (correlation coefficient for regression-based designs),  
214 control and treatment sample size. When the responses of variables to climate drivers  
215 were negative, SMD was negative, and *vice versa* for positive responses. For beta-

216 diversity, we used the absolute value of SMD because it was often difficult to infer the  
217 direction of the response to climate drivers. When no specific p-value was associated  
218 with non-significant values, we used a value of 0.5 for our SMD calculations. We  
219 considered that SMD between -0.20 and 0.20 had a weak effect and that above this  
220 range SMD had a medium to high effect (Cohen, 2013).

221

## 222 **2.4 Bias assessment, sensitivity and statistical analyses**

223 To test for a potential publication bias we did a funnel plot which consisted of plotting  
224 the effect sizes against their standard error (Sterne and Egger, 2001) and we conducted  
225 an Egger's regression test (Egger et al., 1997) using the R package '*metafor*' v4.4-0  
226 (Viechtbauer, 2010; Nair, 2019; Nakagawa et al., 2023). Egger's test is a linear  
227 regression of the intervention effect estimates on their standard errors weighted by their  
228 inverse variance. In the absence of publication bias the regression slope is supposed to  
229 be zero (Rothstein et al., 2006). To test how sensitive our results were to changes in the  
230 experimental approach, peatland type or duration of analysis, we also conducted a  
231 sensitivity analysis. We divided our data into subsets according to the experimental  
232 approach used (e.g. laboratory-based or field-based). Then, we divided our data into  
233 two other random datasets, calculated the SMDs and associated standard errors for  
234 microbial variables, and compared all the results together.

235 We used linear mixed effect models (LMMs) both to quantify the mean  
236 responsiveness of each microbial variable to climate drivers (D), microbial groups (G)  
237 and manipulation magnitude (MM) over all studies (fixed effects), and to analyze  
238 variation in effect size with peatland type, experimentation type, and method used

239 (random effects). Linear mixed effects models were run in *R* using the package  
240 '*lmerTest*' v3.1-3 (Kuznetsova et al., 2017). In addition, we conducted separate  
241 ANOVAs on each microbial variable to test for the potential impact of the random effects  
242 alone. Any significant effect of the random effects was further tested using the Tuckey  
243 HSD test. The models were checked for the homoscedasticity and normality of the  
244 variables and residuals, data were log-transformed when the transformation induced an  
245 improvement in the distribution.

246 All the statistical analyses were performed in *R* (R Core Team, 2022) using  
247 RStudio v12.0 (RStudio Team, 2020) and the graphical representations were done  
248 using '*ggplot2*' v3.4.0 (Wickham, 2016).

249

## 250 **2.5 Meta-analytic Structural Equation Modelling**

251 We exploited the combined power of microbial diversity, biomass across microbial  
252 trophic levels and functions to paint a broad picture of how climate drivers  
253 mechanistically affect multiple microbial C processes using MASEM: Meta-Analytic  
254 Structural Equation Modelling (Cheung and Chan, 2005; Jak and Cheung, 2020).  
255 MASEM technique combines meta-analysis with structural equation modelling, a  
256 method that allows for causal inferences and mechanistic understanding while giving a  
257 synthetic overview of relationships among variables of interest (Cheung and Chan,  
258 2005; Eisenhauer et al., 2015). Generally, MASEM is a two-stage process in which the  
259 meta-analysis data are first used to generate a pooled correlation matrix across studies,  
260 which is then used to fit a structural equation model (Jak and Cheung, 2020). As almost  
261 no match existed between the different strands of microbial data we collected, we used

262 a different approach, more appropriate to the complex and heterogeneous datasets we  
263 generated.

264 As a first step, we constructed an *a priori* MASEM model, which drew from  
265 hypotheses based on current theory of soil microbiomes under climate change (Jansson  
266 and Hofmockel, 2020; Naylor et al., 2020) and accounted for our expectation that  
267 microbial C processes increasingly shift along with climate change intensity because of  
268 increasing changes of microbial diversity, biomass and interactions (Figure S1;  
269 hypotheses: Table S4). To simplify our MASEM model, we included a composite  
270 variable entitled “microbial C-related multifunctionality”, which was the combined  
271 product of microbial CO<sub>2</sub> fixation and respiration, CH<sub>4</sub> oxidation and production, and C-  
272 related enzyme activities (hydrolases and phenoloxidases). Modelling with composites  
273 in structural equation modelling involved a two-step process (Grace et al., 2016).

274 As a first step, we constructed a SEM model to identify the coefficients of the  
275 predictive variables that determine the composite variable ‘microbial C-related  
276 multifunctionality’. To do so, we constructed a SEM model (hereafter ‘latent SEM  
277 model’) with the unmeasured latent variable ‘microbial C-related multifunctionality’  
278 (Figure S1). This latent SEM model was run on a pooled matrix using the *R* package  
279 ‘*lavaan*’ which allows latent variables. The pooled matrix was obtained by iteratively ( $k =$   
280 50) and randomly selecting twelve effect size values and their respective climate  
281 change intensity value for each co-variable across our global database and averaging  
282 these matrices. We diagnosed latent SEM model fit based on chi-squared statistics ( $P >$   
283 0.05), low root-mean-square error of approximation index (RMSEA  $\leq$  0.1), low  
284 standardized root-mean-square residual index (SRMR  $\leq$  0.1) and high comparative fit

285 index ( $CFI \geq 0.95$ ), and included variables in the latent variable based on these fit  
286 indices and Akaike information criterion (AIC) values (low AIC value was preferred for  
287 similar model fit). Second, the resulting standardized estimates of the latent variable  
288 were used to compute the composite index of 'microbial C-related multifunctionality' in  
289 the MASEM model and test its response to shifts in microbial diversity, biomass and  
290 interactions (Figure S1). This procedure was performed on temperature increase and  
291 drought effects separately.

292 In a second step, MASEM was performed iteratively on  $k$  matrices; we used  $k =$   
293 50 for temperature increase and  $k = 10$  for drought.  $k$  was defined according to the  
294 minimum size of covariates for temperature increase and drought sub-matrices. Each  
295 covariate included in the MASEM model was ranked by intensity magnitude before the  
296 random selection. For temperature increase, we ranked data by increasing temperature  
297 increase. For drought, we ranked data by increasing effect size as data on drought  
298 intensity were not easily available in every study selected from our data compilation. For  
299 each iteration, twelve effect size values along with their respective climate change  
300 intensity value, peatland type, experiment type and community type information were  
301 randomly selected for each co-variate. Then, MASEM was fitted with LMMs ran through  
302 piecewise SEM (Lefcheck, 2016). We chose this approach because it allowed us to  
303 account for the variation of the standardized estimates according to various random  
304 effects (e.g. peatland type, experimentation type, method used, and microbial groups).  
305 In addition, compared to covariance-based SEM, this approach allowed us to use the  
306 Shipley's test of d-separation to test whether direct or indirect paths are missing from  
307 the initial model in predicting microbial C-related multifunctionality. The goodness-of-fit



308 of our MASEM model was evaluated using Fisher's C statistic ( $P > 0.05$ ) and AIC for  
309 each iteration.

310

## 311 **2.6 Projections of microbial responses at global peatland scale and under** 312 **climate change scenarios**

313 We projected at the global northern peatland scale ( $>30^{\circ}\text{N}$ ) the responses (*i.e.*, SMDs)  
314 of main microbial functions defining microbial C-related multifunctionality and its main  
315 indirect predictors to forecasted temperature increase. The projected variables were  
316 chosen according to the results from MASEM (see section 3.3). No projections were  
317 made for drought as we were not able to recover enough data on the drought intensity  
318 in every study to build predictive models using IPCC scenarios. Temperature increase  
319 predictions were retrieved from the IPCC Interactive Atlas (IPCC, 2021; Iturbide et al.,  
320 2021) available online at <https://interactive-atlas.ipcc.ch/>. We extracted the mean annual  
321 temperature change in  $^{\circ}\text{C}$  projected from the CMIP6 model under the SSP5-8.5  
322 scenario for  $+1.5^{\circ}\text{C}$  and  $+3^{\circ}\text{C}$  warming relative to the 1850-1900 baseline. Maps were  
323 downloaded with a ground pixel size of 60 arc minutes. As an envelope for predictions,  
324 we used the peatland map from the up-to-date peatland distribution Peat-ML map, a  
325 global raster of peatland fractional coverage at 5 arc minute ground pixel resolution  
326 (Melton et al., 2022). We extracted temperature change for each scenario ( $+1^{\circ}\text{C}$  and  
327  $+3^{\circ}\text{C}$ ) at each peatland pixel where fractional coverage was upper than 0% in the  
328 exclusion of southern and tropical peatlands ( $<30^{\circ}\text{N}$ ), as these areas were non-covered  
329 by our meta-analysis. Each microbial variable has been predicted using generalized  
330 effect models with the SMD as a response variable and the temperature change as an

331 explanatory variable. The models were checked for the homoscedasticity and normality  
332 of the variables and residuals, and the quality of predictions was assessed using  
333 confidence intervals. Confidence intervals of each prediction were retrieved by making  
334 an interval on the scale of the linear predictor, then applying the inverse link function  
335 from the model fit to transform the linear level confidence intervals to the response level  
336 using 2,000 simulations. The probabilities of the predictions to occur were also  
337 calculated and plotted at the global peatland scale.

338

### 339 **3. Results**

#### 340 **3.1 Effects of climate change on peatland's microbial richness and diversity**

341 Overall, microbial richness was weakly impacted by climate change drivers. Most of the  
342 individual responses had low to medium SMDs (Figure 2a). These responses were  
343 dependent on manipulation magnitude (LMMs,  $P < 0.05$ ; Table 2; Table S5). Bacterial  
344 richness was, on average, not affected by temperature increase ( $-0.01 \pm 0.27$ ) and  
345 weakly affected by drought ( $-0.2 \pm 0.3$ ). Temperature increase ( $-0.59 \pm 0.47$ ) and  
346 drought ( $-0.37 \pm 1.12$ ) both decreased micro-eukaryotic richness whereas fungal  
347 richness increased with temperature increase ( $0.96 \pm 0.35$ ) and weakly increased with  
348 drought ( $0.16 \pm 0.39$ ). Responses of microbial richness facing winter warming and  
349 vegetation were all positive and ranged from not significant (bacteria, fungi) to strong  
350 effect (archaea, micro-eukaryotes; Figure S2a; Table S6).

351 The response of microbial alpha-diversity was either positive or negative  
352 depending on the microbial group considered (Table S7). Again, the average response  
353 of microbial alpha-diversity to climate change drivers was weak (Figure 2b).

354 Temperature increase induced a decrease in bacterial alpha-diversity ( $-0.56 \pm 0.48$ )  
355 whereas it increased micro-eukaryotic alpha-diversity ( $0.3 \pm 0.69$ ; Figure 2b). Drought  
356 increased fungal alpha-diversity ( $1.18 \pm 1.62$ ) but had no impact on bacterial and micro-  
357 eukaryotic alpha-diversity ( $0.01 \pm 0.47$  and  $0.003 \pm 0.75$  respectively). Winter warming  
358 increased micro-eukaryotic alpha-diversity although the effect strongly varied ( $0.76 \pm$   
359  $1.16$ ; Figure S2b). LMMs did not show any significant impact of the fixed terms  
360 (microbial group, climate driver and manipulation magnitude;  $P > 0.05$ , Table 2; Table  
361 S5) on microbial alpha-diversity.

362 We found that microbial community structure (beta-diversity) systematically  
363 responded to climate change drivers (Table S8). At the group level, all microbial groups  
364 strongly responded to climate change drivers (Figure 2c). Temperature increase had a  
365 stronger effect on micro-eukaryotic ( $1.16 \pm 0.30$ ) and fungal ( $1.17 \pm 0.17$ ) community  
366 structure than on bacterial community structure ( $0.67 \pm 0.10$ ). Drought showed a very  
367 strong effect on all microbial groups with a mean of SMDs above 1.50. We also  
368 observed that winter warming and vegetation shift induced a strong response to  
369 microbial beta-diversity (mean of SMDs above 0.8; Figure S2c). LMMs further showed  
370 that the microbial group together with climate drivers explained the observed effects ( $P$   
371  $< 0.05$ ; Table 2; Table S5).

372

### 373 **3.2 Effects of climate change on peatlands microbial biomass and** 374 **functions**

375 Overall, the response of microbial biomass to climate change strongly depended on the  
376 trophic group considered and the manipulation magnitude ( $P < 0.01$  and  $P < 0.05$   
377 respectively; Table 2; ; Table S5; Table S9). Most of the effects were medium to strong

378 with a few SMDs within the range of weak effects, notably for drought (Figure 3a; Figure  
379 S3; Figure S4a). The biomass of all microbial groups increased with temperature  
380 increase (means of SMDs between  $0.53 \pm 0.27$  and  $0.85 \pm 0.2$ ). The only exception was  
381 consumers for whom the biomass showed a very weak response ( $0.06 \pm 0.39$ ). Drought  
382 showed a weaker effect than temperature increase on microbial biomasses, except for  
383 photoautotrophs ( $1.01 \pm 0.36$ ) and consumers ( $-0.67 \pm 0.25$ ). Vegetation shift induced a  
384 strong negative response of bacterial and fungal biomasses (SMDs of  $-1.04$  and  $-2.05$ ,  
385 respectively; Figure S4a), and winter warming had negative effects on consumers ( $-0.73$   
386  $\pm 0.25$ ) and weak negative effect on bacteria ( $-0.15 \pm 0.52$ ). In contrast, photoautotroph  
387 biomass increased with winter warming ( $0.53 \pm 0.11$ ). Winter warming had a very weak  
388 impact on fungal biomass ( $0.08 \pm 0.55$ ; Figure S4a).

389         Among microbial consumers, we found that nematodes, ciliates, flagellates and  
390 testate amoebae were particularly sensitive to climate change (Figure 3b; Figure S4b).  
391 While the biomass of ciliates, nematodes and flagellates increased with temperature  
392 increase, testate amoebae showed opposite patterns with a systematic decrease of  
393 their biomass in response to climate change (Table S9). LMMs further showed  
394 significant effects of microbial group together with climate drivers or with manipulation  
395 magnitude on microbial biomass ( $P < 0.001$ ; Table 2).

396         At the functional level, we found that climate change overall boosted microbial  
397 activities (Figure 3c, Figure S4c, Table S10). However, notable differences were found  
398 according to the function considered ( $P < 0.001$ ; Table 2; Table S5). In terms of carbon  
399 emissions, both  $\text{CO}_2$  and  $\text{CH}_4$  emissions increased with temperature increase ( $2.28 \pm$   
400  $0.21$  and  $1.02 \pm 0.25$  respectively; Figure 3c). Drought also increased  $\text{CO}_2$  emissions

401 (1.18 ± 0.32) but decreased CH<sub>4</sub> emissions (-2.01 ± 0.39). We also found that CH<sub>4</sub>  
402 oxidation into CO<sub>2</sub> was less impacted by temperature increase (0.18 ± 0.43) whilst CO<sub>2</sub>  
403 fixation increased with temperature increase and drought (1.05 ± 0.13 and 1.36 ± 1.35;  
404 Figure 3c). Microbial enzyme activities related to C-cycle (e.g. peroxidase, β-  
405 glucosidase, chitinase; Table S3) increased with temperature increase (0.38 ± 0.23) and  
406 drought (1.34 ± 0.61). N-related microbial enzyme activities such as nitrogenase,  
407 aminopeptidase and urease (Table S3) were weakly impacted by temperature increase  
408 (0.2 ± 0.25) but increased with drought (0.48 ± 0.09). The activity of P-related enzymes  
409 (acidic phosphatase activity and P-hydrolase; Table S3) increased with all climate  
410 change drivers (Figure 3c). Winter warming and vegetation shift also drove important  
411 responses of microbial functional activities (Figure S4c). In particular, N-related  
412 enzymes were negatively impacted by vegetation shift (-2.54 ± 3.09). On the opposite,  
413 C mineralisation, CO<sub>2</sub> and CH<sub>4</sub> emissions were positively impacted by vegetation shift  
414 (3.38 ± 1.31; 2.74 ± 1.06 and 0.93 ± 0.48 respectively).

415

### 416 **3.3 Publication bias assessment and sensitivity analysis**

417 We assessed potential bias in publication by conducting an Eggers' regression test and  
418 we found no impact for biomass ( $P = 0.14$ ), richness ( $P = 0.15$ ), alpha-diversity ( $P =$   
419 0.59) and beta-diversity ( $P = 0.54$ ) data. The only significant bias was found for  
420 functions ( $P = 0.02$ ). When carefully looking at each function, we saw that they  
421 responded to climate change drivers toward the same direction which could explain  
422 such a bias. Furthermore, when we compared the dataset used in this meta-analysis  
423 ('complete') to the four different datasets generated ('field', 'laboratory', 'random1' and

424 'random2'), we saw that all the results pointed toward the same effect (except for a few  
425 exceptions, Figure S5-S8).

426

### 427 **3.4 Connections between microbial diversity, biomass and function under** 428 **climate change**

429 Latent SEM models showed that 'microbial C-related multifunctionality' was best defined  
430 by microbial CO<sub>2</sub> fixation and CO<sub>2</sub> and CH<sub>4</sub> emissions under temperature increase  
431 (Figure 4a). Microbial CO<sub>2</sub> and CH<sub>4</sub> emissions, and hydrolytic and oxidative enzyme  
432 activities were the best predictors of microbial C-related multifunctionality under drought  
433 (Figure 4b). We, therefore, used these variables and their respective standardized  
434 estimates to build the composite variable in the MASEMs. MASEMs for temperature  
435 and drought showed overall good fits across iterations (Fisher's C statistic, averaged *P*  
436 > 0.05) and high *R*<sup>2</sup> values (Figure S9a and c). MASEM showed that temperature  
437 increase influenced microbial C-related multifunctionality (averaged *R*<sup>2</sup> = 0.65; Figure  
438 S9a), directly through effects on microbial CO<sub>2</sub> fixation (averaged path = 0.71 ± 0.01)  
439 and emission (averaged path = -0.06 ± 0.03) and CH<sub>4</sub> emission (averaged path = 0.26 ±  
440 0.03), and indirectly through shifts in microbial beta-diversity (averaged path = 0.22 ±  
441 0.08) and the biomass of decomposers (averaged path = 0.09 ± 0.08) and phototrophs  
442 (averaged path = 0.13 ± 0.08; Figure 4c). Shifts in microbial beta-diversity were further  
443 related to shifts in the biomass of decomposers and phototrophs (Figure 4c). Under  
444 drought, MASEM evidenced similar mechanisms (Figure 4d). Variation in microbial C-  
445 related multifunctionality (averaged *R*<sup>2</sup> = 0.96; Figure S9b) was driven by shifts in  
446 microbial beta-diversity (averaged path = 0.13 ± 0.07), decomposer (averaged path =

447 0.69 ± 0.03) and consumer biomass (averaged path = 0.26 ± 0.04; Figure 4d), while  
448 changes in microbial biomass across trophic levels were also explained by shifts in  
449 microbial beta-diversity.

450

### 451 **3.5 Potential future changes in microbial C-related functions**

452 Based on the MASEM results (Figure 4) we chose to predict potential future changes of  
453 microbial C-related functions (including CO<sub>2</sub> emission and fixation, CH<sub>4</sub> emission and  
454 oxidation). Our predictive models showed good results both for CO<sub>2</sub> emissions ( $P =$   
455 0.023 and  $R^2 = 0.36$ ; Table 3; Figure S10) and CO<sub>2</sub> fixation ( $P < 0.001$ ,  $R^2 = 0.73$ ; Table  
456 3; Figure S11). However, the SMDs of CH<sub>4</sub> emission and oxidation did not evidence any  
457 significant relationship with temperature increase ( $P = 0.14$  and  $P = 0.91$  respectively;  
458 Table 3). Therefore, we only made projections for the future of CO<sub>2</sub> emission and  
459 fixation in response to temperature increase.

460 Projected under the SSP5-8.5 scenario, we found that peatland C-related functions  
461 will strongly change as a result of climate warming, although in different directions. We  
462 notably found a global increase in microbial CO<sub>2</sub> emission and CO<sub>2</sub> fixation rates  
463 (Figure 5). Overall, for both projections, SMDs were above the threshold of 0.2 and the  
464 highest SMDs were predicted at the most northern latitudes. Our projections of  
465 microbial CO<sub>2</sub> emission showed that the response of CO<sub>2</sub> emission is temperature  
466 dependent (SMDs between 2 and 4; Figure 5a and b). Indeed, we showed that CO<sub>2</sub>  
467 emission response to increasing temperature at the highest latitudes will be lower under  
468 the 3°C (SMDs around 2.6) than under the 1.5°C scenario (SMDs > 3), although still  
469 increasing with increasing temperature. For CO<sub>2</sub> fixation our predictions showed an  
470 increase of fixation rates along with increasing temperatures at the highest latitudes and

471 across both scenarios (Figure 5c and d). SMDs for CO<sub>2</sub> fixation ranged between 0.5  
472 and 5 with most of the SMDs around 2 for the 1.5°C scenario and around 4 for the 3°C  
473 scenario.

474

## 475 **4 Discussion**

476 Understanding how climate change affects microbial communities and the underlying  
477 functions they drive is a critical issue in climate change and microbiology research  
478 (Jansson and Hofmockel, 2020). By synthesizing the dynamic changes in peatland  
479 microbial communities from 120 studies performed over the past four decades, this  
480 meta-analysis provides explicit evidence that climate change consistently impacts  
481 peatland microbiomes. This agrees with recent findings in other terrestrial systems  
482 (Blankinship et al., 2011; Schindlbacher et al., 2011; Melillo et al., 2017; Romero-  
483 Olivares et al., 2017; Zhou et al., 2020; Gao et al., 2022; W. Li et al., 2022; Robinson et  
484 al., 2023). An interesting outcome of this study demonstrates that climate change  
485 drivers systematically promote microbial functions, such as CO<sub>2</sub> fixation and emissions,  
486 and CH<sub>4</sub> emissions, suggesting a strong impact of climate change on future peatland  
487 biogeochemical cycles. Vegetation shift and winter warming were the least represented  
488 climate drivers in our analysis but led to strong responses of microbial communities and  
489 functions (Figure S2, S3 and S4), highlighting that these two drivers would merit more  
490 attention in future investigations.

491 Our findings show that warming and drought strongly influence microbial  
492 attributes in peatlands, which agrees with findings on other terrestrial systems (Lurgi et  
493 al., 2012a, 2012b; de Vries and Shade, 2013; Meisner et al., 2013; Zhang et al., 2013;



494 Kaisermann et al., 2017; Zhao et al., 2019; Gao et al., 2022). In particular, both warming  
495 and drought reduced bacterial richness and alpha-diversity, while fungal taxonomic  
496 attributes increased (Figure 2a and b). Studies from different terrestrial systems pointed  
497 toward the same results, supporting that soil fungal communities are usually more  
498 resistant than bacteria to drought and warming (Bapiri et al., 2010; de Vries et al., 2012,  
499 2018; de Vries and Shade, 2013; Y. Li et al., 2022). The filamentous structure of fungi  
500 and their ability to produce osmoregulatory solutes to protect their metabolisms against  
501 unfavorable conditions might explain such differences (Maestre et al., 2015; Nielsen et  
502 al., 2015). In addition, our results showed that bacterial and fungal community  
503 composition and biomass always responded to climate drivers (Figure 2c; Figure 3a;  
504 Figure S3), which was further linked to the response of associated ecosystem functions  
505 they drive such as CO<sub>2</sub> and CH<sub>4</sub> emissions (Figure 4; Figure 5).

506 Our results also evidenced a positive response of micro-eukaryotes at  
507 intermediate trophic levels (Figure 3b), especially for ciliates, flagellates and nematodes  
508 which are important bacterial and fungal feeders in microbiomes (Rønn et al., 2012;  
509 Geisen et al., 2018; Neilson et al., 2020; Potapov et al., 2022). This suggests that  
510 climate drivers may increase the strength of bottom-up effects in the microbial food web  
511 and concomitant processes (e.g. activity, growth). In addition, our findings revealed a  
512 possible decrease in the relative importance of top-down effects in structuring microbial  
513 communities with the loss of top-predators such as testate amoebae. The biomass of  
514 testate amoebae systematically and negatively responded to climate change drivers.  
515 Trophic downgrading in response to climate change has been observed in many  
516 systems (Petchey et al., 1999; Dossena et al., 2012; Ohlberger, 2013), and often results

517 from metabolic constraints of larger organisms (Brose et al., 2012; Lurgi et al., 2012a,  
518 2012b). As size ratio is involved in several biological processes, including for instance  
519 metabolism, growth rate and density, trophic flow, biomass fluxes and interaction  
520 strength, changes in community size structure are likely to exert strong feedback on  
521 trophic functioning (Woodward et al., 2005; Brose et al., 2012; Lurgi et al., 2012a;  
522 Jassey et al., 2023). This loss of top-predators suggests that climate drivers can  
523 restructure microbial food webs in peatlands by causing secondary extinctions along the  
524 food web or by altering the diversity and abundance of many taxa from different groups  
525 and trophic levels (Petchey et al., 1999; Woodward et al., 2008; Dossena et al., 2012;  
526 Heckmann et al., 2012; Jassey et al., 2013; Antiqueira et al., 2018; Reczuga et al.,  
527 2018; Romero et al., 2018, 2020). These multiple changes along trophic levels may  
528 strongly affect ecosystem functions (Allison and Martiny, 2008; Antiqueira et al., 2018).  
529 For example, the loss of testate amoebae which feed on a large variety of prey,  
530 including bacteria, fungi, microalgae, ciliates, rotifers and nematodes (Yeates and  
531 Foissner, 1995; Gilbert et al., 2000, 2003; Wilkinson and Mitchell, 2010; Jassey et al.,  
532 2013), may strengthen the interactions between basal species (bacteria and fungi) and  
533 intermediate consumers, which is known to enhance microbial enzyme activity and  
534 metabolic rates (Trap et al., 2015; Sauvadet et al., 2016). Such a hypothesis is  
535 supported by our MASEM models. We showed that increasing shifts in decomposer  
536 biomass resulting from shifts in consumers were related to shifts in microbial C-related  
537 multifunctionality (Figure 4). Hence the restructuring of the microbial food web supports  
538 the hypothesis that peatlands could become emitters of CO<sub>2</sub> in response to climate  
539 change.

540 Overall, we found that warming and drought strongly impacted multifunctionality  
541 related to the C cycle, with a positive response of decomposition (C enzymes) and C  
542 emissions (both CO<sub>2</sub> and CH<sub>4</sub>) except for CH<sub>4</sub> emissions that decreased with drought.  
543 Drought causes aeration of the peat resulting both in unfavourable conditions for  
544 methanogens that are very sensitive to oxygen (Zehnder and Stumm, 1988; Dowrick et  
545 al., 2006; Wu et al., 2020; Barel et al., 2021) and favourable conditions for CH<sub>4</sub>  
546 oxidation (Dowrick et al., 2006; Kang et al., 2018; Perryman et al., 2023). Other meta-  
547 analyses at the global scale also evidenced that warming significantly increases  
548 microbial respiration (Bardgett et al., 2008; Wang et al., 2014; Crowther et al., 2016;  
549 Zhou et al., 2016; Xu and Yuan, 2017; Liu et al., 2020), thus corroborating our results  
550 and suggesting a loss of C from peatlands in response to climate change (Dorrepaal et  
551 al., 2009; Loisel et al., 2020). Now, if we add the response of microbial photoautotrophs  
552 to the global microbial picture, the perception of how peatlands may react to climate  
553 change differs. Recent work showed that peatland microbes can fix on average 8.8 mg  
554 CO<sub>2</sub> hr<sup>-1</sup> m<sup>-2</sup>, a rate equivalent to about 9% of peatlands' gross CO<sub>2</sub> uptake (Hamard et  
555 al. 2021). Our synthesis showed that such a CO<sub>2</sub> fixation rate is likely to increase with  
556 warming and drought. We suggest that the response of photoautotrophs to climate  
557 change may to some extent counterbalance the response of heterotrophic microbes to  
558 climate change and partly mitigate the rise in microbial C emissions. Such a hypothesis  
559 was further supported by our projections of microbial CO<sub>2</sub> emission and fixation at the  
560 global peatland scale based on future scenarios of the IPCC (CMIP6 model with SSP5-  
561 8.5 scenario for +1.5°C and +3°C; Figure 5). Our findings showed a strong and positive  
562 response of microbial CO<sub>2</sub> fixation rate along with warming at the global peatland scale

563 and across scenarios, especially in northern latitudes where peatlands are the most  
564 abundant. This suggests that peatland microbiomes may take up more C along with  
565 temperature increase in the future. This increasingly positive response of microbial CO<sub>2</sub>  
566 fixation to temperature anomalies in northern latitudes may be one of the mechanisms  
567 possibly allowing peatlands to remain C sinks on the long-term, as predicted by recent  
568 model simulations (Gallego-Sala et al., 2018) and experimental studies (Helbig et al.,  
569 2022).

570 On the opposite, our results showed an important increase in the response of  
571 CO<sub>2</sub> emissions, but mostly at +1.5°C scenario (Figure 5a). Indeed, our projection  
572 indicated that the response of microbial CO<sub>2</sub> emissions might decreased in magnitude  
573 under the +3°C scenario (Figure 5b). These results suggest that above a certain  
574 temperature anomaly, the increase in microbial CO<sub>2</sub> emissions may stagnate or even  
575 decrease. Recent meta-analyses in soils found a similar trend with CO<sub>2</sub> emissions  
576 decreasing with warming magnitude after a certain temperature threshold (~+2°C; Xu  
577 and Yuan, 2017; Yang et al., 2023). This suggests that microbial communities might  
578 adapt to climate warming (Rinnan et al., 2009; Melillo et al., 2017; Yang et al., 2023),  
579 probably as a result of physiological adaptation (Bradford et al., 2008; Tucker et al.,  
580 2013) and community changes (Crowther and Bradford, 2013). Another hypothesis that  
581 could explain such a decrease in CO<sub>2</sub> emissions with warming has been suggested by  
582 Walker et al. (2018). First, warming accelerates growth, respiration and C use by  
583 microbial communities, leading to an important release of CO<sub>2</sub>. Then, because of a lack  
584 of C in the system, the first phase is followed by a decrease in microbial biomass,  
585 reducing microbial activities and attenuating CO<sub>2</sub> emission in the long term (Walker et

586 al., 2018). Further studies will be needed to test and verify these hypotheses in  
587 peatlands. Furthermore, although very promising, we caution that our projections are an  
588 extrapolation from a small dataset of SMDs that does not consider the potential effect of  
589 seasons and precipitation changes on microbial C emission and fixation rates. For these  
590 reasons, these results merit further support and must be consolidated with additional  
591 analyses to increase their robustness. Nevertheless, the probability for the values  
592 predicted to be accurate and reliable is relatively high (Figure S12), thus providing some  
593 confidence in the projections.

594 To conclude, our global synthesis demonstrates that climate change strongly  
595 impacts peatland microbial attributes with notably an important effect on microbial  
596 biomass and functions. Our findings underline that considering the microbiome in its  
597 entity (i.e., bacteria, fungi, protists and micro-metazoa) and multiple microbial attributes  
598 (i.e., richness, diversity, biomass and functions) is key to paint a broad picture of how  
599 climate drivers change microbial diversity and trophic interactions, and how these  
600 changes drive shifts in microbial C-related processes. Our findings show that biomass  
601 across trophic levels and changes in community structure are tightly linked, and  
602 together strongly impact microbial functions simultaneously. Therefore, considering  
603 biomass across trophic levels and community structure is key to predict shifts in  
604 microbial C processes. Our results further provide empirical support for the new  
605 hypothesis that microbial CO<sub>2</sub> fixation may regulate microbial climatic feedback to the  
606 peatland C cycle, and yield evidence that incorporating microbial CO<sub>2</sub> fixation process  
607 into global peatland C models, such as ORCHIDEE-PEAT (Qiu et al., 2018) will likely  
608 improve both their mechanistic insight and predictive power. Future studies are needed

609 to build on this foundation, for example, interrogating to what extent microbial CO<sub>2</sub>  
610 fixation counterbalances microbial C losses from CO<sub>2</sub> and CH<sub>4</sub> emissions and  
611 decomposition will be crucial for advancing our predictions of carbon-climate feedback  
612 from peatlands in a warming world.

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618  
619 **Author contributions**

620 VEJJ conceived the study. MLG constructed the database with the help of VEJJ. MLG  
621 and VEJJ performed numerical analyses. RW performed projections maps. MLG and  
622 VEJJ wrote the first draft of the manuscript with the help of BL. All authors reviewed and  
623 contributed to the final form of the manuscript.

624

625 **References**

- 626 Allison, S.D., Martiny, J.B.H., 2008. Resistance, resilience, and redundancy in microbial  
627 communities. *Proceedings of the National Academy of Sciences of the United States of*  
628 *America* 105, 11512–11519.  
629 doi:10.1073/PNAS.0801925105/SUPPL\_FILE/0801925105SI.PDF
- 630 Andersen, R., Chapman, S.J., Artz, R.R.E., 2013. Microbial communities in natural and  
631 disturbed peatlands: A review. *Soil Biology and Biochemistry* 57, 979–994.  
632 doi:10.1016/J.SOILBIO.2012.10.003
- 633 Antiqueira, P.A.P., Petchey, O.L., Romero, G.Q., 2018. Warming and top predator loss  
634 drive ecosystem multifunctionality. *Ecology Letters* 21, 72–82.  
635 doi:10.1111/ELE.12873
- 636 Artz, R.R.E., 2013. Microbial Community Structure and Carbon Substrate use in Northern  
637 Peatlands. *Carbon Cycling in Northern Peatlands* 184, 111–129.  
638 doi:10.1029/2008GM000806
- 639 Bapiri, A., Bååth, E., Rousk, J., 2010. Drying-Rewetting Cycles Affect Fungal and Bacterial  
640 Growth Differently in an Arable Soil. *Microbial Ecology* 60, 419–428.  
641 doi:10.1007/S00248-010-9723-5/
- 642 Bardgett, R.D., Freeman, C., Ostle, N.J., 2008. Microbial contributions to climate change  
643 through carbon cycle feedbacks. *The ISME Journal* 2, 805–814.
- 644 Barel, J.M., Moulia, V., Hamard, S., Sytiuk, A., Jassey, V.E.J., 2021. Come Rain, Come  
645 Shine: Peatland Carbon Dynamics Shift Under Extreme Precipitation. *Frontiers in*  
646 *Environmental Science* 9, 659953. doi:10.3389/FENVS.2021.659953/BIBTEX
- 647 Basińska, A.M., Reczuga, M.K., Gąbka, M., Stróżecki, M., Łuców, D., Samson, M.,  
648 Urbaniak, M., Leśny, J., Chojnicki, B.H., Gilbert, D., Sobczyński, T., Olejnik, J.,  
649 Silvennoinen, H., Juszczak, R., Lamentowicz, M., 2020. Experimental warming and  
650 precipitation reduction affect the biomass of microbial communities in a Sphagnum  
651 peatland. *Ecological Indicators* 112, 106059. doi:10.1016/J.ECOLIND.2019.106059
- 652 Blankinship, J.C., Niklaus, P.A., Hungate, B.A., 2011. A meta-analysis of responses of soil  
653 biota to global change. *Oecologia* 165, 553–565. doi:10.1007/S00442-011-1909-  
654 0/TABLES/3
- 655 Bonn, A., Allott, T., Evans, M., Joosten, H., Stoneman, R., 2016. Peatland restoration and  
656 ecosystem services: An introduction, in: *Peatland Restoration and Ecosystem Services:*  
657 *Science, Policy and Practice*. Cambridge University Press, pp. 1–16.  
658 doi:10.1017/CBO9781139177788.002
- 659 Bradford, M.A., Davies, C.A., Frey, S.D., Maddox, T.R., Melillo, J.M., Mohan, J.E.,  
660 Reynolds, J.F., Treseder, K.K., Wallenstein, M.D., 2008. Thermal adaptation of soil  
661 microbial respiration to elevated temperature. *Ecology Letters* 11, 1316–1327.  
662 doi:10.1111/J.1461-0248.2008.01251.X
- 663 Briske, D.D., Fuhlendorf, S.D., Smeins, F.E., 2006. A unified framework for assessment  
664 and application of ecological thresholds. *Rangeland Ecology and Management* 59,  
665 225–236. doi:10.2111/05-115R.1
- 666 Brose, U., Dunne, J.A., Montoya, J.M., Petchey, O.L., Schneider, F.D., Jacob, U., 2012.  
667 Climate change in size-structured ecosystems. *Philosophical Transactions of the Royal*  
668 *Society B: Biological Sciences* 367, 2903–2912. doi:10.1098/RSTB.2012.0232



669 Cao, R., Chen, Y., Wu, X., Zhou, Q., 2018. The effect of drainage on CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O  
670 emissions in the Zoige peatland: a 40-month in situ study. *Mires and Peat* 21, 1–15.  
671 doi:10.19189/MaP.2017.OMB.292

672 Carrell, A.A., Lawrence, T.J., Cabugao, K.G.M., Carper, D.L., Pelletier, D.A., Lee, J.H.,  
673 Jawdy, S.S., Grimwood, J., Schmutz, J., Hanson, P.J., Shaw, A.J., Weston, D.J., 2022.  
674 Habitat-adapted microbial communities mediate Sphagnum peatmoss resilience to  
675 warming. *New Phytologist* 234, 2111–2125. doi:10.1111/NPH.18072

676 Cheung, M.W.L., Chan, W., 2005. Meta-analytic structural equation modeling: A two-stage  
677 approach. *Psychological Methods* 10, 40–64. doi:10.1037/1082-989X.10.1.40

678 Cohen, J., 2013. *Statistical Power Analysis for the Behavioral Sciences*, Second. ed,  
679 *Statistical Power Analysis for the Behavioral Sciences*. Routledge.  
680 doi:10.4324/9780203771587

681 Crowther, T.W., Bradford, M.A., 2013. Thermal acclimation in widespread heterotrophic  
682 soil microbes. *Ecology Letters* 16, 469–477. doi:10.1111/ELE.12069

683 Crowther, T.W., Todd-Brown, K.E.O., Rowe, C.W., Wieder, W.R., Carey, J.C.,  
684 MacHmuller, M.B., Snoek, B.L., Fang, S., Zhou, G., Allison, S.D., Blair, J.M.,  
685 Bridgham, S.D., Burton, A.J., Carrillo, Y., Reich, P.B., Clark, J.S., Classen, A.T.,  
686 Dijkstra, F.A., Elberling, B., Emmett, B.A., Estiarte, M., Frey, S.D., Guo, J., Harte, J.,  
687 Jiang, L., Johnson, B.R., Kroël-Dulay, G., Larsen, K.S., Laudon, H., Lavallee, J.M.,  
688 Luo, Y., Lupascu, M., Ma, L.N., Marhan, S., Michelsen, A., Mohan, J., Niu, S.,  
689 Pendall, E., Peñuelas, J., Pfeifer-Meister, L., Poll, C., Reinsch, S., Reynolds, L.L.,  
690 Schmidt, I.K., Sistla, S., Sokol, N.W., Templer, P.H., Treseder, K.K., Welker, J.M.,  
691 Bradford, M.A., 2016. Quantifying global soil carbon losses in response to warming.  
692 *Nature* 540, 104–108. doi:10.1038/nature20150

693 Defrenne, C.E., Childs, J., Fernandez, C.W., Taggart, M., Nettles, W.R., Allen, M.F.,  
694 Hanson, P.J., Iversen, C.M., 2021. High-resolution minirhizotrons advance our  
695 understanding of root-fungal dynamics in an experimentally warmed peatland. *Plants*,  
696 *People, Planet* 3, 640–652. doi:10.1002/PPP3.10172

697 Delarue, F., Buttler, A., Bragazza, L., Grasset, L., Jasse, V.E.J., Gogo, S., Laggoun-  
698 Défarge, F., 2015. Experimental warming differentially affects microbial structure and  
699 activity in two contrasted moisture sites in a Sphagnum-dominated peatland. *The*  
700 *Science of the Total Environment* 511, 576–583.  
701 doi:10.1016/J.SCITOTENV.2014.12.095

702 de Vries, F.T., Griffiths, R.I., Bailey, M., Craig, H., Girlanda, M., Gweon, H.S., Hallin, S.,  
703 Kaisermann, A., Keith, A.M., Kretzschmar, M., Lemanceau, P., Lumini, E., Mason,  
704 K.E., Oliver, A., Ostle, N., Prosser, J.I., Thion, C., Thomson, B., Bardgett, R.D., 2018.  
705 Soil bacterial networks are less stable under drought than fungal networks. *Nature*  
706 *Communications* 9, 3033. doi:10.1038/S41467-018-05516-7

707 de Vries, F.T., Liiri, M.E., Bjørnlund, L., Bowker, M.A., Christensen, S., Setälä, H.M.,  
708 Bardgett, R.D., 2012. Land use alters the resistance and resilience of soil food webs to  
709 drought. *Nature Climate Change* 2, 276–280. doi:10.1038/nclimate1368

710 de Vries, F.T., Shade, A., 2013. Controls on soil microbial community stability under  
711 climate change. *Frontiers in Microbiology* 4, 265. doi:10.3389/FMICB.2013.00265

712 Dise, N.B., 2009. Peatland response to global change. *Science* 326, 810–811.  
713 doi:10.1126/SCIENCE.1174268/ASSET/0F9BAE14-4E64-4E49-B91F-  
714 66765AEED122/ASSETS/GRAPHIC/326\_810\_F1.JPEG

715 Dorrepaal, E., Toet, S., van Logtestijn, R.S.P., Swart, E., van de Weg, M.J., Callaghan, T.  
716 V, Aerts, R., 2009. Carbon respiration from subsurface peat accelerated by climate  
717 warming in the subarctic. *Nature* 460, 616–619.

718 Dossena, M., Yvon-Durocher, G., Grey, J., Montoya, J.M., Perkins, D.M., Trimmer, M.,  
719 Woodward, G., 2012. Warming alters community size structure and ecosystem  
720 functioning. *Proceedings of the Royal Society B: Biological Sciences* 279, 3011–3019.  
721 doi:10.1098/RSPB.2012.0394

722 Dowrick, D.J., Freeman, C., Lock, M.A., Reynolds, B., 2006. Sulphate reduction and the  
723 suppression of peatland methane emissions following summer drought. *Geoderma* 132,  
724 384–390. doi:10.1016/J.GEODERMA.2005.06.003

725 Durlak, J.A., 2009. How to Select, Calculate, and Interpret Effect Sizes. *Journal of Pediatric*  
726 *Psychology* 34, 917–928. doi:10.1093/JPEPSY/JSP004

727 Egger, M., Smith, G.D., Schneider, M., Minder, C., 1997. Bias in meta-analysis detected by  
728 a simple, graphical test. *BMJ* 315, 629–634. doi:10.1136/BMJ.315.7109.629

729 Eisenhauer, N., Bowker, M.A., Grace, J.B., Powell, J.R., 2015. From patterns to causal  
730 understanding: Structural equation modeling (SEM) in soil ecology. *Pedobiologia* 58,  
731 65–72. doi:10.1016/J.PEDOBI.2015.03.002

732 Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Björk, R.G., Bjorkman, A.D., Callaghan,  
733 T. V., Collier, L.S., Cooper, E.J., Cornelissen, J.H.C., Day, T.A., Fosaa, A.M., Gould,  
734 W.A., Grétarsdóttir, J., Harte, J., Hermanutz, L., Hik, D.S., Hofgaard, A., Jarrad, F.,  
735 Jónsdóttir, I.S., Keuper, F., Klanderud, K., Klein, J.A., Koh, S., Kudo, G., Lang, S.I.,  
736 Loewen, V., May, J.L., Mercado, J., Michelsen, A., Molau, U., Myers-Smith, I.H.,  
737 Oberbauer, S.F., Pieper, S., Post, E., Rixen, C., Robinson, C.H., Schmidt, N.M.,  
738 Shaver, G.R., Stenström, A., Tolvanen, A., Totland, Ø., Troxler, T., Wahren, C.H.,  
739 Webber, P.J., Welker, J.M., Wookey, P.A., 2012. Global assessment of experimental  
740 climate warming on tundra vegetation: Heterogeneity over space and time. *Ecology*  
741 *Letters* 15, 164–175. doi:10.1111/J.1461-0248.2011.01716.X

742 Frank, Dorothea, Reichstein, M., Bahn, M., Thonicke, K., Frank, David, Mahecha, M.D.,  
743 Smith, P., van der Velde, M., Vicca, S., Babst, F., Beer, C., Buchmann, N., Canadell,  
744 J.G., Ciais, P., Cramer, W., Ibrom, A., Miglietta, F., Poulter, B., Rammig, A.,  
745 Seneviratne, S.I., Walz, A., Wattenbach, M., Zavala, M.A., Zscheischler, J., 2015.  
746 Effects of climate extremes on the terrestrial carbon cycle: concepts, processes and  
747 potential future impacts. *Global Change Biology* 21, 2861–2880.  
748 doi:10.1111/gcb.12916

749 Gallego-Sala, A. V., Charman, D.J., Brewer, S., Page, S.E., Prentice, I.C., Friedlingstein, P.,  
750 Moreton, S., Amesbury, M.J., Beilman, D.W., Björck, S., Blyakharchuk, T.,  
751 Bohicchio, C., Booth, R.K., Bunbury, J., Camill, P., Carless, D., Chimner, R.A.,  
752 Clifford, M., Cressley, E., Courtney-Mustaphi, C., De Vleeschouwer, F., de Jong, R.,  
753 Fialkiewicz-Kozziel, B., Finkelstein, S.A., Garneau, M., Githumbi, E., Hribljan, J.,  
754 Holmquist, J., Hughes, P.D.M., Jones, C., Jones, M.C., Karofeld, E., Klein, E.S.,  
755 Kokfelt, U., Korhola, A., Lacourse, T., Le Roux, G., Lamentowicz, M., Large, D.,  
756 Lavoie, M., Loisel, J., Mackay, H., MacDonald, G.M., Makila, M., Magnan, G.,  
757 Marchant, R., Marcisz, K., Martínez Cortizas, A., Massa, C., Mathijssen, P., Mauquoy,  
758 D., Mighall, T., Mitchell, F.J.G., Moss, P., Nichols, J., Oksanen, P.O., Orme, L.,  
759 Packalen, M.S., Robinson, S., Roland, T.P., Sanderson, N.K., Sannel, A.B.K., Silva-  
760 Sánchez, N., Steinberg, N., Swindles, G.T., Turner, T.E., Uglow, J., Väliranta, M., van

761 Bellen, S., van der Linden, M., van Geel, B., Wang, G., Yu, Z., Zaragoza-Castells, J.,  
762 Zhao, Y., 2018. Latitudinal limits to the predicted increase of the peatland carbon sink  
763 with warming. *Nature Climate Change* 8, 907–913. doi:10.1038/s41558-018-0271-1  
764 Gao, S., Song, Y., Song, C., Wang, X., Ma, X., Gao, J., Cheng, X., Du, Y., 2022. Effects of  
765 temperature increase and nitrogen addition on the early litter decomposition in  
766 permafrost peatlands. *Catena* 209. doi:10.1016/J.CATENA.2021.105801  
767 Gavazov, K., Albrecht, R., Buttler, A., Dorrepaal, E., Garnett, M.H., Gogo, S., Hagedorn,  
768 F., Mills, R.T.E., Robroek, B.J.M., Bragazza, L., 2018. Vascular plant-mediated  
769 controls on atmospheric carbon assimilation and peat carbon decomposition under  
770 climate change. *Global Change Biology* 24, 3911–3921. doi:10.1111/GCB.14140  
771 Geisen, S., Mitchell, E.A.D., Adl, S., Bonkowski, M., Dunthorn, M., Ekelund, F.,  
772 Fernández, L.D., Jousset, A., Krashevskaya, V., Singer, D., Spiegel, F.W., Walochnik, J.,  
773 Lara, E., 2018. Soil protists: a fertile frontier in soil biology research. *FEMS*  
774 *Microbiology Reviews* 42, 293–323. doi:10.1093/FEMSRE/FUY006  
775 Gilbert, D., Amblard, C., Bourdier, G., Francez, A.J., Mitchell, E.A.D., 2000. Le régime  
776 alimentaire des Thécamoebiens (Protista, Sarcodina). *L'Année Biologique* 39, 57–68.  
777 doi:10.1016/S0003-5017(00)80001-X  
778 Gilbert, D., Mitchell, E., Amblard, C., Bourdier, G., Francez, A.-J., D Mitchell, E.A., 2003.  
779 Population dynamics and food preferences of the testate amoeba *Nebela tinctoria* major-  
780 *bohemica-collaris* complex (Protozoa) in a Sphagnum peatland. *Acta Protozoologica*  
781 42, 99–104.  
782 Grace, J.B., Anderson, T.M., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S.,  
783 Hautier, Y., Hillebrand, H., Lind, E.M., Pärtel, M., Bakker, J.D., Buckley, Y.M.,  
784 Crawley, M.J., Damschen, E.I., Davies, K.F., Fay, P.A., Firn, J., Gruner, D.S., Hector,  
785 A., Knops, J.M.H., MacDougall, A.S., Melbourne, B.A., Morgan, J.W., Orrock, J.L.,  
786 Prober, S.M., Smith, M.D., 2016. Integrative modelling reveals mechanisms linking  
787 productivity and plant species richness. *Nature* 529, 390–393.  
788 doi:10.1038/nature16524  
789 Hamard, S., Céréghino, R., Barret, M., Sytiuk, A., Lara, E., Dorrepaal, E., Kardol, P.,  
790 Küttim, M., Lamentowicz, M., Leflaive, J., Le Roux, G., Tuittila, E.S., Jasey, V.E.J.,  
791 2021. Contribution of microbial photosynthesis to peatland carbon uptake along a  
792 latitudinal gradient. *Journal of Ecology* 109, 3424–3441. doi:10.1111/1365-  
793 2745.13732  
794 Harris, L.I., Richardson, K., Bona, K.A., Davidson, S.J., Finkelstein, S.A., Garneau, M.,  
795 McLaughlin, J., Nwaishi, F., Olefeldt, D., Packalen, M., Roulet, N.T., Southee, F.M.,  
796 Strack, M., Webster, K.L., Wilkinson, S.L., Ray, J.C., 2022. The essential carbon  
797 service provided by northern peatlands. *Frontiers in Ecology and the Environment* 20,  
798 222–230. doi:10.1002/FEE.2437  
799 Heckmann, L., Drossel, B., Brose, U., Guill, C., 2012. Interactive effects of body-size  
800 structure and adaptive foraging on food-web stability. *Ecology Letters* 15, 243–250.  
801 doi:10.1111/J.1461-0248.2011.01733.X  
802 Hedges, L., Olkin, I., 1985. *Statistical Methods for Meta-Analysis - 1st Edition*.  
803 Hollister, R.D., Elphinstone, C., Henry, G.H.R., Bjorkman, A.D., Klanderud, K., Björk,  
804 R.G., Björkman, M.P., Bokhorst, S., Carbognani, M., Cooper, E.J., Dorrepaal, E.,  
805 Elmendorf, S.C., Fetcher, N., Gallois, E.C., Guoðmundsson, J., Healey, N.C.,  
806 Jónsdóttir, I.S., Klarenberg, I.J., Oberbauer, S.F., Macek, P., May, J.L., Mereghetti, A.,

807 Molau, U., Petraglia, A., Rinnan, R., Rixen, C., Wookey, P.A., 2023. A review of open  
808 top chamber (OTC) performance across the ITEX Network. *Arctic Science* 9, 331–  
809 344. doi:10.1139/AS-2022-0030/ASSET/IMAGES/AS-2022-0030\_F9.JPG

810 Hopple, A.M., Wilson, R.M., Kolton, M., Zalman, C.A., Chanton, J.P., Kostka, J., Hanson,  
811 P.J., Keller, J.K., Bridgham, S.D., 2020. Massive peatland carbon banks vulnerable to  
812 rising temperatures. *Nature Communications* 11, 1–7. doi:10.1038/s41467-020-16311-  
813 8

814 IPCC, 2023. *Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II*  
815 *and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate*  
816 *Change* [Core Writing Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva,  
817 Switzerland, 184 pp., doi: 10.59327/IPCC/AR6-9789291691647.

818 IPCC, 2021. *Climate Change 2021: The Physical Science Basis. Contribution of Working*  
819 *Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate*  
820 *Change*[Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N.  
821 Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R.  
822 Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)].  
823 Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA,  
824 In press,. doi:10.1017/9781009157896

825 Iturbide, M., Fernández, J., Gutiérrez, J.M., Bedía, J., Cimadevilla, E., Díez-Sierra, J.,  
826 Manzanas, R., Casanueva, A., Baño-Medina, J., Milovac, J., Herrera, S., Cofiño, A.S.,  
827 San Martín, D., García-Díez, M., Hauser, M., Huard, D., Yelekci, Ö., 2021. Repository  
828 supporting the implementation of FAIR principles in the IPCC-WGI Atlas.  
829 doi:10.5281/ZENODO.5171760

830 Jak, S., Cheung, M.W.L., 2020. Meta-analytic structural equation modeling with  
831 moderating effects on SEM parameters. *Psychological Methods* 25, 430–455.  
832 doi:10.1037/MET0000245

833 Jansson, J.K., Hofmockel, K.S., 2020. Soil microbiomes and climate change. *Nature*  
834 *Reviews Microbiology* 18, 35–46. doi:10.1038/s41579

835 Jassey, V.E.J., Chiapusio, G., Binet, P., Buttler, A., Laggoun-Défarge, F., Delarue, F.,  
836 Bernard, N., Mitchell, E.A., Toussaint, M.L., Francez, A.J., Gilbert, D., 2013. Above-  
837 and belowground linkages in Sphagnum peatland: climate warming affects plant-  
838 microbial interactions. *Global Change Biology* 19, 811–823. doi:10.1111/GCB.12075

839 Jassey, V.E.J., Lamentowicz, M., Bragazza, L., Hofsommer, M.L., Mills, R.T.E., Buttler,  
840 A., Signarbieux, C., Robroek, B.J.M., 2016. Loss of testate amoeba functional  
841 diversity with increasing frost intensity across a continental gradient reduces microbial  
842 activity in peatlands. *European Journal of Protistology* 55, 190–202.  
843 doi:10.1016/J.EJOP.2016.04.007

844 Jassey, V.E.J., Petchey, O.L., Binet, P., Buttler, A., Chiapusio, G., Delarue, F., Laggoun-  
845 Défarge, F., Gilbert, D., Mitchell, E.A.D., Barel, J.M., 2023. Food web structure and  
846 energy flux dynamics, but not taxonomic richness, influence microbial ecosystem  
847 functions in a Sphagnum-dominated peatland. *European Journal of Soil Biology* 118,  
848 103532. doi:10.1016/J.EJSOBI.2023.103532

849 Jassey, V.E.J., Reczuga, M.K., Zielińska, M., Słowińska, S., Robroek, B.J.M., Mariotte, P.,  
850 Seppely, C.V.W., Lara, E., Barabach, J., Słowiński, M., Bragazza, L., Chojnicki, B.H.,  
851 Lamentowicz, M., Mitchell, E.A.D., Buttler, A., 2018. Tipping point in plant–fungal

852 interactions under severe drought causes abrupt rise in peatland ecosystem respiration.  
853 *Global Change Biology* 24, 972–986. doi:10.1111/GCB.13928

854 Jassey, V.E.J., Signarbieux, C., Hättenschwiler, S., Bragazza, L., Buttler, A., Delarue, F.,  
855 Fournier, B., Gilbert, D., Laggoun-Défarge, F., Lara, E., T. E. Mills, R., Mitchell,  
856 E.A.D., Payne, R.J., Robroek, B.J.M., 2015. An unexpected role for mixotrophs in the  
857 response of peatland carbon cycling to climate warming. *Scientific Reports* 5, 1–10.  
858 doi:10.1038/srep16931

859 Jiang, L., Song, Y., Sun, L., Song, C., Wang, X., Ma, X., Liu, C., Gao, J., 2020. Effects of  
860 warming on carbon emission and microbial abundances across different soil depths of  
861 a peatland in the permafrost region under anaerobic condition. *Applied Soil Ecology*  
862 156. doi:10.1016/J.APSOIL.2020.103712

863 Juottonen, H., 2020. Disentangling the effects of methanogen community and environment  
864 on peatland greenhouse gas production by a reciprocal transplant experiment.  
865 *Functional Ecology* 34, 1268–1279. doi:10.1111/1365-2435.13536/SUPPINFO

866 Juottonen, H., Kieman, M., Fritze, H., Hamberg, L., Laine, A.M., Merilä, P., Peltoniemi, K.,  
867 Putkinen, A., Tuittila, E.S., 2022. Integrating Decomposers, Methane-Cycling  
868 Microbes and Ecosystem Carbon Fluxes Along a Peatland Successional Gradient in a  
869 Land Uplift Region. *Ecosystems* 25, 1249–1264. doi:10.1007/S10021-021-00713-  
870 W/FIGURES/5

871 Kaisermann, A., de Vries, F.T., Griffiths, R.I., Bardgett, R.D., 2017. Legacy effects of  
872 drought on plant–soil feedbacks and plant–plant interactions. *New Phytologist* 215,  
873 1413–1424. doi:10.1111/NPH.14661

874 Kang, X., Yan, L., Cui, L., Zhang, X., Hao, Y., Wu, H., Zhang, Y., Li, W., Zhang, K., Yan,  
875 Z., Li, Y., Wang, J., 2018. Reduced Carbon Dioxide Sink and Methane Source under  
876 Extreme Drought Condition in an Alpine Peatland. *Sustainability* 10, 4285.  
877 doi:10.3390/SU10114285

878 Kip, N., Van Winden, J.F., Pan, Y., Bodrossy, L., Reichart, G.J., Smolders, A.J.P., Jetten,  
879 M.S.M., Damsté, J.S.S., Op Den Camp, H.J.M., 2010. Global prevalence of methane  
880 oxidation by symbiotic bacteria in peat-moss ecosystems. *Nature Geoscience* 3, 617–  
881 621. doi:10.1038/ngeo939

882 Koricheva, J., Gurevitch, J., Mengersen, K.L., 2013. *Handbook of meta-analysis in ecology  
883 and evolution*. Princeton University Press.

884 Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: Tests in  
885 Linear Mixed Effects Models. *Journal of Statistical Software* 82, 1–26.  
886 doi:10.18637/JSS.V082.I13

887 Laiho, R., 2006. Decomposition in peatlands: Reconciling seemingly contrasting results on  
888 the impacts of lowered water levels. *Soil Biology and Biochemistry* 38, 2011–2024.  
889 doi:10.1016/J.SOILBIO.2006.02.017

890 Lamentowicz, M., Bragazza, L., Buttler, A., Jassey, V.E.J., Mitchell, E.A.D., 2013.  
891 Seasonal patterns of testate amoeba diversity, community structure and species–  
892 environment relationships in four Sphagnum-dominated peatlands along a 1300 m  
893 altitudinal gradient in Switzerland. *Soil Biology and Biochemistry* 67, 1–11.

894 Lamit, L.J., Romanowicz, K.J., Potvin, L.R., Lennon, J.T., Tringe, S.G., Chimner, R.A.,  
895 Kolka, R.K., Kane, E.S., Lilleskov, E.A., 2021. Peatland microbial community  
896 responses to plant functional group and drought are depth-dependent. *Molecular  
897 Ecology* 30, 5119–5136. doi:10.1111/MEC.16125

898 Lefcheck, J.S., 2016. piecewiseSEM: Piecewise structural equation modelling in r for  
899 ecology, evolution, and systematics. *Methods in Ecology and Evolution* 7, 573–579.  
900 doi:10.1111/2041-210X.12512

901 Liu, S., Zheng, Y., Ma, R., Yu, K., Han, Z., Xiao, S., Li, Z., Wu, S., Li, S., Wang, J., Luo,  
902 Y., Zou, J., 2020. Increased soil release of greenhouse gases shrinks terrestrial carbon  
903 uptake enhancement under warming. *Global Change Biology* 26, 4601–4613.  
904 doi:10.1111/GCB.15156

905 Li, W., Shi, R., Yuan, L., Lan, X., Feng, D., Chen, H., 2022. Effect of short-term warming  
906 and drought on the methanogenic communities in degraded peatlands in Zoige Plateau.  
907 *Frontiers in Microbiology* 13, 4139. doi:10.3389/FMICB.2022.880300/BIBTEX

908 Li, Y., Ma, J., Yu, Y., Li, Yijia, Shen, X., Huo, S., Xia, X., 2022. Effects of multiple global  
909 change factors on soil microbial richness, diversity and functional gene abundances: A  
910 meta-analysis. *Science of The Total Environment* 815, 152737.  
911 doi:10.1016/J.SCITOTENV.2021.152737

912 Loisel, J., Gallego-Sala, A. V., Amesbury, M.J., Magnan, G., Anshari, G., Beilman, D.W.,  
913 Benavides, J.C., Blewett, J., Camill, P., Charman, D.J., Chawchai, S., Hedgpeth, A.,  
914 Kleinen, T., Korhola, A., Large, D., Mansilla, C.A., Müller, J., van Bellen, S., West,  
915 J.B., Yu, Z., Bubier, J.L., Garneau, M., Moore, T., Sannel, A.B.K., Page, S., Väiliranta,  
916 M., Bechtold, M., Brovkin, V., Cole, L.E.S., Chanton, J.P., Christensen, T.R., Davies,  
917 M.A., De Vleeschouwer, F., Finkelstein, S.A., Frolking, S., Gałka, M., Gandois, L.,  
918 Girkin, N., Harris, L.I., Heinemeyer, A., Hoyt, A.M., Jones, M.C., Joos, F., Juutinen,  
919 S., Kaiser, K., Lacourse, T., Lamentowicz, M., Larmola, T., Leifeld, J., Lohila, A.,  
920 Milner, A.M., Minkinen, K., Moss, P., Naafs, B.D.A., Nichols, J., O'Donnell, J.,  
921 Payne, R., Philben, M., Piilo, S., Quillet, A., Ratnayake, A.S., Roland, T.P.,  
922 Sjögersten, S., Sonntag, O., Swindles, G.T., Swinnen, W., Talbot, J., Treat, C.,  
923 Valach, A.C., Wu, J., 2020. Expert assessment of future vulnerability of the global  
924 peatland carbon sink. *Nature Climate Change* 11, 70–77. doi:10.1038/s41558-020-  
925 00944-0

926 Lurgi, M., López, B.C., Montoya, J.M., 2012a. Novel communities from climate change.  
927 *Philosophical Transactions of the Royal Society B: Biological Sciences* 367, 2913–  
928 2922. doi:10.1098/RSTB.2012.0238

929 Lurgi, M., López, B.C., Montoya, J.M., 2012b. Climate change impacts on body size and  
930 food web structure on mountain ecosystems. *Philosophical Transactions of the Royal*  
931 *Society B: Biological Sciences* 367, 3050–3057. doi:10.1098/RSTB.2012.0239

932 Maestre, F.T., Delgado-Baquerizo, M., Jeffries, T.C., Eldridge, D.J., Ochoa, V., Gozalo, B.,  
933 Quero, J.L., García-Gómez, M., Gallardo, A., Ulrich, W., Bowker, M.A., Arredondo,  
934 T., Barraza-Zepeda, C., Bran, D., Florentino, A., Gaitán, J., Gutiérrez, J.R., Huber-  
935 Sannwald, E., Jankju, M., Mau, R.L., Miriti, M., Naseri, K., Ospina, A., Stavi, I.,  
936 Wang, D., Woods, N.N., Yuan, X., Zaady, E., Singh, B.K., 2015. Increasing aridity  
937 reduces soil microbial diversity and abundance in global drylands. *Proceedings of the*  
938 *National Academy of Sciences of the United States of America* 112, 15684–15689.  
939 doi:10.1073/PNAS.1516684112/SUPPL\_FILE/PNAS.201516684SI.PDF

940 Malinauskaite, L., Cook, D., Davíðsdóttir, B., Ögmundardóttir, H., Roman, J., 2019.  
941 Ecosystem services in the Arctic: a thematic review. *Ecosystem Services* 36, 100898.  
942 doi:10.1016/j.ecoser.2019.100898

943 McCalley, C.K., Woodcroft, B.J., Hodgkins, S.B., Wehr, R.A., Kim, E.H., Mondav, R.,  
944 Crill, P.M., Chanton, J.P., Rich, V.I., Tyson, G.W., Saleska, S.R., 2014. Methane  
945 dynamics regulated by microbial community response to permafrost thaw. *Nature* 514,  
946 478–481. doi:10.1038/nature13798

947 Meisner, A., Bååth, E., Rousk, J., 2013. Microbial growth responses upon rewetting soil  
948 dried for four days or one year. *Soil Biology and Biochemistry* 66, 188–192.  
949 doi:10.1016/J.SOILBIO.2013.07.014

950 Melillo, J.M., Frey, S.D., DeAngelis, K.M., Werner, W.J., Bernard, M.J., Bowles, F.P.,  
951 Pold, G., Knorr, M.A., Grandy, A.S., 2017. Long-term pattern and magnitude of soil  
952 carbon feedback to the climate system in a warming world. *Science* 358, 101–105.  
953 doi:10.1126/SCIENCE.AAN2874/SUPPL\_FILE/AAN2874\_MELILLO\_SM.PDF

954 Melton, J.R., Chan, E., Millard, K., Fortier, M., Winton, R.S., Martín-López, J.M., Cadillo-  
955 Quiroz, H., Kidd, D., Verchot, L. V., 2022. A map of global peatland extent created  
956 using machine learning (Peat-ML). *Geoscientific Model Development* 15, 4709–4738.  
957 doi:10.5194/GMD-15-4709-2022

958 Mpmah, P.A., Taipale, S., Rissanen, A.J., Biasi, C., Nykänen, H.K., 2017. The impact of  
959 long-term water level draw-down on microbial biomass: A comparative study from  
960 two peatland sites with different nutrient status. *European Journal of Soil Biology* 80,  
961 59–68. doi:10.1016/J.EJSOBI.2017.04.005

962 Nair, A., 2019. Publication bias - Importance of studies with negative results! *Indian*  
963 *Journal of Anaesthesia* 63, 505. doi:10.4103/IJA.IJA\_142\_19

964 Nakagawa, S., Yang, Y., Macartney, E.L., Spake, R., Lagisz, M., 2023. Quantitative  
965 evidence synthesis: a practical guide on meta-analysis, meta-regression, and  
966 publication bias tests for environmental sciences. *Environmental Evidence* 12, 1–19.  
967 doi:10.1186/S13750-023-00301-6

968 Naylor, D., Sadler, N., Bhattacharjee, A., Graham, E.B., Anderton, C.R., McClure, R.,  
969 Lipton, M., Hofmockel, K.S., Jansson, J.K., 2020. Soil Microbiomes Under Climate  
970 Change and Implications for Carbon Cycling. *Annual Review of Environment and*  
971 *Resources* 45, 29–59. doi:10.1146/ANNUREV-ENVIRON-012320-082720

972 Neilson, R., Caul, S., Fraser, F.C., King, D., Mitchell, S.M., Roberts, D.M., Giles, M.E.,  
973 2020. Microbial community size is a potential predictor of nematode functional group  
974 in limed grasslands. *Applied Soil Ecology* 156, 103702.  
975 doi:10.1016/J.APSOIL.2020.103702

976 Nichols, J.E., Peteet, D.M., 2019. Rapid expansion of northern peatlands and doubled  
977 estimate of carbon storage. *Nature Geoscience* 12, 917–921. doi:10.1038/s41561-019-  
978 0454-z

979 Nielsen, U.N., Wall, D.H., Six, J., 2015. Soil Biodiversity and the Environment. *Annual*  
980 *Review of Environment and Resources* 40, 63–90. doi:10.1146/ANNUREV-  
981 ENVIRON-102014-021257

982 Ohlberger, J., 2013. Climate warming and ectotherm body size – from individual  
983 physiology to community ecology. *Functional Ecology* 27, 991–1001.  
984 doi:10.1111/1365-2435.12098

985 Peltoniemi, K., Laiho, R., Juottonen, H., Kiikkilä, O., Mäkiranta, P., Minkkinen, K.,  
986 Pennanen, T., Penttilä, T., Sarjala, T., Tuittila, E.S., Tuomivirta, T., Fritze, H., 2015.  
987 Microbial ecology in a future climate: effects of temperature and moisture on microbial

988 communities of two boreal fens. *FEMS Microbiology Ecology* 91, 062.  
989 doi:10.1093/FEMSEC/FIV062

990 Perryman, C.R., McCalley, C.K., Shorter, J.H., Perry, A.L., White, N., Dziurzynski, A.,  
991 Varner, R.K., 2023. Effect of Drought and Heavy Precipitation on CH<sub>4</sub> Emissions and  
992 δ<sup>13</sup>C–CH<sub>4</sub> in a Northern Temperate Peatland. *Ecosystems* 1–18. doi:10.1007/S10021-  
993 023-00868-8/FIGURES/5

994 Petchey, O.L., McPhearson, P.T., Casey, T.M., Morin, P.J., 1999. Environmental warming  
995 alters food-web structure and ecosystem function. *Nature* 402, 69–72.  
996 doi:10.1038/47023

997 Potapov, A.M., Beaulieu, F., Birkhofer, K., Bluhm, S.L., Degtyarev, M.I., Devetter, M.,  
998 Goncharov, A.A., Gongalsky, K.B., Klärner, B., Korobushkin, D.I., Liebke, D.F.,  
999 Maraun, M., Mc Donnell, R.J., Pollierer, M.M., Schaefer, I., Shrubovych, J.,  
1000 Semenyuk, I.I., Sendra, A., Tuma, J., Tůmová, M., Vassilieva, A.B., Chen, T.W.,  
1001 Geisen, S., Schmidt, O., Tiunov, A. V., Scheu, S., 2022. Feeding habits and  
1002 multifunctional classification of soil- associated consumers from protists to  
1003 vertebrates. *Biological Reviews* 97, 1057–1117. doi:10.1111/BRV.12832

1004 Qiu, C., Ciais, P., Zhu, D., Guenet, B., Peng, S., Petrescu, A.M.R., Lauerwald, R.,  
1005 Makowski, D., Gallego-Sala, A. V., Charman, D.J., Brewer, S.C., 2021. Large  
1006 historical carbon emissions from cultivated northern peatlands. *Science Advances* 7.  
1007 doi:10.1126/SCIADV.ABF1332

1008 Qiu, C., Zhu, D., Ciais, P., Guenet, B., Krinner, G., Peng, S., Aurela, M., Bernhofer, C.,  
1009 Brümmer, C., Bret-Harte, S., Chu, H., Chen, J., Desai, A.R., Dušek, J., Euskirchen,  
1010 E.S., Fortuniak, K., Flanagan, L.B., Friborg, T., Grygoruk, M., Gogo, S., Grünwald, T.,  
1011 Hansen, B.U., Holl, D., Humphreys, E., Hurkuck, M., Kiely, G., Klatt, J., Kutzbach,  
1012 L., LARGERON, C., Laggoun-Défarge, F., Lund, M., Lafleur, P.M., Li, X., Mammarella,  
1013 I., Merbold, L., Nilsson, M.B., Olejnik, J., Ottosson-Löfvenius, M., Oechel, W.,  
1014 Parmentier, F.J.W., Peichl, M., Pirk, N., Peltola, O., Pawlak, W., Rasse, D., Rinne, J.,  
1015 Shaver, G., Peter Schmid, H., Sottocornola, M., Steinbrecher, R., Sachs, T., Urbaniak,  
1016 M., Zona, D., Ziemblinska, K., 2018. ORCHIDEE-PEAT (revision 4596), a model for  
1017 northern peatland CO<sub>2</sub>, water, and energy fluxes on daily to annual scales.  
1018 *Geoscientific Model Development* 11, 497–519. doi:10.5194/GMD-11-497-2018

1019 Qiu, C., Zhu, D., Ciais, P., Guenet, B., Peng, S., 2020. The role of northern peatlands in the  
1020 global carbon cycle for the 21st century. *Global Ecology and Biogeography* 29, 956–  
1021 973. doi:10.1111/GEB.13081

1022 Raghoebarsing, A.A., Smolders, A.J.P., Schmid, M.C., Rijnstra, W.I.C., Wolters-Arts, M.,  
1023 Derksen, J., Jetten, M.S.M., Schouten, S., Damsté, J.S.S., Lamers, L.P.M., Roelofs,  
1024 J.G.M., Op Den Camp, H.J.M., Strous, M., 2005. Methanotrophic symbionts provide  
1025 carbon for photosynthesis in peat bogs. *Nature* 436, 1153–1156.  
1026 doi:10.1038/NATURE03802

1027 R Core Team, 2022. R: A language and environment for statistical computing. R  
1028 Foundation for Statistical Computing, Vienna, Austria.

1029 Re ACD, 2013. compute.es: Compute Effect Sizes.

1030 Reczuga, M.K., Lamentowicz, M., Mulot, M., Mitchell, E.A.D., Buttler, A., Chojnicki, B.,  
1031 Słowiński, M., Binet, P., Chiapusio, G., Gilbert, D., Słowińska, S., Jassey, V.E.J.,  
1032 2018. Predator–prey mass ratio drives microbial activity under dry conditions in  
1033 Sphagnum peatlands. *Ecology and Evolution* 8, 5752–5764. doi:10.1002/ECE3.4114



1034 Rinnan, R., Stark, S., Tolvanen, A., 2009. Responses of vegetation and soil microbial  
1035 communities to warming and simulated herbivory in a subarctic heath. *Journal of*  
1036 *Ecology* 97, 788–800. doi:10.1111/J.1365-2745.2009.01506.X

1037 Robinson, C., Ritson, J., Alderson, D., Malik, A.A., Griffiths, R.I., Heinemeyer, A.,  
1038 Gallego-Sala, A. V., Quillet, A., Robroek, B.J.M., Evans, C., Chandler, D.M., Elliott,  
1039 D.R., Shuttleworth, E.L., Lilleskov, E.A., Kitson, E., Cox, F., Worrall, F., Clay, G.,  
1040 Crosher, I., Pratscher, J., Bird, J., Walker, J., Belyea, L.R., Dumont, M.G., Bell,  
1041 N.G.A., Artz, R.R.E., Bardgett, R., Andersen, R., Hutchinson, S.M., Page, S.E., Thom,  
1042 T.J., Burn, W., Evans, M.G., 2023. Aspects of microbial communities in peatland  
1043 carbon cycling under changing climate and land use pressures. *Mires and Peat*.

1044 Romero, G.Q., Gonçalves-Souza, T., Kratina, P., Marino, N.A.C., Petry, W.K., Sobral-  
1045 Souza, T., Roslin, T., 2018. Global predation pressure redistribution under future  
1046 climate change. *Nature Climate Change* 8, 1087–1091. doi:10.1038/S41558-018-0347-  
1047 Y

1048 Romero, G.Q., Marino, N.A.C., MacDonald, A.A.M., Céréghino, R., Trzcinski, M.K.,  
1049 Mercado, D.A., Leroy, C., Corbara, B., Farjalla, V.F., Barberis, I.M., Dézerald, O.,  
1050 Hammill, E., Atwood, T.B., Piccoli, G.C.O., Bautista, F.O., Carrias, J.F., Leal, J.S.,  
1051 Montero, G., Antiquiera, P.A.P., Freire, R., Realpe, E., Amundrud, S.L., de Omena,  
1052 P.M., Campos, A.B.A., Kratina, P., O’Gorman, E.J., Srivastava, D.S., 2020. Extreme  
1053 rainfall events alter the trophic structure in bromeliad tanks across the Neotropics.  
1054 *Nature Communications* 11, 1–8. doi:10.1038/s41467-020-17036-4

1055 Romero-Olivares, A.L., Allison, S.D., Treseder, K.K., 2017. Soil microbes and their  
1056 response to experimental warming over time: A meta-analysis of field studies. *Soil*  
1057 *Biology and Biochemistry* 107, 32–40. doi:10.1016/J.SOILBIO.2016.12.026

1058 Rønn, R., Vestergård, M., Ekelund, F., 2012. Interactions Between Bacteria, Protozoa and  
1059 Nematodes in Soil. *Acta Protozoologica* 51, 223–235.  
1060 doi:10.4467/16890027AP.12.018.0764

1061 Rothstein, H.R., Sutton, A.J., Borenstein, M., 2006. Publication bias in meta-analysis:  
1062 Prevention, assessment and adjustments. *wiley*. doi:10.1002/0470870168

1063 RStudio Team, 2020. RStudio: Integrated Development for R.

1064 Sauvadet, M., Chauvat, M., Cluzeau, D., Maron, P.A., Villenave, C., Bertrand, I., 2016. The  
1065 dynamics of soil micro-food web structure and functions vary according to litter  
1066 quality. *Soil Biology and Biochemistry* 95, 262–274.  
1067 doi:10.1016/J.SOILBIO.2016.01.003

1068 Schindlbacher, A., Rodler, A., Kuffner, M., Kitzler, B., Sessitsch, A., Zechmeister-  
1069 Boltenstern, S., 2011. Experimental warming effects on the microbial community of a  
1070 temperate mountain forest soil. *Soil Biology & Biochemistry* 43, 1417–1425.  
1071 doi:10.1016/J.SOILBIO.2011.03.005

1072 Smith, D.M., Screen, J.A., Deser, C., Cohen, J., Fyfe, J.C., García-Serrano, J., Jung, T.,  
1073 Kattsov, V., Matei, D., Msadek, R., Peings, Y., Sigmond, M., Ukita, J., Zhang, X.,  
1074 2019. The Polar Amplification Model Intercomparison Project (PAMIP) contribution  
1075 to CMIP6: Investigating the causes and consequences of polar amplification.  
1076 *Geoscientific Model Development* 12, 1139–1164. doi:10.5194/GMD-12-1139-2019

1077 Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M.,  
1078 Millor, H.L., 2007. Contribution of Working Group I to the Fourth Assessment Report

1079 of the Intergovernmental Panel on Climate Change, 2007. Cambridge University Press,  
1080 Cambridge, United Kingdom and New York, NY, USA.

1081 Song, Y., Liu, C., Song, C., Wang, X., Ma, X., Gao, J., Gao, S., Wang, L., 2021. Linking  
1082 soil organic carbon mineralization with soil microbial and substrate properties under  
1083 warming in permafrost peatlands of Northeastern China. *Catena* 203, 105348.  
1084 doi:10.1016/J.CATENA.2021.105348

1085 Sterne, J.A.C., Egger, M., 2001. Funnel plots for detecting bias in meta-analysis: guidelines  
1086 on choice of axis. *Journal of Clinical Epidemiology* 54, 1046–1055.  
1087 doi:10.1016/S0895-4356(01)00377-8

1088 Strack, M., Davidson, S.J., Hirano, T., Dunn, C., 2022. The Potential of Peatlands as  
1089 Nature-Based Climate Solutions. *Current Climate Change Reports* 8, 71–82.  
1090 doi:10.1007/S40641-022-00183-9

1091 Swindles, G.T., Morris, P.J., Mullan, D.J., Payne, R.J., Roland, T.P., Amesbury, M.J.,  
1092 Lamentowicz, M., Turner, T.E., Gallego-Sala, A., Sim, T., Barr, I.D., Blaauw, M.,  
1093 Blundell, A., Chambers, F.M., Charman, D.J., Feurdean, A., Galloway, J.M., Gałka,  
1094 M., Green, S.M., Kajukalo, K., Karofeld, E., Korhola, A., Lamentowicz, Ł., Langdon,  
1095 P., Marcisz, K., Mauquoy, D., Mazei, Y.A., McKeown, M.M., Mitchell, E.A.D.,  
1096 Novenko, E., Plunkett, G., Roe, H.M., Schoning, K., Sillasoo, Ü., Tsyganov, A.N., van  
1097 der Linden, M., Väliranta, M., Warner, B., 2019. Widespread drying of European  
1098 peatlands in recent centuries. *Nature Geoscience* 12, 922–928. doi:10.1038/s41561-  
1099 019-0462-z

1100 Trap, J., Bonkowski, M., Plassard, C., Villenave, C., Blanchart, E., 2015. Ecological  
1101 importance of soil bacterivores for ecosystem functions. *Plant and Soil* 398, 1–24.  
1102 doi:10.1007/S11104-015-2671-6

1103 Tucker, C.L., Bell, J., Pendall, E., Ogle, K., 2013. Does declining carbon-use efficiency  
1104 explain thermal acclimation of soil respiration with warming? *Global Change Biology*  
1105 19, 252–263. doi:10.1111/GCB.12036

1106 Viechtbauer, W., 2010. Conducting Meta-Analyses in R with the metafor Package. *Journal*  
1107 *of Statistical Software* 36, 1–48. doi:10.18637/JSS.V036.I03

1108 Walker, T.W.N., Kaiser, C., Strasser, F., Herbold, C.W., Leblans, N.I.W., Woebken, D.,  
1109 Janssens, I.A., Sigurdsson, B.D., Richter, A., 2018. Microbial temperature sensitivity  
1110 and biomass change explain soil carbon loss with warming. *Nature Climate Change* 8,  
1111 885–889. doi:10.1038/S41558-018-0259-X

1112 Wang, K., Peng, C., Zhu, Q., Zhou, X., Wang, M., Zhang, K., Wang, G., 2017. Modeling  
1113 Global Soil Carbon and Soil Microbial Carbon by Integrating Microbial Processes into  
1114 the Ecosystem Process Model TRIPLEX-GHG. *Journal of Advances in Modeling*  
1115 *Earth Systems* 9, 2368–2384. doi:10.1002/2017MS000920

1116 Wang, X., Liu, L., Piao, S., Janssens, I.A., Tang, J., Liu, W., Chi, Y., Wang, J., Xu, S.,  
1117 2014. Soil respiration under climate warming: differential response of heterotrophic  
1118 and autotrophic respiration. *Global Change Biology* 20, 3229–3237.  
1119 doi:10.1111/GCB.12620

1120 Wickham, H., 2016. *ggplot2 Elegant Graphics for Data Analysis* 211.

1121 Wilkinson, D.M., Mitchell, E.A.D., 2010. Testate Amoebae and Nutrient Cycling with  
1122 Particular Reference to Soils. *Geomicrobiology Journal* 27, 520–533.  
1123 doi:10.1080/01490451003702925

1124 Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A.,  
1125 Warren, P.H., 2005. Body size in ecological networks. *Trends in Ecology & Evolution*  
1126 20, 402–409. doi:10.1016/J.TREE.2005.04.005

1127 Woodward, Guy, Papantoniou, G., Edwards, François, Lauridsen, Rasmus B, Woodward,  
1128 G, Papantaniou, G., Edwards, F, Lauridsen, R B, 2008. Trophic trickles and cascades  
1129 in a complex food web: impacts of a keystone predator on stream community structure  
1130 and ecosystem processes. *Oikos* 117, 683–692. doi:10.1111/J.0030-  
1131 1299.2008.16500.X

1132 Wu, H., Yan, L., Li, Y., Zhang, K., Hao, Y., Wang, J., Zhang, X., Yan, Z., Zhang, Y., Kang,  
1133 X., 2020. Drought-induced reduction in methane fluxes and its hydrothermal  
1134 sensitivity in alpine peatland. *PeerJ* 8, 8874. doi:10.7717/PEERJ.8874/FIG-3

1135 Xue, D., Liu, T., Chen, H., Liu, J., Hu, J., Liu, L., 2021. Fungi are more sensitive than  
1136 bacteria to drainage in the peatlands of the Zoige Plateau. *Ecological Indicators* 124,  
1137 107367. doi:10.1016/J.ECOLIND.2021.107367

1138 Xu, W., Yuan, W., 2017. Responses of microbial biomass carbon and nitrogen to  
1139 experimental warming: A meta-analysis. *Soil Biology and Biochemistry* 115, 265–274.  
1140 doi:10.1016/J.SOILBIO.2017.08.033

1141 Yang, L., Pan, J., Wang, J., Tian, D., Zhang, C., Zhao, X., Hu, J., Yang, W., Yan, Y., Ma,  
1142 F., Chen, W., Quan, Q., Wang, P., Niu, S., 2023. Soil microbial respiration adapts to  
1143 higher and longer warming experiments at the global scale. *Environmental Research*  
1144 *Letters* 18, 034044. doi:10.1088/1748-9326/ACBECB

1145 Yeates, G.W., Foissner, W., 1995. Testate amoebae as predators of nematodes. *Biology and*  
1146 *Fertility of Soils* 20, 1–7. doi:10.1007/BF00307834

1147 Yu, Z., Joos, F., Bauska, T.K., Stocker, B.D., Fischer, H., Loisel, J., Brovkin, V., Hugelius,  
1148 G., Nehrbass-Ahles, C., Kleinen, T., 2021. No support for carbon storage of >1000  
1149 GtC in northern peatlands. *Nature Geoscience* 14, 465–467.  
1150 doi:10.31223/OSF.IO/HYNM7

1151 Zehnder, A.J.B., Stumm, W., 1988. Geochemistry and biogeochemistry of anaerobic  
1152 habitats., in: *Biology of Anaerobic Microorganisms*. pp. 1–38. doi:10.3/JQUERY-  
1153 UIJS

1154 Zhang, N., Liu, W., Yang, H., Yu, X., Gutknecht, J.L.M., Zhang, Z., Wan, S., Ma, K., 2013.  
1155 Soil microbial responses to warming and increased precipitation and their implications  
1156 for ecosystem C cycling. *Oecologia* 173, 1125–1142. doi:10.1007/S00442-013-2685-  
1157 9/FIGURES/7

1158 Zhao, J., Tian, L., Wei, H., Sun, F., Li, R., 2019. Negative responses of ecosystem  
1159 autotrophic and heterotrophic respiration to experimental warming in a Tibetan semi-  
1160 arid alpine steppe. *CATENA* 179, 98–106. doi:10.1016/J.CATENA.2019.04.002

1161 Zhou, L., Zhou, X., Shao, J., Nie, Y., He, Y., Jiang, L., Wu, Z., Hosseini Bai, S., 2016.  
1162 Interactive effects of global change factors on soil respiration and its components: a  
1163 meta-analysis. *Global Change Biology* 22, 3157–3169. doi:10.1111/GCB.13253

1164 Zhou, Z., Wang, C., Luo, Y., 2020. Meta-analysis of the impacts of global change factors  
1165 on soil microbial diversity and functionality. *Nature Communications* 11, 1–10.  
1166 doi:10.1038/s41467-020-16881-7

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1169 **Table 1. Description of the climate drivers retained in this synthesis.**

<b>Climate drivers</b>	<b>Complete name</b>	<b>Description</b>
TI	Temperature increase	Natural gradient, transplantation, experimental warming, in the field or in laboratory
WW	Winter warming	Natural or experimental warming during the winter season, snow removal or addition
DR	Drought	Drought, reduced precipitation or reduction of water availability
VS	Vegetation shift	Climate-change-induced change of vegetation (for instance removing of some plants)

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1172 **Table 2. Summary of the response of richness, alpha-diversity, beta-diversity, biomass and function to**  
 1173 **climate drivers (linear mixed effects models, LMMs).** Groups, climate drivers and manipulation magnitude were  
 1174 retained as fixed effect terms, whilst the peatland type, experimentation type, method used and study type were  
 1175 retained as random effect terms. G<sup>a</sup> = microbial group for richness, alpha-diversity, beta-diversity and biomass, and  
 1176 the type of function for microbial function, D = climate drivers, MM= manipulation magnitude. Peatland type = bog,  
 1177 fen, mire, other or several; experimentation = laboratory or field; method = method used to estimate alpha-diversity,  
 1178 beta-diversity and biomass and/or measure microbial functions (see Methods). \*\*\* *P* < 0.001, \*\* *P* < 0.01, \* *P* < 0.05.  
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Fixed effects terms								Random effects terms
Response variable	G <sup>a</sup>	D	MM	D x MM	G <sup>a</sup> x D	G <sup>a</sup> x MM	G <sup>a</sup> x D x MM	
Richness			*					Peatland type, Experimentation, Method
Alpha-diversity								Peatland type, Experimentation, Method
Beta-diversity					*			Peatland type, Experimentation, Method
Biomass	**		*		***	***		Peatland type, Experimentation, Method
Functions	***				***			Peatland type, Experimentation, Study

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**Table 3. Summary of the predictive models used for projections at global peatland scale**

<b>Parameters</b>	<b>CO<sub>2</sub> emission</b>	<b>CO<sub>2</sub> fixation</b>	<b>CH<sub>4</sub> emission</b>	<b>CH<sub>4</sub> oxidation</b>
<b>Number of observations</b>	42	15	41	16
<b><i>P</i>-value</b>	0.023	0.001	0.14	0.91
<b>R<sup>2</sup></b>	0.36	0.73	0.17	0.18

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1198 **Figure captions**

1199 **Figure 1. Peatland coverage and data.** Estimated area coverage (in percentage) of peatlands based on  
1200 the Peat-ML distribution map (Melton et al., 2022). Geometric forms show the global distribution of the  
1201 experimental sites according to different climate change drivers used in this meta-analysis. TI =  
1202 temperature increase (n = 41), WW = winter warming (n = 3), DR = drought (n = 32), VS = vegetation shift  
1203 (n = 2), and MIX = combination of several drivers (n = 42). MIX included TI-DR (n = 25), TI-WW (n = 8),  
1204 TI-VS (n = 4), DR-VS (n = 4), and TI-DR-VS (n = 1). The map shows only latitude above 30°N.  
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1206 **Figure 2. Standardized mean difference (SMD) showing the response of peatland microbial**  
1207 **richness (a), alpha-diversity (b) and beta-diversity (c) to temperature increase (TI) and drought**  
1208 **(DR).** The black dot shows the mean of SMDs and the bars represent the associated standard error. The  
1209 filled line shows the null effect size (equal to zero), the grey area with dotted blue lines represents the  
1210 range [-0.2;0.2] in which SMDs are considered weak. Outside this range SMDs are considered to have  
1211 medium to high effect. Numbers between brackets indicate the number of observations used to calculate  
1212 the SMDs.  
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1214 **Figure 3. Standardized mean difference (SMD) showing the response of peatland microbial**  
1215 **biomass grouped by microbial functional groups to temperature increase (TI) and drought (DR)**  
1216 **(a), with a focus on consumers (b). SMD showing the response of peatland microbial functions to**  
1217 **temperature increase (TI) and drought (DR) (c).** The black dot shows the mean of SMDs and the bars  
1218 represent the standard error associated. The filled line shows the null effect size (equal to zero), the grey  
1219 area with dotted blue lines represents the range [-0.2;0.2] in which SMDs are considered weak. Outside  
1220 this range SMDs are considered to have medium to high effect. Numbers between brackets indicate the  
1221 number of observations used to calculate the SMDs.

1222 **Figure 4. Microbial species turnover and biomass across trophic levels are complementary facets**  
1223 **of the response of peatlands' functions to climate change.** Latent SEMs showing the best functions  
1224 defining microbial C-related multifunctionality under **(a)** temperature increase ( $\chi^2 = 0.35$ ,  $df = 1$ ,  $P = 0.55$ ;  
1225 CFI = 1, RMSEA = 0, SRMR = 0.031) and **(b)** drought ( $\chi^2 = 0.27$ ,  $df = 1$ ,  $P = 0.60$ ; CFI = 1, RMSEA = 0,  
1226 SRMR = 0.01). Unmeasured latent variable 'microbial C-related multifunctionality' is represented by a  
1227 circle while measured variables are represented by squares. Numbers next to each arrow indicated the  
1228 standardized estimates of the model. Standardized estimates derived from the MASEM models under **(c)**  
1229 temperature increase and **(d)** drought. Circles are the mean of  $k$  iterations for each path of the model and  
1230 the bars indicate the standard error derived from the  $k$  iterations ( $k = 50$  for temperature increase;  $k = 10$   
1231 for drought, more details can be found in Methods). Fit of the MASEM models are given in supplementary  
1232 Figure S9. TI = temperature increase, div = alpha-diversity, bdiv = beta-diversity, photot = biomass of  
1233 phototrophs, dec = biomass of bacteria and/or fungi, cons = biomass of consumers, C = microbial C-

1234 related multifunctionality. A priori MASEM model and hypotheses behind paths are given in Figure S1 and  
1235 Table S4.

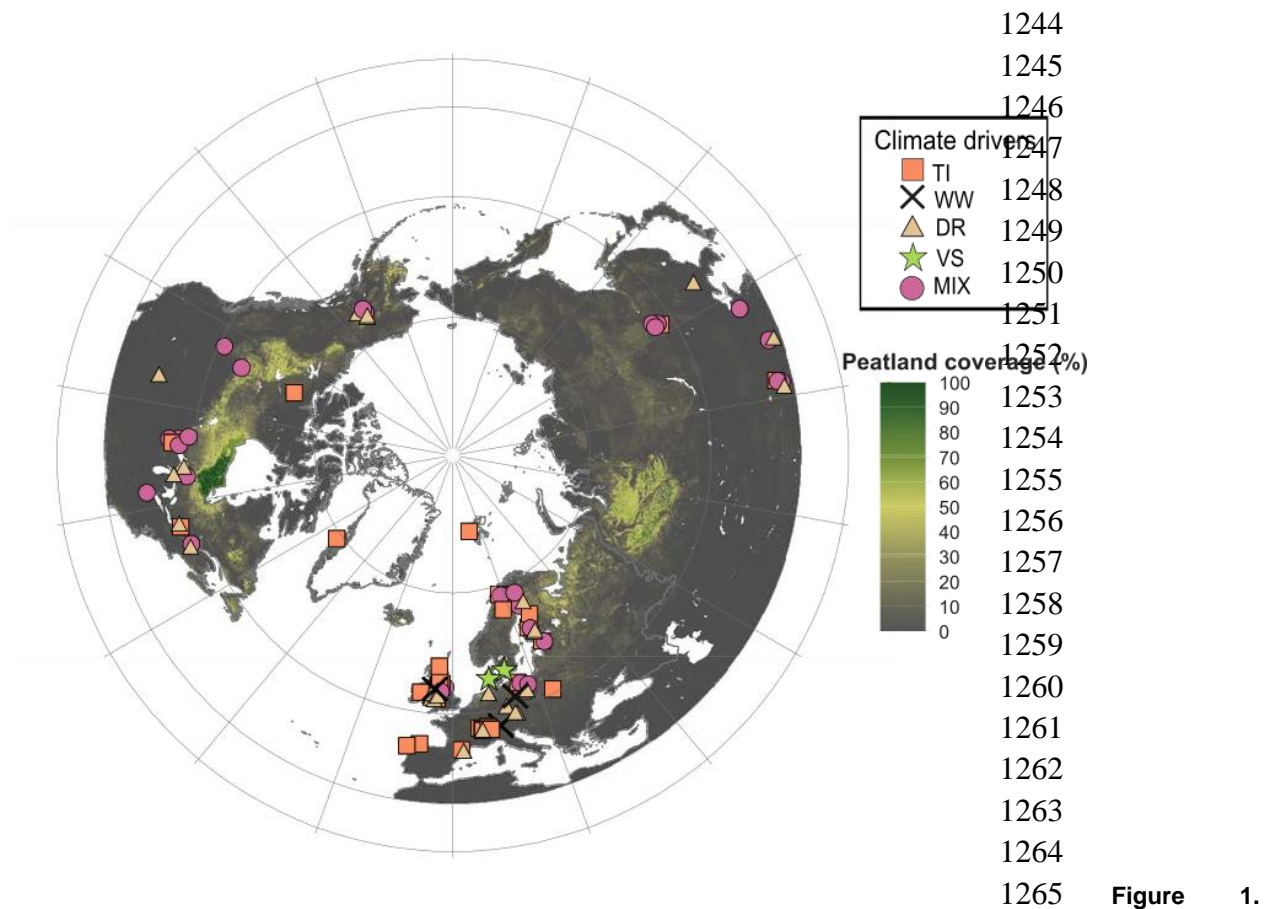
1236 **Figure 5. Predicted standardized mean difference (SMD) for the effect of increasing temperatures**  
1237 **+1.5°C (a) and (c) and +3.0°C (b) and (d) on CO<sub>2</sub> emissions (a) and (b) and CO<sub>2</sub> fixation (c) and (d).**

1238 Peatland distribution was retrieved from the peatland distribution Peat-ML map (Melton et al., 2022),  
1239 CMIP6 model under the SSP5-8.5 scenario for +1.5°C and +3°C warming related to the 1850-1900  
1240 baseline was used.

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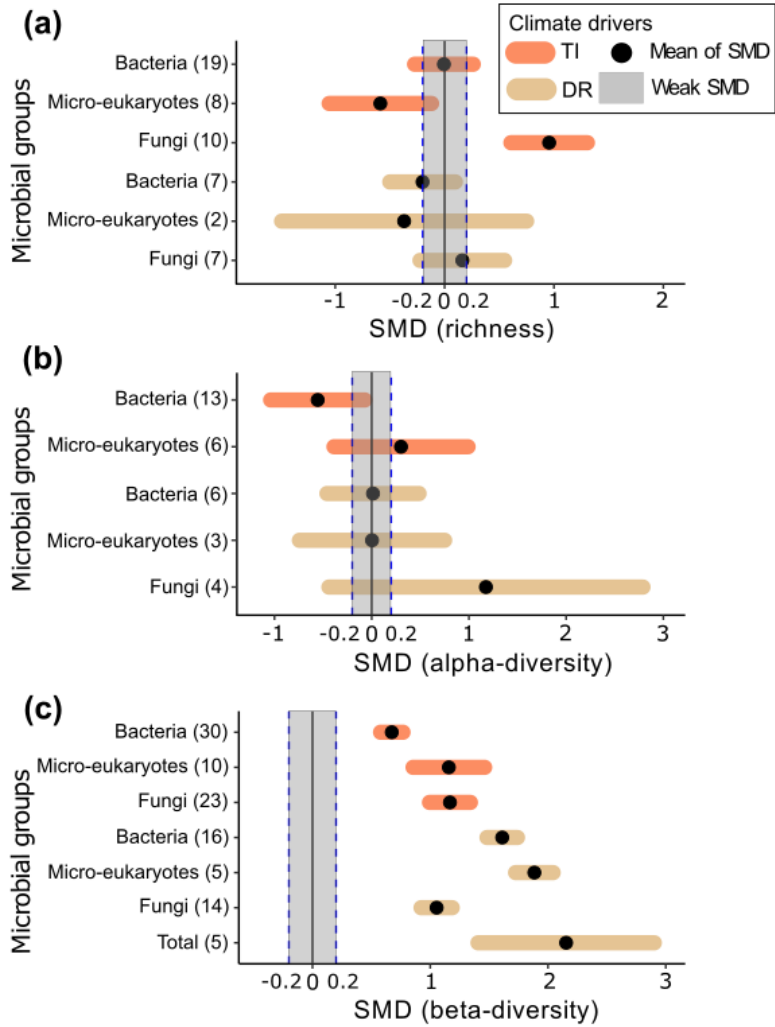
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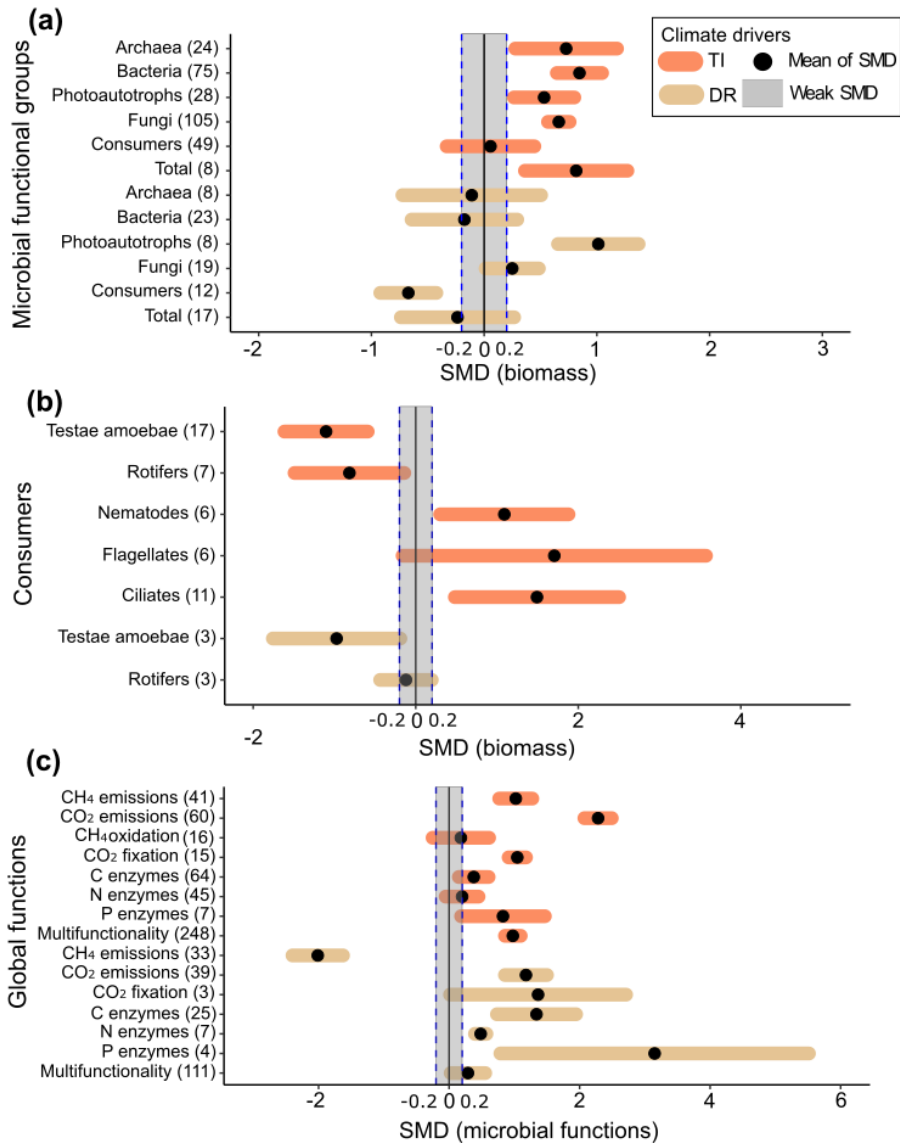
1266 **Peatland coverage and data.** Estimated area coverage (in percentage) of peatlands based on the Peat-ML  
 1267 distribution map (Melton et al., 2022). Geometric forms show the global distribution of the experimental sites  
 1268 according to different climate change drivers used in this meta-analysis. TI = temperature increase (n = 41), WW =  
 1269 winter warming (n = 3), DR = drought (n = 32), VS = vegetation shift (n = 2), and MIX = combination of several drivers  
 1270 (n = 42). MIX included TI-DR (n = 25), TI-WW (n = 8), TI-VS (n = 4), DR-VS (n = 4), and TI-DR-VS (n = 1). The map  
 1271 shows only latitude above 30°N.

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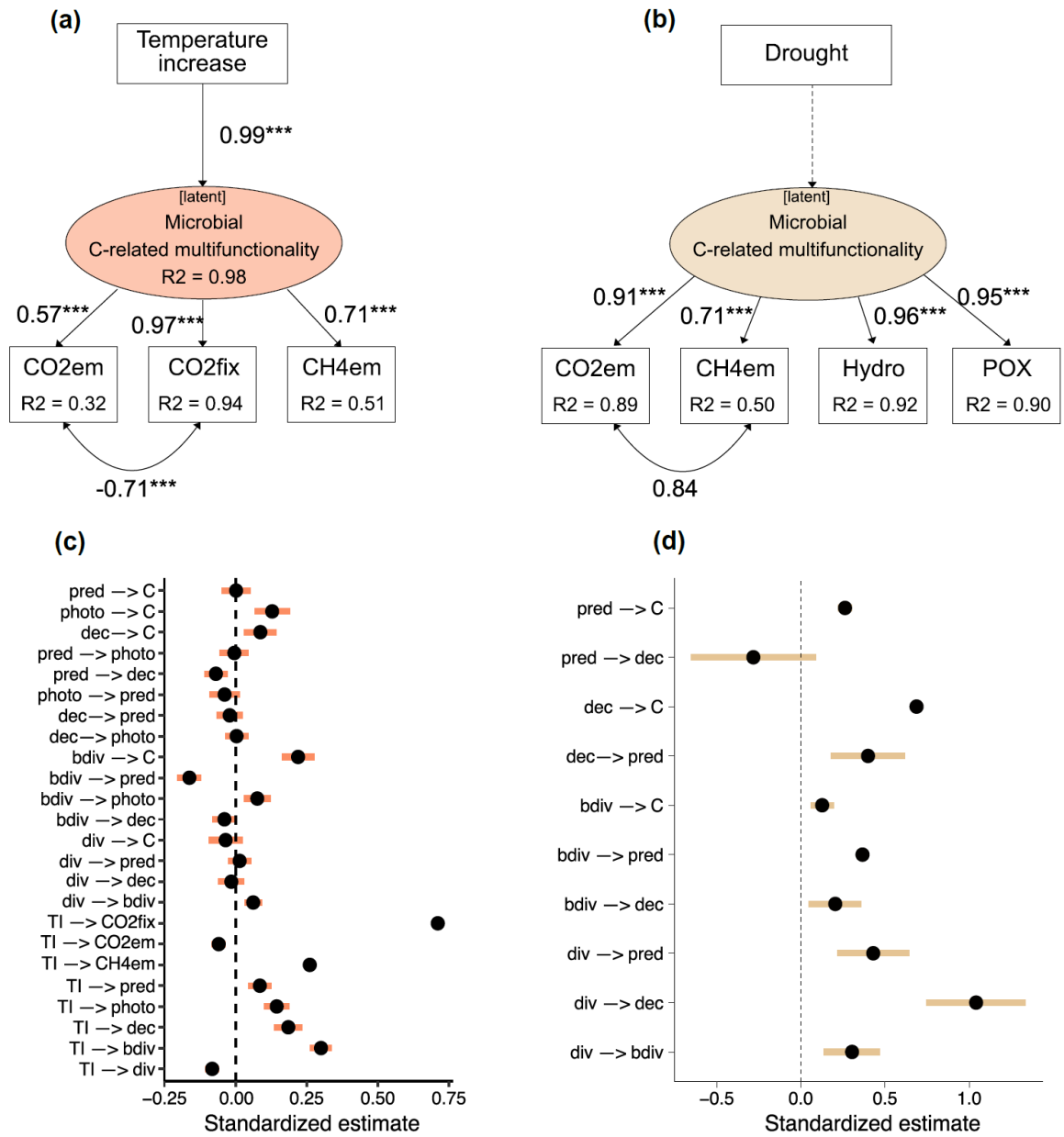
**Figure 2. Standardized mean difference (SMD) representing the response of peatland microbial richness (a), alpha-diversity (b) and beta-diversity (c) to temperature increase (TI) and drought (DR).** The black dot shows the mean of SMD and the bars represent the associated standard error. The filled line shows the null effect size (equal to zero), the grey area with dotted blue lines represents the range [-0.2;0.2] in which SMDs are considered weak. Outside this range SMDs are considered to have medium to high effect. Numbers between brackets indicate the number of observations used to calculate SMDs.

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**Figure 3. Standardized mean difference (SMD) showing the response of peatland microbial biomass grouped by functional type to temperature increase (TI) and drought (DR) (a), with a focus on consumers (b). SMD showing the response of peatland microbial functions to temperature increase (TI) and drought (DR) (c). The black dot shows the mean of SMD and the bars represent the standard error associated. The filled line shows the null effect size (equal to zero), the grey area with dotted blue lines represents the range [-0.2;0.2] in which SMDs are considered weak. Outside this range SMDs are considered to have medium to high effect. Numbers between brackets indicate the number of observations used to calculate SMDs.**

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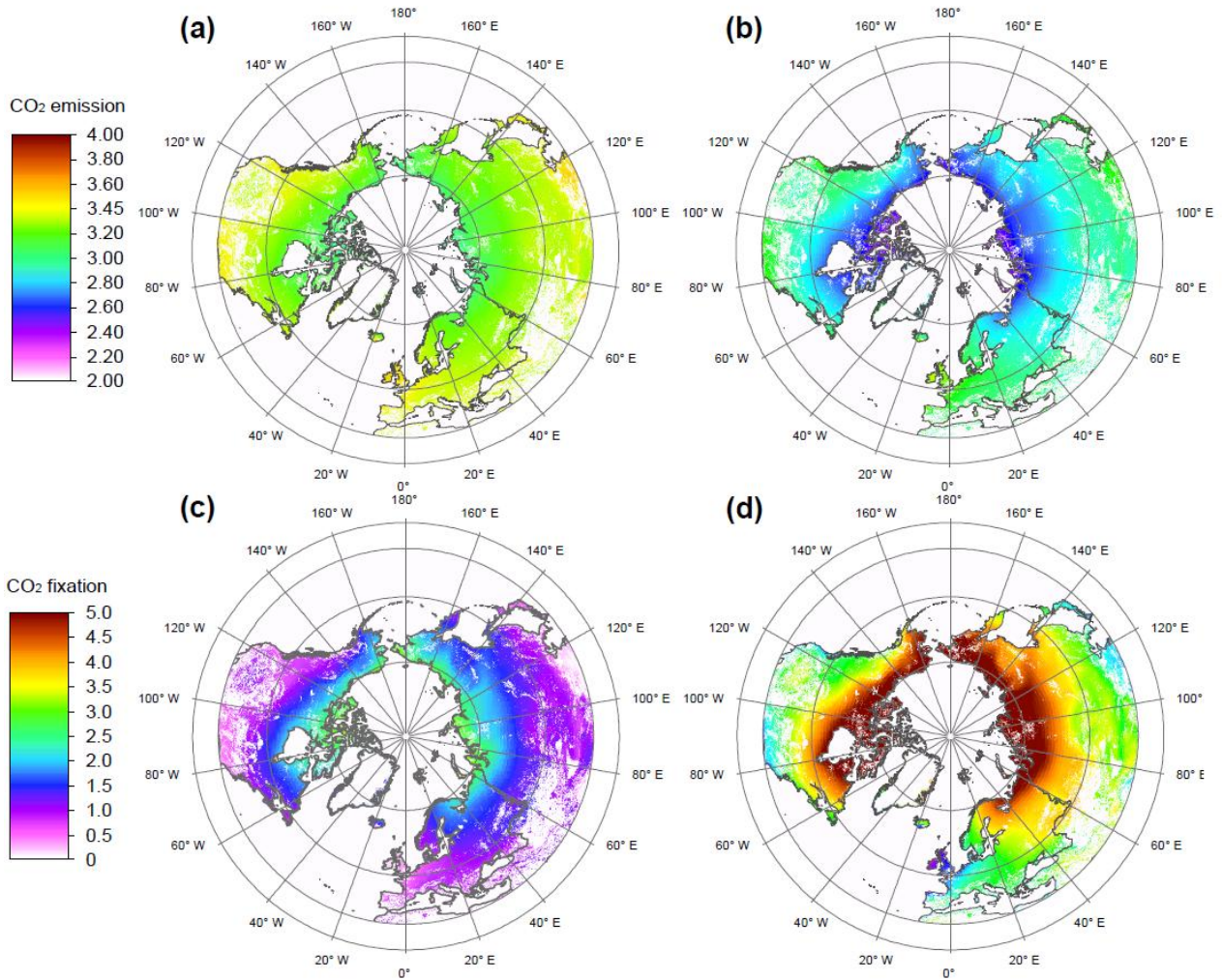
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**Figure 4. Microbial species turnover and biomass across trophic levels are complementary facets of the response of peatland’s functions to climate change.** Latent SEMs showing the best functions defining microbial C-related multifunctionality under (a) temperature increase ( $\chi^2 = 0.35$ ,  $df = 1$ ,  $P = 0.55$ ; CFI = 1, RMSEA = 0, SRMR = 0.031) and (b) drought ( $\chi^2 = 0.27$ ,  $df = 1$ ,  $P = 0.60$ ; CFI = 1, RMSEA = 0, SRMR = 0.01). Unmeasured latent variable ‘microbial C-related multifunctionality’ is represented by a circle while measured variables are represented by squares. Numbers next to each arrow indicated the standardized estimates of the model. Standardized estimates derived from the MASEM models under (c) temperature increase and (d) drought. Circles are the mean of  $k$  iterations for each path of the model and the bars indicate the standard error derived from the  $k$  iterations ( $k = 50$  for temperature increase;  $k = 10$  for drought, more details can be found in methods). Fit of the MASEM models are given

1398 in supplementary Figure S9. TI = temperature increase, div = alpha-diversity, bdiv = beta-diversity, photot = biomass  
1399 of phototrophs, dec = biomass of bacteria and/or fungi, cons = biomass of consumers, C = microbial C-related  
1400 multifunctionality. A priori MASEM model and hypotheses behind paths are given in Figure S1 and Table S4.

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**Figure 5. Predicted standardized mean difference (SMD) for the effect of increasing temperatures +1.5°C (a and c) and +3.0°C (b and d) on CO<sub>2</sub> emissions (a and b) and CO<sub>2</sub> fixation (c and d). Peatland distribution was retrieved from the peatland distribution Peat-ML map (Melton et al., 2022), CMIP6 model under the SPP8.5 scenario for +1.5°C and +3°C warming related to the 1850-1900 baseline was used.**