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

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13
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 CO₂ 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 CO₂ fixation increased for each
30 degree in air temperature gained, while the response of microbial CO₂ 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 CO₂ fixation to temperature anomalies in northern latitudes might
34 compensate to some extent for the possible loss of C from microbial CO₂ 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 CO₂ 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 CH₄ oxidation into CO₂ (Raghoebarsing et
75 al., 2005; Kip et al., 2010), CH₄ emissions (Juottonen, 2020; Juottonen et al., 2022) and
76 CO₂ emissions (Dorrepaal et al., 2009; Hoppo et al., 2020). Recent studies further
77 showed the importance of microbial CO₂ fixation in peatlands, which could approximate
78 c. 10% of peatlands CO₂ 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, CO₂ and CH₄ 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), CO₂ respiration and fixation,
197 CH₄ production and oxidation and N₂ 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 CO₂ fixation and respiration, CH₄ 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 ± 0.27) and
345 weakly affected by drought (-0.2 ± 0.3). Temperature increase (-0.59 ± 0.47) and
346 drought (-0.37 ± 1.12) both decreased micro-eukaryotic richness whereas fungal
347 richness increased with temperature increase (0.96 ± 0.35) and weakly increased with
348 drought (0.16 ± 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 ± 0.48)
355 whereas it increased micro-eukaryotic alpha-diversity (0.3 ± 0.69 ; Figure 2b). Drought
356 increased fungal alpha-diversity (1.18 ± 1.62) but had no impact on bacterial and micro-
357 eukaryotic alpha-diversity (0.01 ± 0.47 and 0.003 ± 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 ± 0.30) and fungal (1.17 ± 0.17) community
366 structure than on bacterial community structure (0.67 ± 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 ± 0.27 and 0.85 ± 0.2). The only exception was
381 consumers for whom the biomass showed a very weak response (0.06 ± 0.39). Drought
382 showed a weaker effect than temperature increase on microbial biomasses, except for
383 photoautotrophs (1.01 ± 0.36) and consumers (-0.67 ± 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 ± 0.25) and weak negative effect on bacteria (-0.15 ± 0.52). In contrast, photoautotroph
387 biomass increased with winter warming (0.53 ± 0.11). Winter warming had a very weak
388 impact on fungal biomass (0.08 ± 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 CO_2 and CH_4 emissions increased with temperature increase ($2.28 \pm$
400 0.21 and 1.02 ± 0.25 respectively; Figure 3c). Drought also increased CO_2 emissions

401 (1.18 ± 0.32) but decreased CH₄ emissions (-2.01 ± 0.39). We also found that CH₄
402 oxidation into CO₂ was less impacted by temperature increase (0.18 ± 0.43) whilst CO₂
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, CO₂ and CH₄ 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 CO₂ fixation and CO₂ and CH₄ emissions under temperature increase
431 (Figure 4a). Microbial CO₂ and CH₄ 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^2 values (Figure S9a and c). MASEM showed that temperature
437 increase influenced microbial C-related multifunctionality (averaged $R^2 = 0.65$; Figure
438 S9a), directly through effects on microbial CO₂ fixation (averaged path = 0.71 ± 0.01)
439 and emission (averaged path = -0.06 ± 0.03) and CH₄ emission (averaged path = $0.26 \pm$
440 0.03), and indirectly through shifts in microbial beta-diversity (averaged path = $0.22 \pm$
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 $R^2 = 0.96$; 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 CO₂ emission and fixation, CH₄ emission and
454 oxidation). Our predictive models showed good results both for CO₂ emissions ($P =$
455 0.023 and $R^2 = 0.36$; Table 3; Figure S10) and CO₂ fixation ($P < 0.001$, $R^2 = 0.73$; Table
456 3; Figure S11). However, the SMDs of CH₄ 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 CO₂ 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 CO₂ emission and CO₂ 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 CO₂ emission showed that the response of CO₂ emission is temperature
466 dependent (SMDs between 2 and 4; Figure 5a and b). Indeed, we showed that CO₂
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 CO₂ 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 CO₂ 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 CO₂ fixation and emissions,
486 and CH₄ 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 CO₂ and CH₄ 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; Antikeira 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; Antikeira 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 CO₂ 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 CO₂ and CH₄) except for CH₄ 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 CH₄
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 CO₂ hr⁻¹ m⁻², a rate equivalent to about 9% of peatlands' gross CO₂ uptake (Hamard et
555 al. 2021). Our synthesis showed that such a CO₂ 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 CO₂ 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 CO₂ 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 CO₂
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 CO₂ emissions, but mostly at +1.5°C scenario (Figure 5a). Indeed, our projection
572 indicated that the response of microbial CO₂ 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 CO₂ emissions may stagnate or even
575 decrease. Recent meta-analyses in soils found a similar trend with CO₂ 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 CO₂ 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 CO₂. 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 CO₂ 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 CO₂ fixation may regulate microbial climatic feedback to the
606 peatland C cycle, and yield evidence that incorporating microbial CO₂ 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 CO₂
610 fixation counterbalances microbial C losses from CO₂ and CH₄ 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

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

Climate drivers	Complete name	Description
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^a = 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 ^a	D	MM	D x MM	G ^a x D	G ^a x MM	G ^a 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

Parameters	CO₂ emission	CO₂ fixation	CH₄ emission	CH₄ oxidation
Number of observations	42	15	41	16
<i>P</i>-value	0.023	0.001	0.14	0.91
R²	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.

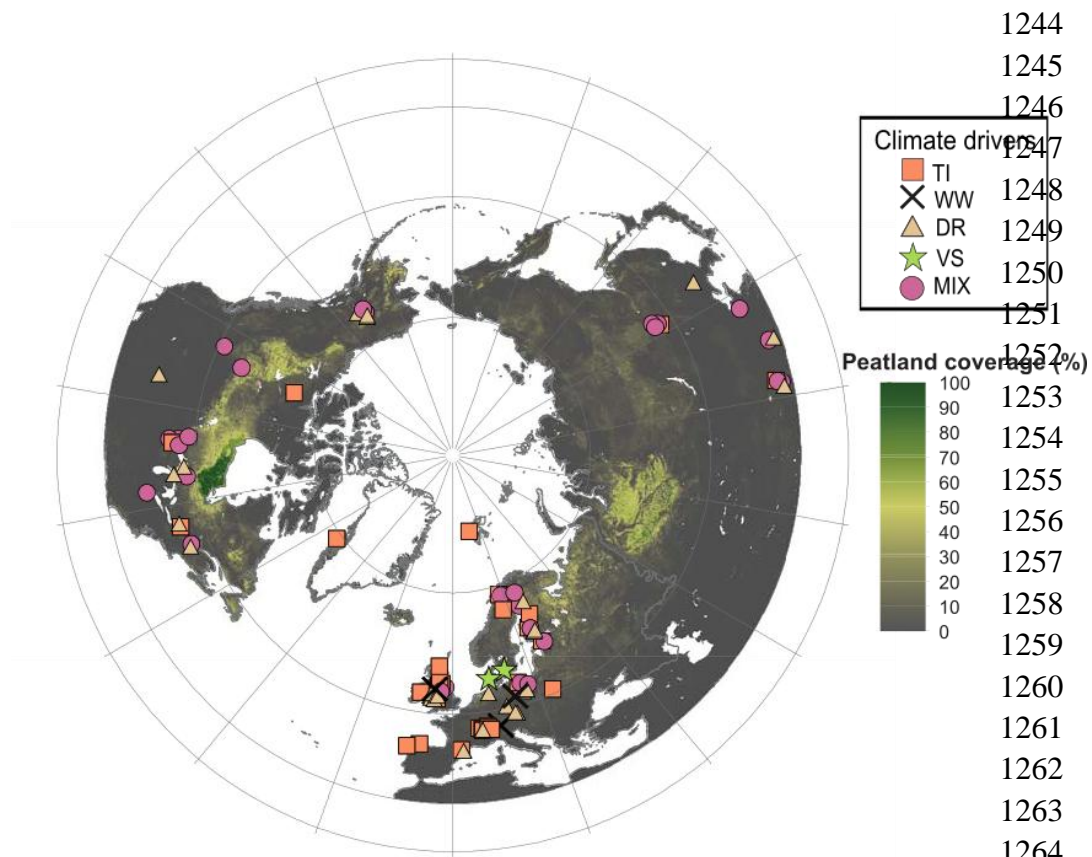
1222 **Figure 4. Microbial species turnover and biomass across trophic levels are complementary facets**
1223 **of the response of peatlands' functions to climate change.** Latent SEMs showing the best functions
1224 defining microbial C-related multifunctionality under **(a)** temperature increase ($\chi^2 = 0.35$, $df = 1$, $P = 0.55$;
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 CO₂ emissions (a) and (b) and CO₂ 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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 1265 **Figure 1.**

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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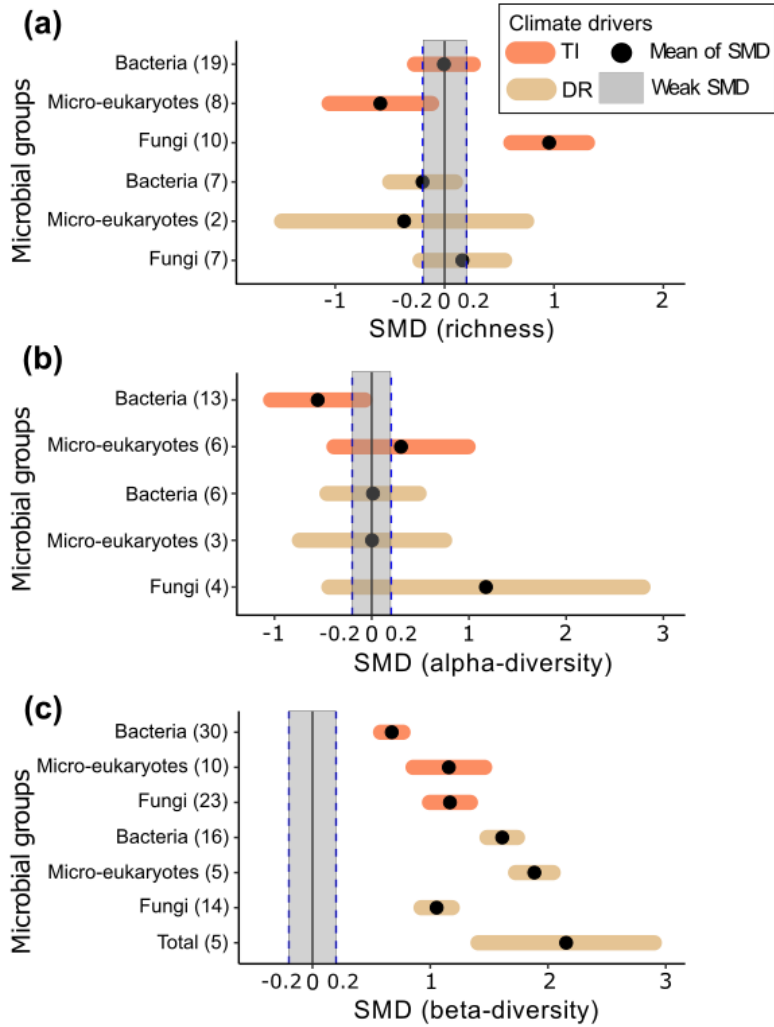


Figure 2. Standardized mean difference (SMD) representing the response of peatland microbial richness (a), alpha-diversity (b) and beta-diversity (c) to temperature increase (TI) and drought (DR). The black dot shows the mean of SMD and the bars represent the associated standard error. The filled line 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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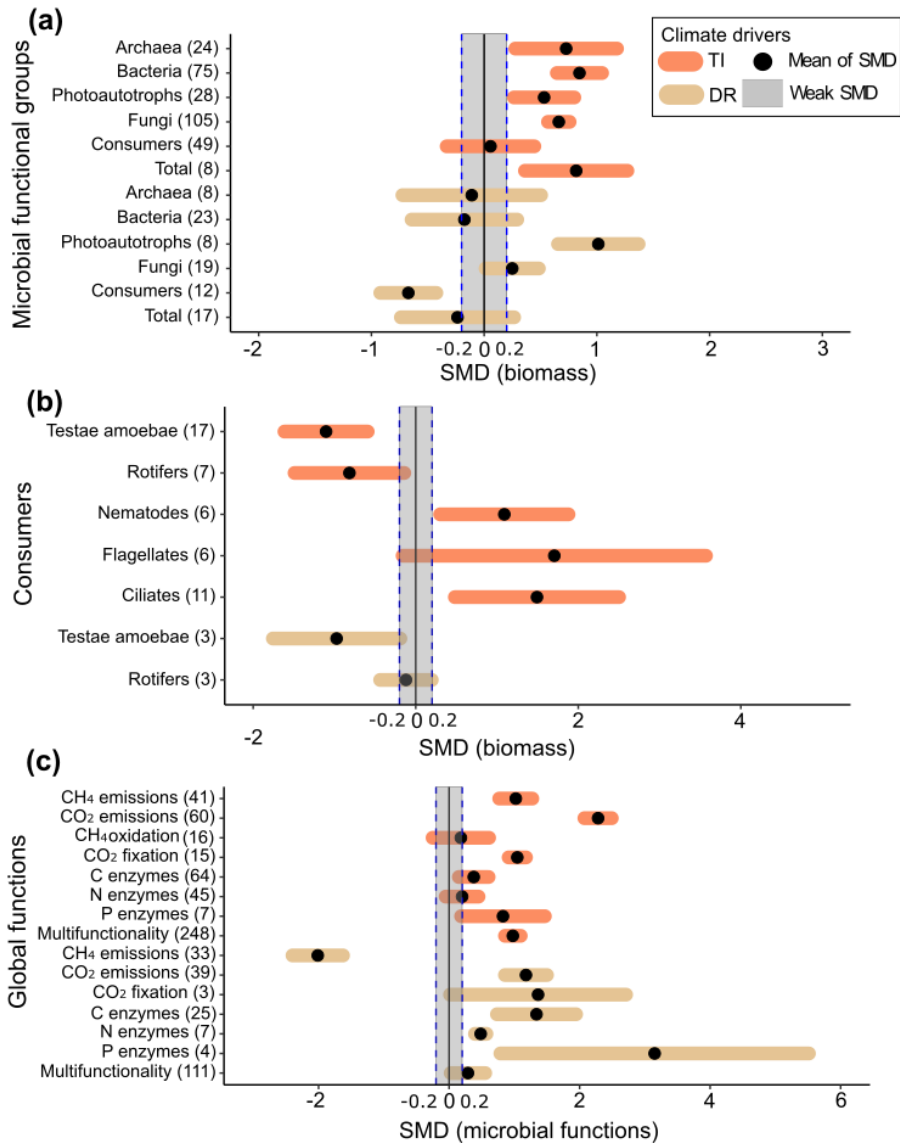
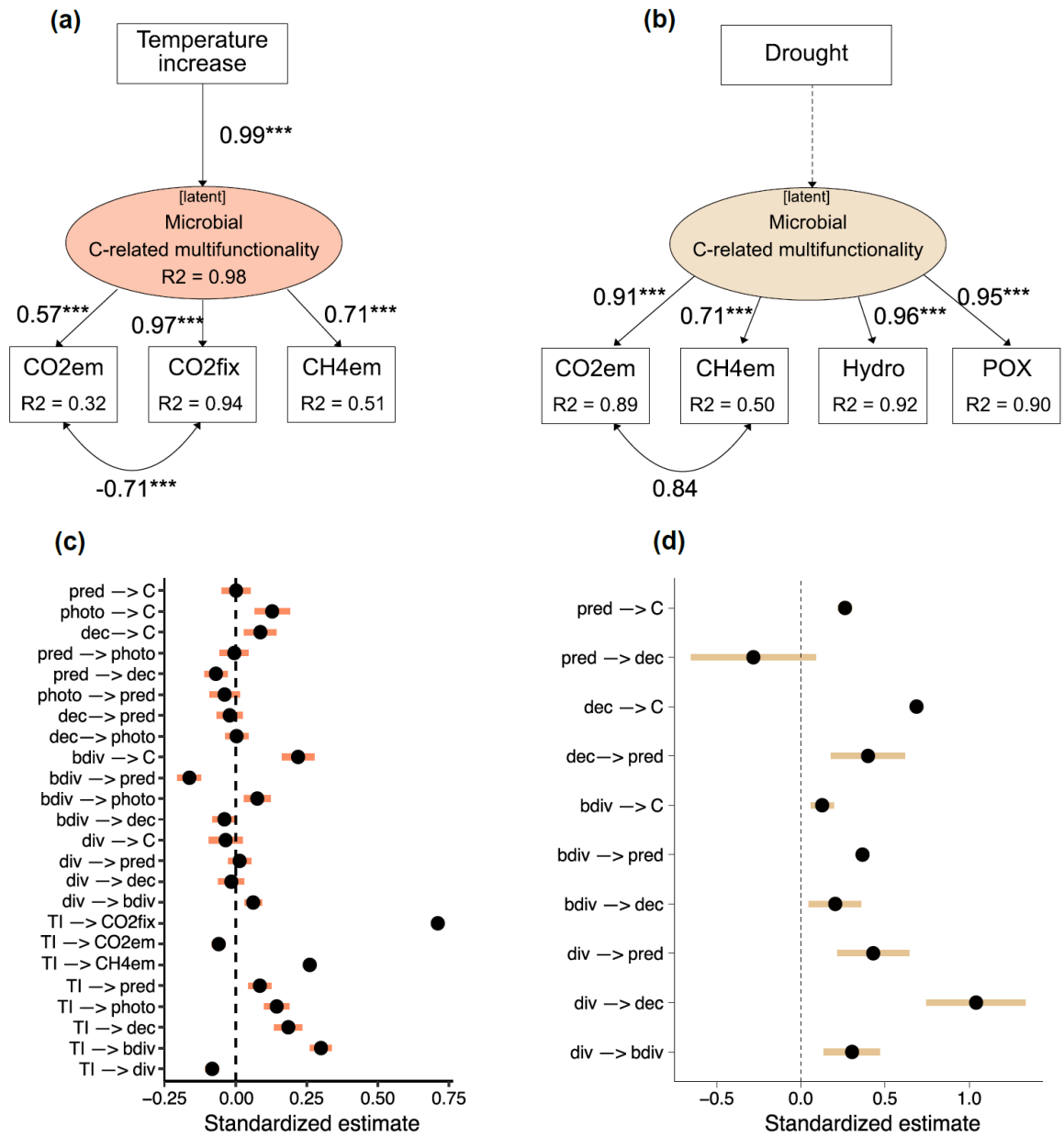


Figure 3. Standardized mean difference (SMD) showing the response of peatland microbial biomass grouped by functional type to temperature increase (TI) and drought (DR) (a), with a focus on consumers (b). SMD showing the response of peatland microbial functions to temperature increase (TI) and drought (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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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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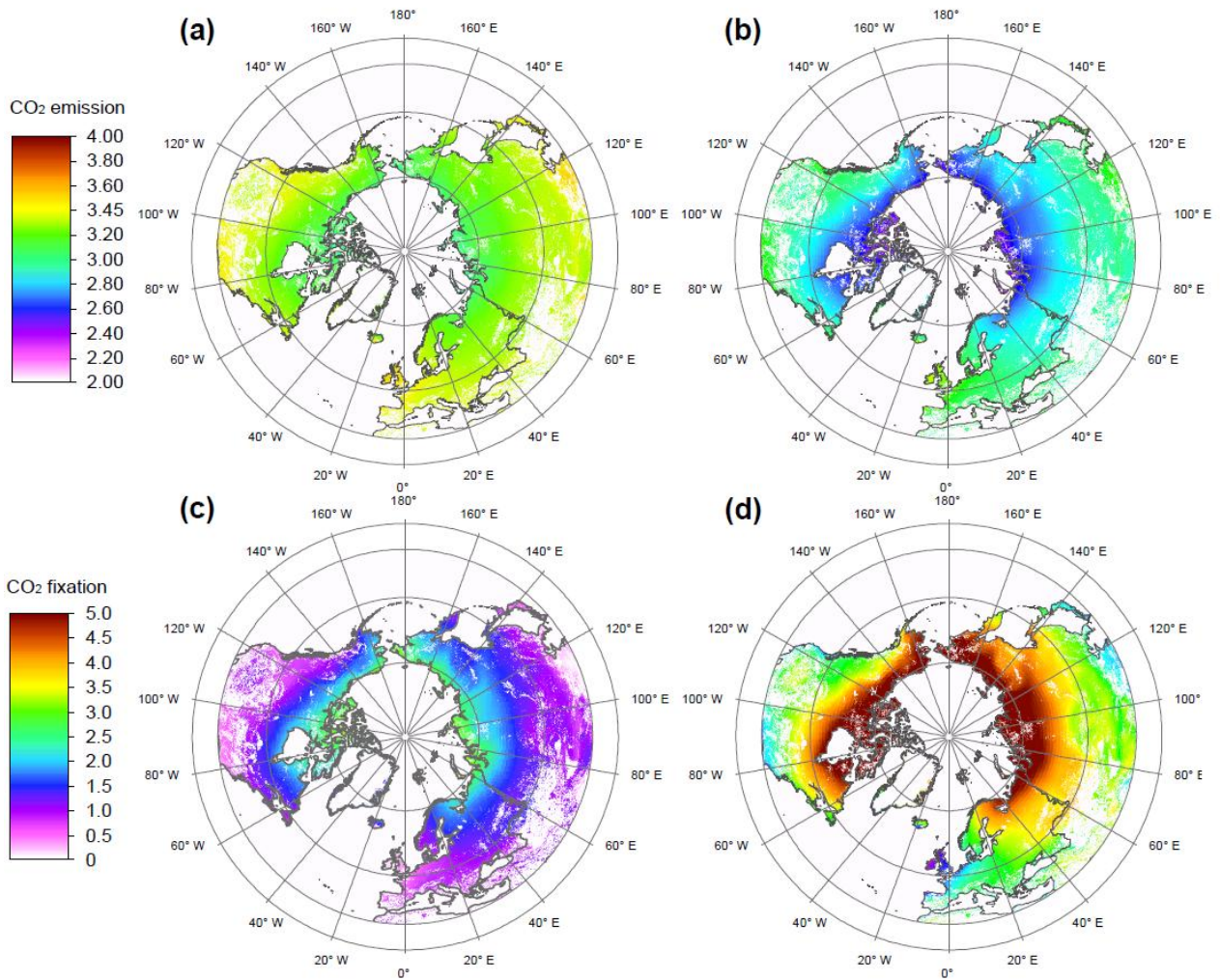


Figure 5. Predicted standardized mean difference (SMD) for the effect of increasing temperatures +1.5°C (a and c) and +3.0°C (b and d) on CO₂ emissions (a and b) and CO₂ fixation (c and d). Peatland distribution was retrieved from the peatland distribution Peat-ML map (Melton et al., 2022), CMIP6 model under the SPP8.5 scenario for +1.5°C and +3°C warming related to the 1850-1900 baseline was used.