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1 **Contribution of microbial photosynthesis to peatland carbon uptake along a**  
2 **latitudinal gradient**

3

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28 **ABSTRACT**

29 1. Phototrophic microbes, also known as micro-algae, display a high abundance in many terrestrial  
30 surface soils. They contribute to atmospheric carbon dioxide fluxes through their photosynthesis, and  
31 thus regulate climate similar to plants. However, microbial photosynthesis remains overlooked in most  
32 terrestrial ecosystems. Here, we hypothesize that phototrophic microbes significantly contribute to  
33 peatland C uptake, unless environmental conditions limit their development and their photosynthetic  
34 activity.

35 2. To test our hypothesis, we studied phototrophic microbial communities in five peatlands distributed  
36 along a latitudinal gradient in Europe. By means of metabarcoding, microscopy and cytometry  
37 analyses, as well as measures of photosynthesis, we investigated the diversity, absolute abundance  
38 and photosynthetic rates of the phototrophic microbial communities.

39 3. We identified 351 photosynthetic prokaryotic and eukaryotic operational taxonomic units (OTU)  
40 across the five peatlands. We found that water availability and plant composition were important  
41 determinants of the composition and the structure of phototrophic microbial communities. Despite  
42 environmental shifts in community structure and composition, we showed that microbial C-fixation  
43 rates remained similar along the latitudinal gradient. Our results further revealed that phototrophic  
44 microbes accounted for approximately 10% of peatland C uptake.

45 4. *Synthesis*. Our findings show that phototrophic microbes are extremely diverse and abundant in  
46 peatlands. While species turnover with environmental conditions, microbial photosynthesis similarly  
47 contributed to peatland C uptake at all latitudes. We estimate that phototrophic microbes take up  
48 around 75 MT CO<sub>2</sub> per year in northern peatlands. This amount roughly equals the magnitude of  
49 projected peatland C loss due to climate warming and highlight the importance of phototrophic  
50 microbes for the peatland C cycle.

51

52 **KEYWORDS**

53 Algae, Carbon cycle, Metabarcoding, Microbial diversity, Peatland, Photosynthesis, Phototrophs,  
54 Primary productivity.

55

56 **1 INTRODUCTION**

57 Microbes only represent one-sixth of the living biomass on Earth (93 PgC for fungi, protists, bacteria  
58 and archaea; Bar-On et al., 2018) but they drive some of the most important carbon (C) fluxes at the  
59 global scale (Caron et al., 2017; Fierer, 2017; Singh et al., 2010). For instance, oceanic phytoplankton  
60 contributes to one third of the global photosynthetic CO<sub>2</sub> fixation with 50 PgC fixed each year, while  
61 the remaining amount is consensually attributed to terrestrial plants (Ciais et al., 2013). The input of  
62 organic matter to oceanic and terrestrial food webs is therefore attributed to the photosynthetic  
63 activity of either oceanic phytoplankton or terrestrial plants, respectively (Krumins et al., 2013; Liang  
64 et al., 2017; Worden et al., 2015). This consensus, however, ignores terrestrial photosynthetic  
65 microorganisms also known as micro-algae (hereafter, phototrophic microbes), which are natural  
66 components of the soil flora (Bates et al., 2013; Cano-Díaz et al., 2019; Oliverio et al., 2020), and can  
67 reach several millions of individuals per gram of soil (Zancan et al., 2006).

68         Soil phototrophic microbes display myriads of species with a wide range of morphologies and  
69 life styles (Caron et al., 2017; Delgado-Baquerizo et al., 2018; Oliverio et al., 2020). Prokaryotes and  
70 eukaryotes that compose the soil phototrophic microbial communities can be either photo-autotrophs  
71 (i.e., strict phototrophs using only mineral C as C source), photo-heterotrophs (i.e., using only organic  
72 C; Geisen et al., 2018; Lynn et al., 2017), or mixotrophs (i.e., using both mineral and organic C; Mitra  
73 et al., 2016). Recent studies suggest that phototrophic microbes could account for large amounts of  
74 net primary production, and play a much larger role in terrestrial C dynamics than previously  
75 acknowledged (Elbert et al., 2012). However, our understanding of their contribution to the C balance  
76 and productivity of terrestrial ecosystems is largely restricted to drylands (Elbert et al., 2012; Maier et

77 al., 2018). Phototrophic microbial contribution to total C fixation remains largely unexplored in most  
78 other ecosystems, especially in C-accreting systems such as peatlands.

79 Peatlands play an important role in the global C cycle as they are major C sinks and store a  
80 large pool of soil C (500 – 1000 PgC; Bridgham et al., 2006; Nichols & Peteet, 2019; Yu, 2012). Peat  
81 mosses (i.e., *Sphagnum* spp.) serve a variety of key functions in peatlands, notably primary production  
82 and C sequestration (Turetsky, 2003; van Breemen, 1995). *Sphagnum* mosses also provide a habitat  
83 for a large diversity of microbes living either inside or at the surface of *Sphagnum* leaves (Gilbert et al.,  
84 1998). This association between *Sphagnum* mosses and microbes forms the bryosphere (Lindo &  
85 Gonzalez, 2010). *Sphagnum*-associated phototrophic microbes include bacteria (e.g., Cyanobacteria,  
86 Alphaproteobacteria), protists (e.g., Chlorophyta) and other mixotrophic micro-eukaryotes (e.g., many  
87 Ochrophyta or endosymbiotic Lobosa) (Gilbert et al., 1998; Gilbert & Mitchell, 2006; Jassey et al., 2015;  
88 Lara et al., 2011; Tian et al., 2019) and can be highly abundant. For instance, the biomass of  
89 phototrophic microbes in surface peat (0.5 mg C.l<sup>-1</sup>; Gilbert & Mitchell, 2006) can exceed the  
90 phytoplankton biomass of some of the most productive oceanic locations (c.a. 0.08 mg C.l<sup>-1</sup>;  
91 Behrenfeld, 2014). Yet, despite such high abundance, only a handful studies focused on algal  
92 productivity in peatlands, mostly in water-logged rich fens (Gilbert et al., 1998; Goldsborough &  
93 Robinson, 1996; Wyatt et al., 2012). Phototrophic microbial productivity remains largely overlooked  
94 in all other peatland types including *Sphagnum*-dominated bogs and poor fens, which constitute the  
95 largest part of peatlands at a global scale (Hugelius et al., 2020). *Sphagnum*-dominated peatlands  
96 occupy extensive areas of land at different latitudes and across a wide variety of climates (Halsey et  
97 al., 2000; Robroek et al., 2017). Hence, improving our understanding of the spatial and environmental  
98 patterns of phototrophic microbial contribution to bryosphere C uptake across environmental  
99 gradients is likely to improve our understanding of biogeochemical cycles in peatlands.

100 Here, we explore the diversity of phototrophic microbes and their primary productivity in  
101 different peatlands under varying climates and peatland conditions, using a latitudinal transect

102 covering a broad range of environmental conditions. Specifically, we tested the relationships between  
103 phototrophic microbial community composition, structure, and photosynthetic rate in five European  
104 *Sphagnum*-dominated peatlands distributed from southern France to northern Sweden. We  
105 hypothesized (i) that phototrophic microbes make a significant contribution to the bryosphere C  
106 uptake, and that (ii) this contribution depends on environmental conditions such as climate  
107 (temperature, precipitation) and/or edaphic factors. More specifically, we expected (iii) that  
108 environmental conditions strongly influence the taxonomic composition of phototrophic microbial  
109 communities, affecting community structure with cascading effects on phototrophic abundance and C  
110 fixation rates. We analysed phototrophic microbial community composition by means of  
111 environmental 16S and 18S rDNA gene sequencing for prokaryotes and eukaryotes, respectively. We  
112 further evaluated phototrophic microbial abundance through flux cytometry and microscopy, and we  
113 assessed phototrophic microbial C fixation rates by measuring their photosynthetic efficiency and  
114 photosynthetic pigments content.

115

## 116 **2 METHODS**

### 117 **2.1 Sites description and sampling**

118 We collected samples in five European peatlands distributed along a latitudinal gradient ranging from  
119 42 °N (south of France) to 68°N (north of Sweden) in July 2018. From south to north (3000 km as the  
120 crow flies), the five peatlands were Counozouls (Lapazeuil) in France (42°41'16 N, 2°14'18 E, 1350 m  
121 a.s.l.), Kusowo (Kusowkie Bagno) in Poland (53°48'48 N, 16°35'12 E, 250 m a.s.l.), Männikjärve in  
122 Estonia (58°52'30 N, 26°15'04 E, 78 m a.s.l.), Siikaneva in Finland (61°50'00 N, 24°11'32 E, 170 m a.s.l.)  
123 and Abisko (Stordalen) in Sweden (68°20'54 N, 19°04'09 E, 350 m a.s.l.) (Fig. 1A). These sites were  
124 characterised by flat topographies on a local scale and were associated with different peatland types.  
125 Counozouls is a minerotrophic fen, Kusowo and Männikjärve are ombrotrophic bogs, Siikaneva is a  
126 boreal oligotrophic fen, and Abisko a palsa mire. The vegetation at all five sites contained a sparse

127 vascular plant layer, and was dominated by bryophytes from the *Sphagnum* genus: *S. warnstorffii* in  
128 Counozouls, *S. magellanicum* and *S. fallax* in Kusowo, *S. rubellum*, *S. magellanicum* and *S. fuscum* in  
129 Männikjärve, *S. papillosum* in Siikaneva and *S. balticum* in Abisko. At each site, we selected five  
130 homogeneous plots (50 x 50 cm). In each plot we sampled the apical part of *Sphagnum* mosses (0-3  
131 cm from the capitulum) for analysis of microbial diversity, abundance and biomass as well as  
132 photosynthetic rates. We further quantified bryosphere C fixation rates from the same location (see  
133 below).

134

## 135 **2.2 Vegetation, climatic and edaphic parameters**

136 The vegetation cover (Supplementary Table S1) was assessed in each site and in each plot by taking  
137 four pictures of each plot as explained in Sytiuk et al. (2020). The quality and quantity of *Sphagnum*  
138 water-extractable organic matter (Supplementary Table S2) was assessed in each site according to  
139 Jassey et al. (2018). Several physico-chemical properties were analysed including pH, dissolved organic  
140 carbon and total nitrogen (measured by combustion on a Shimadzu TOC-L), ion concentration  
141 (measured on Dionex Ics-5000+ and Dionex DX-120) and dissolved organic matter quality (measured  
142 by spectrometry and fluorescence following Hansen et al. (2016). All values were corrected by a blank  
143 consisting of demineralized water. *Sphagnum* shoots were weighted fresh just after sampling. Then  
144 they were oven-dried (60°C for 48 hours) and weighted after extraction to calculate *Sphagnum* water  
145 content and to express the variables per g of *Sphagnum* dry weight (g DW). *Sphagnum* water content  
146 was expressed in g of water per g of *Sphagnum* DW. Finally, long-term bioclimatic variables such as  
147 mean annual temperature, annual precipitation and temperature seasonality were retrieved from  
148 WorldClim 2.0 (Supplementary Table S3).

149

150

151

152

## 153 **2.3 Diversity and community structure of peatland phototrophic microbes**

### 154 2.3.1 Microbial DNA extraction

155 Three shoots of *Sphagnum* (0-3 cm) were sampled with sterile equipment from each plot, cut into  
156 small pieces and placed into sterile 5 mL tubes containing 3 mL of Lifeguard (Qiagen). For each sample,  
157 DNA was extracted using the DNeasy PowerSoil Pro Kit (Qiagen) and following the manufacturer's  
158 instructions. A negative extraction (i.e., without *Sphagnum*) was performed to control for possible  
159 contaminations during extraction. For mechanical lysis of the cells, we included two runs of bead  
160 beating on a FastPrep FP120 Instrument (MP Biomedicals) for 40 s at speed 5.0 m.s<sup>-1</sup>. DNA was eluted  
161 in 70 µl of final solution and DNA concentration in each extract was quantified using a Nanodrop ND-  
162 1000 spectrophotometer. Extracts were stored at -80°C before proceeding with DNA amplification.

163

### 164 2.3.2 Microbial DNA sequencing

165 To investigate prokaryote communities, we amplified a part of the 16S rDNA gene, using the primers  
166 PCR1\_515F and PCR1\_928R (Wang & Qian, 2009). Eukaryote communities were investigated by  
167 amplifying a part of the 18S rDNA gene with the primers TAREuk454FWD1 and TAREukREV3 (Tanabe  
168 et al., 2016). Both prokaryotic and eukaryotic pairs of primers were tagged with Illumina adapter  
169 sequences. PCRs were conducted in a total volume of 50 µl containing 13 µl of Mastermix AmpliTaq  
170 Gold (ThermoFisher), 1µl of each primer from the chosen pair (0.4 µM final concentration), 35 ng of  
171 DNA (up to 10 µl) and supplemented to 50 µl with DNA-free water. The primers' sequences and the  
172 PCR programs used are presented in Supplementary Table S4. All PCR products were checked on an  
173 agarose gel and samples were then frozen at -80°C until sequencing was performed by the GeT-PlaGe  
174 platform (Genotoul, Toulouse, France) with Illumina MiSeq technology and using the V3 chemistry  
175 (2x250 bp).

176 Paired-end fastq sequences (851 910 prokaryotic reads and 891 422 eukaryotic reads for 25  
177 samples) were analysed using the FROGS pipeline (Find Rapidly Operational Taxonomic Units Galaxy  
178 Solution) on the Galaxy platform (Escudié et al., 2018). Paired-end reads were merged using Vsearch



179 (10% of mismatch; Rognes et al., 2016). Sequences were filtered based on their length and primer  
180 mismatches were removed, leading to a total of 770 602 prokaryotic sequences and 813 098 eukaryotic  
181 sequences for all samples. Sequences were then de-replicated and clustered into operational  
182 taxonomic units (OTUs) using the Swarm clustering method with an aggregation distance of 3 (Mahé  
183 et al., 2014). Chimera were identified and removed using Vsearch. Filters were then applied to remove  
184 singletons. In total 677 947 sequences clustered in 2 063 OTUs were kept for prokaryotes, and 718 684  
185 sequences clustered in 2 050 OTUs were kept for eukaryotes. OTUs were assigned at different  
186 taxonomic levels using Blast. We used the Silva 138 database (Quast et al., 2013) for prokaryotic  
187 assignation and the PR<sup>2</sup> v4.12.0 database (Guillou et al., 2013) for eukaryotic assignation.

188

### 189 2.3.3 Identification of phototrophic OTUs

190 Further analyses were done using the Phyloseq R package (McMurdie & Holmes, 2013). Prokaryotic  
191 and micro-eukaryotic sequences were retrieved by removing chloroplast, mitochondria and plant  
192 associated sequences. The 25 samples were further rarefied to a total of 50 400 prokaryotic sequences  
193 clustered into 1 172 operational taxonomy units (OTUs), and 21 672 micro-eukaryotic sequences  
194 clustered in 622 OTUs. Microbial phototrophic OTUs were identified at the genus level, and we  
195 outlined the structure of phototrophic microbial communities from the relative abundance of  
196 phototrophic OTUs. We considered that an OTU was phototrophic if its affiliated genus was referred  
197 as photoautotrophic, photoheterotrophic or mixotrophic in the literature (e.g. (Jia et al., 2015;  
198 Kulichevskaya et al., 2014; Li et al., 1999; Okamura et al., 2009; Yurkov et al., 1993)). For instance, we  
199 included endosymbiotic mixotrophs (Mitra et al., 2016) among phototrophic OTUs such as the testate  
200 amoeba *Archerella flavum* and *Hyalosphenia papilio*. Further, OTUs of Chrysophyceae were specifically  
201 aligned with the GenBank database using BLAST v. 2.9.0+ as implemented on the NCBI website in order  
202 to obtain a precise functional assignation. Indeed, Chrysophyceae have swapped trophic modes  
203 several times during their evolutionary history (Graupner et al., 2018). The overwhelming majority of  
204 Chrysophyceae OTUs were phototrophic or mixotrophic.

## 205 **2.4 Absolute abundance of phototrophic microbes**

206 To determine the absolute abundance of phototrophs in every site, we sampled five shoots of  
207 *Sphagnum* (0-3 cm) in each plot, fixed them in 20 ml of glutaraldehyde (2% final concentration), and  
208 extracted microorganisms from *Sphagnum* tissues following the method of Jassey et al. (2011). Then,  
209 we quantified the absolute abundance of phototrophic microbes from microbial extracts by means of  
210 either flow cytometry or microscope analyses according to microbial body size.

211 Phototrophic microbes with a body length smaller than 40  $\mu\text{m}$  were enumerated using flow  
212 cytometry. To do so, we filtrated 300  $\mu\text{l}$  aliquots of microbial extract with 40  $\mu\text{m}$  Nitex<sup>®</sup> filters, and  
213 placed them in a 96-well microplate. Then, aliquots were run unstained in a Guava<sup>®</sup> easyCyte<sup>™</sup> 11HT  
214 cytometer at a flow of 0.59  $\mu\text{l}\cdot\text{s}^{-1}$ . A maximum of 5000 events were recorded in each sample. Forward  
215 and side light scatter (size indication) as well as green fluorescence (presence or absence of  
216 chlorophyll) were used to discriminate photosynthetic microorganisms from non-photosynthetic  
217 microorganisms (bacteria) (Olson et al., 1989).

218 Phototrophic microbes with a body size larger than 40  $\mu\text{m}$  as well as all Cyanobacteria were  
219 identified and counted directly using an inverted microscope. In our samples, Cyanobacteria formed  
220 colonies and/or long filaments over 40  $\mu\text{m}$  that were not counted by flow cytometry. We double  
221 checked that the subsamples filtrated at 40  $\mu\text{m}$  did not contain Cyanobacteria under the microscope.  
222 Under the microscope, we identified and enumerated phototrophic microbe until species level when  
223 possible. We differentiated between strictly phototrophic microbes (microalgae, Cyanobacteria), and  
224 mixotrophic microbes (endosymbiotic microbes). Mixotrophic species included testate amoebae (e.g.  
225 *Archerella flavum*, *Amphitrema wrightianum*, *Heleopera sphagni* and *Hyalosphenia papilio*) and ciliates  
226 (e.g. *Paramecium bursaria* and *Platyophrya sphagni*).

227 Flow cytometry and inverted microscope abundance data were expressed as the number of  
228 individuals per gram of *Sphagnum* dry weight (DW). We further converted abundance data to C  
229 biomass ( $\mu\text{g}$  C per gram of *Sphagnum* DW) by measuring the biovolume of each species using  
230 geometrical shapes under microscope (Gilbert et al., 1998; Mitchell et al., 2003). Biovolumes were

231 then converted to C biomass using conversion factors from the literature (Borsheim & Bratbak, 1987;  
232 Gilbert et al., 1998; Weisse et al., 1990).

233

## 234 **2.5 Microbial photosynthetic rates**

235 Chlorophyll *a* (Chl *a*) concentrations and the quantum yield of photosystem II ( $\Phi_{\text{PSII}}$ ) were measured in  
236 each plot. Chl *a* concentrations provide an estimate of the amount of photosynthetic machinery, while  
237  $\Phi_{\text{PSII}}$  gives the fraction of the absorbed quanta that are used for photosynthetic electron transport and  
238 thus provides a measure of photosynthetic efficiency (Wilken et al., 2013). For these analyses, five  
239 shoots of *Sphagnum* (0-3 cm) were sampled in each plot and immersed in 20 mL demineralized water.  
240 Samples were kept at 4°C in the dark and microorganisms were extracted immediately upon return to  
241 the laboratory. Samples were shaken at 150 rpm for 1.5 h and then squeezed to extract  
242 microorganisms. The remaining solution was filtered at 100  $\mu\text{m}$  with Nitex® filters to remove any  
243 *Sphagnum* residue, while the remaining *Sphagnum* material was dried at 80°C for 48 h and weighted.  
244 Each microbial extract was filtered on a GF/F Whatman® filter (0.7  $\mu\text{m}$ ) to recover the microbial  
245 community.

246 We measured  $\Phi_{\text{PSII}}$  of the microbial community with a Phyto-PAM (Walz, Effeltrich, Germany) after  
247 exposing filters to low light for 30 min (PAR, 32  $\mu\text{mol photons.m}^{-2}.\text{s}^{-1}$ ). We chose a PAR of 32  $\mu\text{mol}$   
248  $\text{photons.m}^{-2}.\text{s}^{-1}$  following light response curve analyses previously ran on test samples (Supplementary  
249 Fig. S1). We further quantified the microbial photosynthetic rates in each plot by calculating the  
250 photosynthetic electron transport rate (ETR) as described in Wilken et al. (2013), and following  
251 Falkowski & Raven (2013):

$$252 \quad (1) \text{ ETR} = 0.5 \times I \times \frac{\text{Chla}}{\text{cell}} \times \Phi_{\text{PSII}} \times a^*$$

253 where ETR is the photosynthetic rate, expressed per cell as a measure of the community-weighted  
254 mean photosynthetic rate. It was calculated at a light intensity (*I*) of 32  $\mu\text{mol.m}^{-2}.\text{s}^{-1}$ . The calculation of  
255 ETR relies on the importance of the microbial photosynthetic machinery (cellular Chl*a* content,  $\frac{\text{Chla}}{\text{cell}}$ )

256 and on its photosynthetic efficiency (effective quantum yield of photosystem II,  $\Phi_{PSII}$ , measured at a  
257 PAR of  $32 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ). Here,  $a^*$  was the spectrally averaged chlorophyll-specific absorption cross  
258 section, for which we took a value of  $26.86 \text{ m}^2\cdot\text{g Chla}^{-1}$  as estimated in (Wilken et al., 2013). The ETR  
259 was expressed in  $\text{mol e}^-\cdot\text{cell}^{-1}\cdot\text{s}^{-1}$ .

260 To obtain Chl *a* concentrations, the filters used for microbial photosynthetic efficiency and  
261 containing microbial communities were frozen at  $-80^\circ\text{C}$  and freeze-dried in the dark. Adapting the  
262 methodology from Capdeville et al. (2019), we soaked lyophilized filters in 1.5 ml of methanol buffered  
263 with 2 %v of ammonium acetate ( $1 \text{ mol}\cdot\text{l}^{-1}$ ). Samples were sonicated for 2 min in an ice bath, then  
264 cooled at  $-20^\circ\text{C}$  in the dark for 15 min and centrifuged for 5 min at 10 000 rpm. The supernatant was  
265 recovered (solution 1) while 1 ml of buffered methanol was added to the pellet (solution 2). The  
266 process was repeated for solution 2 and its supernatant was merged with solution 1. Then, 1.5 ml of  
267 this composite solution was filtered at  $0.2 \mu\text{m}$  with a syringe filter and frozen at  $-80^\circ\text{C}$  before analysis  
268 on an HPLC (Barlow et al., 1997). We assessed the concentration of several pigments including Chl *a*,  
269 pheophytin *a* and pheophorbide *a*. As pheophytin *a* and pheophorbide *a* are alteration products of Chl  
270 *a* (Jeffrey et al., 1997), we summed the abundance of these three pigments to have an estimate of  
271 overall Chl *a* in the samples (hereafter named Chl *a*). Chl *a* was expressed in mg per g of *Sphagnum*  
272 DW and divided by phototroph abundance to have an estimate of cellular Chl *a* content (expressed in  
273  $\text{mg}\cdot\text{cell}^{-1}$ ).

274

## 275 **2.6 Microbial C fixation rate and contribution to bryosphere C fixation rate**

276 Phototrophic microbial C fixation rates ( $C_{\text{fixed}}$ ) were calculated in each plot from ETR:

$$277 \quad (2) \quad C_{\text{fixed}} = 0.25 \times \text{ETR} \times \text{cell} \times \text{Area}_{\text{DW}}$$

278 where we assumed a maximum fixation of  $0.25 \text{ mol CO}_2$  per mol of electron (Wilken et al., 2013), and  
279 took into account phototrophic microbial abundance (*cell*) and specific surface of *Sphagnum* ( $\text{Area}_{\text{DW}}$ )

280 measured in each plot as the area per gram of *Sphagnum* DW (0-3 cm). Carbon fixation rates were  
281 expressed in mg of CO<sub>2</sub> fixed per hour and per m<sup>2</sup> of *Sphagnum*.

282 We measured the bryosphere photosynthetic capacity ( $A_{MAX}$ , maximum net CO<sub>2</sub> assimilation  
283 rate) in each plot from three *Sphagnum* shoots as described in Jassey & Signarbieux (2019). The  $A_{MAX}$   
284 was measured with an open-path infrared gas analyser (IRGA) system connected to a 2.5 cm<sup>2</sup> PLC-5  
285 chamber (TARGAS-1; PP-Systems) under optimum conditions for light (i.e., 600 μmol of photons m<sup>-2</sup> .s<sup>-1</sup>  
286 <sup>1</sup>, which was previously determined in the field). Bryosphere C fixation was expressed in mg CO<sub>2</sub> h<sup>-1</sup> .m<sup>-2</sup>  
287 <sup>2</sup>, allowing comparisons with microbial C fixation rates. To estimate bryosphere C fixation per Chl *a*, we  
288 also estimated the Chl *a* content of *Sphagnum* in each plot. We extracted Chl *a* from two lyophilized  
289 *Sphagnum* shoots and followed the same extraction method as for phototrophic microbes.

290

## 291 **2.7 Numerical analyses**

292 Meta-barcoding data were used to explore the diversity and taxonomy of phototrophic microbes, and  
293 their community composition. Biostatistics were conducted separately on prokaryotic and eukaryotic  
294 microbial communities. Alpha-diversity, non-metric multidimensional scaling (NMDS), and beta-  
295 diversity metrics based on Bray-Curtis dissimilarity were used to estimate diversity and species  
296 turnover between sites. Environmental drivers of phototrophic microbial species turnover were tested  
297 using generalized dissimilarity modelling (GDM). The environmental matrix included a selection of  
298 variables such as plant community composition (Supplementary Table S1), *Sphagnum* physico-  
299 chemical parameters (Supplementary Table S2), and climatic variables (Supplementary Table S3). We  
300 selected the most representative and least collinear environmental variables using the package  
301 ClustOfVar (12) with an ascendant hierarchical clustering of all available environmental variables. To  
302 maximise the stability of partition, nine clusters of variables were retained. In each cluster, the most  
303 representative variables were kept for GDM (Supplementary Fig. S2). Variable significance in GDM was  
304 determined using matrix permutations and comparing models with each variable permuted and un-  
305 permuted. At each step, the least important variables were dropped until all non-significant predictors

306 were removed. The GDM was then fit using only significant environmental predictors, and model  
307 significance was checked.

308 All data were tested for normality and transformed if necessary. We tested variation of  
309 phototrophic microbial abundance, chlorophyll content, electron transport rate, and C fixation rates  
310 between sites (explicative qualitative variable) using analysis of variance (ANOVA). Further, we used  
311 linear mixed effects models to test the effects of environmental variables (mean annual temperature,  
312 water table depth, annual precipitation; fixed effects) on phototrophic microbial abundance, while  
313 accounting for measurements repeated in the same sites (random effect).

314 The variability of phototrophic C fixation can be determined by numerous interconnected eco-  
315 physiological mechanisms that operate simultaneously at different individual to community scales  
316 (Padfield et al., 2018; Yvon-Durocher et al., 2015). One approach to studying such complex interactions  
317 is Structural Equation Modelling (SEM; Grace et al. 2014). Following current knowledge on  
318 phototrophic eco-physiology (Huete-Ortega et al., 2012; Kalchev et al., 1996; Padfield et al., 2018), we  
319 developed an *a priori* model of hypothesized relationships (Supplementary Fig. S3) within a path  
320 diagram allowing a causal interpretation of microbial C fixation rates in relation to microbial  
321 community structure (bacteria and protists), to allometric features (abundance, community-weighted  
322 mean body size) and metabolic parameters (Chl *a*, photosynthetic rate) (Supplementary Table S5). In  
323 this diagram, each path is a component of the model, and represent a linear model between the  
324 explanatory and the explained variable. All components of the model were united using the `psem`  
325 function from the `piecewiseSEM` R package (Lefcheck, 2016). The goodness-of-fit of our *a priori* SEM  
326 model was evaluated using Fisher's statistic and Akaike Information Criterion (AIC). Based on the  
327 outputs of the *a priori* model and by step-wise exclusion and selection of variables, we found the model  
328 with the lowest AIC value. The main drivers of microbial C fixation were determined from this final  
329 model. We used the first axes of phototrophic prokaryotic and eukaryotic NMDS as indicators of  
330 microbial community structure, and electron transport rate (ETR) as indicator of photosynthetic  
331 activity. To test to what extent environmental variables affected microbial C fixation and the

332 phototrophic mechanisms underpinning it, we ran our SEM model a second time with microbial  
333 variables corrected for the co-varying environmental variables (residual data). To correct microbial  
334 variables for environmental conditions, we used the residuals of linear models computed between  
335 every microbial variable and the environmental variables identified in the GDM (i.e., precipitation,  
336 *Sphagnum* water content, plant community composition and dissolved organic carbon).

337 All statistical analyses were performed using R version 3.6.2 (R Core Team, 2019).

338

339

### 340 **3 RESULTS**

#### 341 **3.1 Diversity and community composition of phototrophic microbes**

342 The relative abundance of phototrophic microbes varied strongly across sites (Fig. 1A; Supplementary  
343 Fig. S4). Phototrophic bacteria represented on average 12% of the prokaryotic microbial community,  
344 and had their largest relative abundance in Counozouls (34% of prokaryotic gene copies) compared to  
345 the other sites (<13 %;  $F_{(4,12)} = 6.21$ ,  $P = 0.006$ ). Phototrophic protists constituted a large part of the  
346 micro-eukaryotic community, with on average 30% of micro-eukaryotes gene copies. The relative  
347 abundance of phototrophic protists ranged from 53% in Männikjärve to 17% in Siikaneva ( $F_{(4,12)} = 9.53$ ,  
348  $P = 0.001$ ).

349 Overall, we observed 74 OTUs of phototrophic bacteria and 277 OTUs of phototrophic protists.  
350 For phototrophic bacteria, Counozouls had by far the highest OTU richness with on average 30 species  
351 per sample ( $F_{(4,12)} = 28.0$ ,  $P < 0.001$ ; Fig. 2B), whilst Siikaneva had the lowest richness (10 species per  
352 sample on average). Despite significant variation in OTU richness, we found that phototrophic bacteria  
353 diversity (Shannon's entropy) was stable across sites ( $F_{(4,12)} = 0.9$ ,  $P = 0.48$ , Fig. 2B). For phototrophic  
354 protists, we found the highest OTU richness in Männikjärve (52 species) ( $F_{(4,12)} = 3.2$ ,  $P = 0.05$ ; Fig. 2B)  
355 and the lowest in Abisko (31 species). Phototrophic protist diversity followed the latitudinal gradient  
356 with a slight but significant decrease from Counozouls to Abisko ( $F_{(4,12)} = 4.6$ ,  $P = 0.02$ ; Fig. 2B).

357 We identified four phyla of phototrophic bacteria, distributed in four classes and eight orders  
358 (Supplementary Fig. S5). Proteobacteria and Cyanobacteria dominated phototrophic bacteria across  
359 sites. Proteobacteria ( $F_{(4,12)} = 113.24$ ,  $P < 0.001$ ) were relatively more abundant in Kusowo,  
360 Männikjärve and Siikaneva (>80 %), while Cyanobacteria ( $F_{(4,12)} = 10.4$ ,  $P < 0.001$ ) relatively dominated  
361 in Counozouls (60.8 %) and Abisko (68.5 %) (Fig. 2A). Gemmatimonadetes and Chloroflexi were only  
362 present in Counozouls (Fig. 2A). Proteobacteria were primarily represented by the orders  
363 Acetobacterales and Rhizobiales, whereas Cyanobacteria were mostly represented by Nostocales  
364 (Supplementary Fig. S5). We further identified seven phyla of phototrophic protists, distributed in 13  
365 classes and 21 orders (Supplementary Fig. S5). Chlorophyta (75.1 % of the average phototrophic protist  
366 relative abundance), Ochrophyta (15.3 %) and Streptophyta (7.4 %) were the three most relatively  
367 abundant phyla (Fig. 2A, Supplementary Fig. S5). At the class level, Chlorophyta were mainly  
368 represented by Trebouxiophyceae and Chlorophyceae; Ochrophyta by Chrysophyceae; and  
369 Streptophyta by Zygnemophyceae and Klebsormidiophyceae. The relative abundance of the different  
370 classes varied significantly along the latitudinal gradient (Fig. 2A, Supplementary Fig. S5).

371 Both phototrophic bacteria and protist assemblages clustered at the site level (NMDS with  
372 Bray-Curtis dissimilarity; Fig. 1B and Fig. 1C). Pairwise comparisons of beta-diversity based on Bray-  
373 Curtis dissimilarity showed substantial species turnover between sites (Supplementary Table S6). More  
374 than half of all phototrophic microbial OTUs identified were indeed found in only one site  
375 (Supplementary Fig. S6) and only 13 OTUs (6 affiliated to bacteria and 7 to protists) were found in all  
376 sites. Furthermore, we found that both phototrophic bacteria and protist turnover (i.e., pairwise  
377 community compositional dissimilarity) increased with environmental distance among sites (i.e.,  
378 pairwise environmental dissimilarity; Fig. 3A, 3C). Phototrophic microbial communities of both  
379 domains were increasingly dissimilar as shrubs replaced herbaceous plants in the vegetation (Fig. 3B,  
380 3D). Phototrophic bacteria turnover was also driven by an increase in precipitation and dissolved  
381 organic carbon (Fig. 3B), while the turnover of phototrophic protists was strongly driven by changes in  
382 *Sphagnum* water content (Fig. 3D).



383

### 384 **3.2 Absolute abundance, biomass and size structure of phototrophs**

385 The absolute abundance of phototrophic microbes strongly decreased along the latitudinal gradient  
386 with a drop from  $194.0 \times 10^6$  ind.g<sup>-1</sup> DW in COUNZOULS to  $45.3 \times 10^6$  ind.g<sup>-1</sup> DW in ABISKO ( $F_{(4,16)} = 25.1$ ,  
387  $P < 0.001$ ; Fig. 4A). This pattern was mostly driven by phototrophic microbes with a body size  $< 40 \mu\text{m}$   
388 that constituted the majority of microbial phototrophs (98.5 %, Supplementary Fig. S7). Large  
389 phototrophic microbes and large mixotrophs (body size  $> 40 \mu\text{m}$ ) were less abundant and showed  
390 opposite patterns with an increase of their absolute abundance toward high latitudes ( $F_{(4,16)} = 11.8$ ,  $P$   
391  $< 0.001$  and  $F_{(4,16)} = 20.3$ ,  $P < 0.001$  respectively, Supplementary Fig. S7, Fig. 4B). Consequently, the  
392 community-weighted mean body size per cell increased toward high latitudes ( $F_{(4,16)} = 20.3$ ,  $P < 0.001$ ),  
393 with phototrophic microbes being on average 28 times larger in Abisko than in COUNZOULS (Fig. 4C).  
394 On the whole, the total biomass of the phototrophic community tended to increase toward high  
395 latitudes, from  $1049 \mu\text{gC.g}^{-1}\text{DW}$  in COUNZOULS to  $1634 \mu\text{gC.g}^{-1}\text{DW}$  in ABISKO ( $F_{(4,16)} = 46.3$ ,  $P < 0.001$ ;  
396 Fig. 4D). Within the phototrophic community, Cyanobacteria had a higher absolute abundance in  
397 COUNZOULS and in ABISKO ( $1.04 \times 10^6 \pm 0.01$  ind.g<sup>-1</sup> DW) than in the other sites ( $0.20 \times 10^6 \pm 0.04$  ind.g<sup>-1</sup>  
398 DW) ( $F_{(4,16)} = 20.3$ ,  $P < 0.001$ ; Supplementary Fig. S8). However, considering biomasses, the ratio  
399 Cyanobacteria to phototrophic microbes was higher in COUNZOULS and KUSOWO ( $0.61 \pm 0.17$ ) compared  
400 to the other sites ( $0.13 \pm 0.03$ ) ( $F_{(4,16)} = 16.9$ ,  $P < 0.001$ ; Supplementary Fig. S8).

401 Phototrophic microbial abundance correlated positively with annual precipitation ( $r = 0.75$ ,  
402  $F_{(1,23)} = 29.4$ ,  $P < 0.001$ ), and to a lesser extent with plant composition ( $r = 0.55$ ,  $F_{(1,23)} = 10.29$ ,  $P = 0.004$ ),  
403 phototrophic microbes being more abundant when shrubs were absent. The abundance of large  
404 phototrophic microbes was negatively correlated with the water table depth ( $r = -0.80$ ,  $F_{(1,23)} = 15.05$ ,  
405  $P < 0.001$ ), meaning that large phototrophic microbes were more abundant when water was close to  
406 the surface. The abundance of large mixotrophs correlated negatively with both annual precipitation  
407 ( $r = -0.87$ ,  $F_{(1,23)} = 73.83$ ,  $P < 0.001$ ) and mean annual temperature ( $r = -0.83$ ,  $F_{(1,23)} = 51.10$ ,  $P < 0.001$ ).

408

409

### 410 **3.3 Photosynthetic rates and C fixation of phototrophic microbial communities**

411 The chlorophyll content of phototrophic microbes increased along the gradient (+400 % between  
412 COUNOZOULS and ABISKO;  $F_{(4,16)} = 5.78$ ,  $P = 0.005$ ; Fig. 4E). Similar patterns were found for photosynthetic  
413 rates (+380 % ;  $F_{(4,16)} = 3.7$ ,  $P = 0.02$ ; Fig. 4F). On average, phototrophic microbes fixed 8.8 (3.8 – 16.2)  
414 mg CO<sub>2</sub>.h<sup>-1</sup>.m<sup>-2</sup> over the gradient. Phototrophic microbial C fixation varied between sites, from 16.2 mg  
415 CO<sub>2</sub>.h<sup>-1</sup>.m<sup>-2</sup> in MÄNNIKJÄRVE to 3.8 mg CO<sub>2</sub>.h<sup>-1</sup>.m<sup>-2</sup> in KUSOWO, but differences among sites were not  
416 significant ( $F_{(4,12)} = 1.10$ ,  $P = 0.39$ ; Fig. 5A).

417 Our SEM model showed that microbial C fixation was directly mediated by the direct influence  
418 of phototrophic abundance (path = 0.42) and metabolism (photosynthetic rate, path = 0.70) (Fig. 6).  
419 Indirectly, microbial C fixation was mediated by the community structure of phototrophic bacteria and  
420 protists, which influenced phototrophic allometry. In particular, community structure influenced the  
421 microbial abundance (path = 1.09 and path = -0.43 for bacteria and protist community structure,  
422 respectively) and the community-weighted mean body size (path = -0.46 and path = 0.70 for bacteria  
423 and protist community structure, respectively), which had cascading effects on phototrophs  
424 metabolism (chlorophyll content per individual, and finally photosynthetic rate). A comparison with  
425 the SEM model corrected from environmental variables did not reveal strong alterations of the  
426 pathways (Supplementary Fig. S9). This indicated that the phototrophic mechanisms identified in our  
427 SEM model were independent from environmental changes.

428 In comparison with microbial C fixation, bryosphere C fixation showed a different latitudinal  
429 pattern with higher C uptake in the three northern sites compared to the two southern sites  
430 ( $F_{(4,12)} = 6.70$ ,  $P = 0.002$ ; Fig. 5A). The bryosphere fixed on average 111.5 mg CO<sub>2</sub>.h<sup>-1</sup>.m<sup>-2</sup>. The microbial  
431 C fixation normalised by Chl *a* showed that phototrophic microbes fixed nearly four times more C than  
432 the bryosphere for a given amount of Chl *a* ( $F_{(1,48)} = 79.15$ ,  $P < 0.001$ ; Fig. 5B). We further estimated  
433 that phototrophic microbes contributed by 9.4% (1.1% - 37.5%) to the bryosphere C fixation across all

434 sites (Fig. 5C). This contribution ranged on average from 4.1% in Siikaneva to 12.4% in Abisko (Fig. 5C),  
435 but differences among sites were not significant ( $F_{(4,12)} = 1.44$ ,  $P = 0.27$ ).

436

437

## 438 **4 DISCUSSION**

439 Microbial communities play an important role in maintaining multiple ecosystem functions that are  
440 important for C cycling. Whilst methanogens, fungi and other bacteria are known for their key role in  
441 C mineralization and respiration (e.g., (Galand et al., 2005; Myers et al., 2012; Thormann, 2006)), we  
442 show that, across a wide range of climatic conditions, phototrophic microbial communities are  
443 important for peatland C dynamics through their contribution to C uptake. Our study revealed that  
444 phototrophic microbes were phylogenetically diverse and highly abundant in peatlands throughout  
445 the latitudinal gradient. The structure and abundance of phototrophic microbial communities varied  
446 along the latitudinal gradient, driven by shifts in biotic and abiotic environmental factors (e.g., climate,  
447 plant composition). Despite microbial species turnover, our findings demonstrated a constant  
448 microbial CO<sub>2</sub> fixation along the gradient. Our results therefore provide the first *in situ* evidence for  
449 the role of phototrophic microbes in peatland C uptake at a continental scale.

450

### 451 **4.1 Phototrophy is a dominant microbial process in surface peat**

452 On average, we found  $7.5 \times 10^7$  microbial phototrophic cells per gram of dry moss in the top 3 cm of  
453 the *Sphagnum* carpet. This number is in line with previous studies, where phototrophic microbial  
454 abundance typically ranged between  $10^6$  and  $10^8$  cells per gram of dry moss (Basińska et al., 2020;  
455 Jassey et al., 2015). We found that phototrophic microbes represented an approximate biomass of 1.0  
456 mg C per gram of dry moss. This is, by comparison, higher than the heterotrophic bacterial biomass  
457 (approximately 0.5 mg C per g DW), or the biomass of heterotrophic protists (approximately 0.15 mg  
458 C per g DW) found in peatlands at the same depth (Jassey et al., 2011, 2015; Mitchell et al., 2003).  
459 Phototrophic microbes constitute therefore the most important component of microbial C biomass in

460 the apical part of the *Sphagnum* carpet, which suggests that phototrophy is a dominant microbial  
461 process in the upper peatland layer.

462 In terms of community composition, we found that, on average, 12% of prokaryotic sequences  
463 and 30% of micro-eukaryotic sequences belonged to phototrophic microbial lineages. These relative  
464 proportions were unexpectedly high, especially compared to previous meta-barcoding studies where  
465 phototrophic microbes represented less than 1% of prokaryotes (Bragina et al., 2012, 2014) and only  
466 10% of micro-eukaryotes (Geisen et al., 2015; Heger et al., 2018). These high relative abundances of  
467 phototrophic microbes most probably result from our experimental design. We indeed sampled the  
468 top 3 cm of the *Sphagnum* carpet, where light conditions are favourable for phototrophic microbial  
469 abundance and activity (Jassey et al., 2013; Reczuga et al., 2020; Robroek et al., 2009).

470 Our results further revealed that both communities of phototrophic bacteria and protists were  
471 relatively more abundant in peatlands than in other terrestrial ecosystems (Cano-Díaz et al., 2019;  
472 Oliverio et al., 2020). This alters our perception of the global distribution of soil phototrophic microbes,  
473 as until now, drylands were considered as the main phototrophic microbial hotspots (Bates et al., 2013;  
474 Oliverio et al., 2020). These findings therefore highlight the potential importance of peatland  
475 phototrophic microbes for the global C cycle.

476

#### 477 **4.2 Peatland phototrophic communities are diverse and environment-specific**

478 We identified 351 phototrophic microbial OTUs over the gradient, belonging to diverse prokaryotic  
479 and eukaryotic taxonomic clades. While phototrophic communities were relatively dominated by  
480 Chlorophyta (micro-eukaryote) and Alphaproteobacteria (prokaryotes), we nevertheless identified  
481 seven phyla of phototrophic micro-eukaryote, and four out of the seven existing phyla of phototrophic  
482 prokaryotes (Zeng et al., 2014). In link with this high taxonomic diversity, we identified a wide range of  
483 photosynthetic pathways. Within micro-eukaryotes, we found strict phototrophic organisms (e.g.,  
484 phototrophic Ochrophyta, Chlorophyta) and mixotrophic organisms (e.g., endosymbiotic Ciliophora,  
485 Lobosa). Within prokaryotes, the OTUs identified formed a continuum between photoautotrophy and

486 photoheterotrophy (Kulichevskaya et al., 2014; Yurkov et al., 1993), with uncertainty about the levels  
487 of autotrophy. For instance, Cyanobacteria can acquire organic C and downregulate their  
488 photosynthesis when in symbiosis with other plants (Black & Osborne, 2004), while some phototrophic  
489 Proteobacteria can grow both photoautotrophically and photoheterotrophically (Tang et al., 2011).  
490 Even though the occurrence of Cyanobacteria and phototrophic Proteobacteria is generally accepted  
491 in peatlands, they remain poorly explored and this calls for a deeper consideration of their role in  
492 peatland C cycling.

493         Beyond the high taxonomic diversity, our results revealed that phototrophic microbial  
494 communities were site-specific due to a high species turnover across sites. Species turnover was largely  
495 driven by water availability (precipitation and *Sphagnum* water content), plant cover and dissolved  
496 organic C. This indicates that complex interactions among climate, *Sphagnum* properties and  
497 vegetation determine the community structure of phototrophic microbes in peatlands. For instance,  
498 by reducing light availability at the *Sphagnum* surface, vascular plant cover could structure  
499 phototrophic microbial communities as shown in other terrestrial systems such as grasslands or alpine  
500 deserts (Davies et al., 2013; Řeháková et al., 2017). Moreover, this close link between phototrophic  
501 microbial and plant communities suggests that plants affect phototrophic microbes through the  
502 nutrients and numerous allelochemical compounds they release in their surrounding environment, by  
503 favouring or inhibiting specific taxa (Asao & Madigan, 2010; Hamard et al., 2019; Řeháková et al., 2017;  
504 Stoler & Relyea, 2011; Sytiuk et al., 2021).

505

#### 506 **4.3 The microbial C fixation depends on the community structure of phototrophic microbes**

507 Our structural equation modelling revealed the links by which species turnover affected microbial C  
508 fixation rates. We identified two indirect pathways: first, microbial community structure influenced C  
509 fixation rates through an alteration of microbial abundance; and second, through an alteration of  
510 community-weighted mean body size and individual-level photosynthetic rates. Both pathways were  
511 antagonists: when the phototrophic community structure shifted and induced an increase of the

512 microbial abundance, it also led to a decrease of the community-weighted mean body size and a  
513 decrease of the individual-level photosynthetic rates. This compensation resulted in constant C fixation  
514 rates across the gradient. This result is in line with previous studies where isometric laws between  
515 body size, metabolic rates and abundance of phytoplankton have been found (Cermeño et al., 2006;  
516 Huete-Ortega et al., 2012). Altogether, these findings suggest that the total energy processed by  
517 phototrophic microbes in peatlands for C fixation was constant across our large latitudinal gradient.

518         The influence of microbial community structure on C fixation rates could be related to specific  
519 mechanisms on the two identified pathways. For instance, the presence of certain species, such as  
520 colonial phototrophic microbes, could increase the abundance of phototrophic microbes (Finkel et al.,  
521 2010). Some colonial phototrophic species (e.g. *Anabaena* sp.) can indeed form long filaments  
522 composed by numerous cells (Gilbert & Mitchell, 2006). These filaments are hardly eaten by grazers  
523 (DeColibus et al., 2017), thus favouring phototrophic abundance. In addition, the community-weighted  
524 mean body size, and hence, the size of the photosynthetic apparatus at the individual level (Finkel et  
525 al., 2010; Kalchev et al., 1996), depends on the phototrophic species present in the community.  
526 Therefore, communities composed of larger phototrophic microbes had higher individual-level  
527 photosynthetic rates, as was the case in the northern sites, where large mixotrophic species were  
528 present. This result suggests that mixotrophic species are key organisms by their size, driving microbial  
529 photosynthesis rates and C uptake in peatlands. This is in line with previous studies on the contribution  
530 of mixotrophic testate amoebae to bryosphere C fixation (Jassey et al., 2015). It also echoes  
531 observations in oceanic environments where mixotrophic plankton plays a paramount role in  
532 ecosystem primary productivity (Ward & Follows, 2016; Worden et al., 2015).

533

#### 534 **4.4 Implications of microbial C fixation for peatland C dynamics**

535 Phototrophic microbes fixed on average 8.8 (3.8 – 16.2) mg CO<sub>2</sub> h<sup>-1</sup> m<sup>-2</sup> across sites, which represented  
536 on average 9% (4% - 12%) of the total bryosphere C fixation. This contribution might seem relatively  
537 high considering the low C biomass of phototrophs in *Sphagnum* (1 mg C.g<sup>-1</sup> DW). Yet, the

538 photosynthetic rate per chlorophyll content of phototrophs is four to ten times higher than for  
539 *Sphagnum*. It explains why phototrophic microbes contribute significantly to the bryosphere C fixation  
540 despite their small size and biomass. It further indicates that the small fraction of C found in  
541 phototrophic biomass does not reflect the amount of C they fix. This result is in line with a previous  
542 study suggesting that Cyanobacteria and green algae can display a 50-fold higher efficiency in CO<sub>2</sub>  
543 fixation compared to plants due to their faster growth rate (Rossi et al., 2015).

544         Regarding the proportion of C fixed by phototrophic microbes, we argue it is very likely that  
545 phototrophic microbes play an important– and until now overlooked– role in peatland C cycling.  
546 Assuming that our data are representative for northern peatlands, we roughly estimated that  
547 phototrophic microbes would fix a global amount of *ca.* 75 MT C per year in northern peatlands  
548 (Supplementary Methods, Supplementary Table S7). By comparison, this amount is about the same  
549 magnitude as C loss from northern peatlands in response to climate warming (Dorrepaal et al., 2009).  
550 We note that our estimates of microbial contribution to annual peatland C uptake are based on several  
551 assumptions that might lead to uncertainty. For example, seasonal climatic variation in microbial  
552 phototrophic activity could influence the values that we present here. In particular, water availability  
553 and *Sphagnum* water content vary over the year, and thus shape the community structure and C  
554 fixation rates of phototrophic microbes accordingly. Yet, phototrophic microbial communities respond  
555 fast to water availability changes in peatlands (less than two weeks, Reczuga et al., 2018). We thus  
556 believe that our estimations are representative of the summer conditions at the time we sampled.  
557 Moreover, phototrophic microbial abundance have been shown to peak in spring and autumn  
558 (Reczuga et al., 2020), when their abundance can double (Rober et al., 2014). This suggests that the  
559 annual C fixation by microbial phototrophs might therefore be higher than expected. We also  
560 acknowledge that our fluorescence-based measurements of microbial photosynthesis could introduce  
561 some bias in our estimates. In particular, the high proportion of Cyanobacteria in some sites could lead  
562 to an underestimation of photosynthetic rates, as chlorophyll fluorescence measurements are often  
563 underestimated in Cyanobacteria due to their prokaryotic nature (Ogawa et al., 2017; Schuurmans et

564 al., 2015). We however did not observed this effect in our samples (Supplementary Fig. S10). Similarly,  
565 measurements of chlorophyll fluorescence do not take into account the photosynthesis performed by  
566 the bacteriochlorophyll of phototrophic prokaryotes. However, microbial C fixation rates estimated  
567 using fluorescence were of the same magnitude as C fixation rates quantified using a gas analyser  
568 (Supplementary Fig. S11). Finally, we caution that the estimate of peatland surface used for upscaling  
569 (Leifeld & Menichetti, 2018) is not restricted to *Sphagnum*-dominated peatlands and includes rich fens.  
570 However, *Sphagnum*-dominated peatlands (ombrotrophic bogs and poor fens) represent a high  
571 proportion of total peatlands, accounting for instance for more than 65% in North America (Hugelius  
572 et al., 2020). Further, phototrophic microbial C fixation in rich fens has been found of either similar or  
573 higher magnitude than our estimates (Wyatt et al., 2012). Despite these limitations, our findings clearly  
574 underline the importance of phototrophic microbes for peatland C cycle through the large amount of  
575 C they fix.

576

#### 577 **4.5 Conclusions and perspectives**

578 The current consensus on C pathways in terrestrial ecosystems is that plants are the only or at least  
579 the main route for soil C uptake (Krumins et al., 2013; Liang et al., 2017). Our study questions this  
580 assumption and shows that phototrophic microbial photosynthesis could represent about 10% of  
581 peatland primary productivity, demonstrating that phototrophic microbes cannot be ignored in  
582 peatland C dynamics. Their role remains nevertheless obscure in terms of C sequestration, as the fate  
583 of microbial-fixed C in peatlands is currently unknown. The only study to date suggests that microbial  
584 fixed C would not promote peatland C accumulation. This study shows that phototrophic microbes in  
585 a fen ecosystem release 20 to 40% of the C they fix as exudates (Wyatt & Turetsky, 2015), contributing  
586 to DOC concentrations and promoting heterotrophic respiration (Wyatt et al., 2014; Wyatt & Turetsky,  
587 2015). The fate of the remaining C fixed (60 to 80%) is however unknown. If less labile than exudates,  
588 this C could contribute to peat formation. We show here that our current understanding of peatland  
589 C dynamics is missing a large piece of the jigsaw puzzle, highlighting the urgent need to further explore



590 phototrophic microbes. Including microbial C uptake in biogeochemical peatland C models would  
591 certainly improve predictions of the peatland C balance under future global changes. Particular  
592 attention should be given to seasonal variation across phototrophic microbial communities, and to the  
593 fate of the C they fix. The incorporation of these aspects in future ecological models to refine our  
594 understanding of peatland C biogeochemical cycles is a worthy challenge.

595

596

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610

## 611 **CONFLICT OF INTEREST**

612 The authors declare that the research was conducted in the absence of any commercial or financial  
613 relationships that could be construed as a potential conflict of interest.

614

615 **AUTHOR CONTRIBUTION**

616 VEJJ conceived the ideas and designed methodology with the help of SH. VEJJ choose the sites with  
617 the help of ML, MK, EST, GIR and ED. VEJJ and SH collected the data with the help of MK. SH and VEJJ  
618 proceeded to laboratory work with the help of MB, AS, JL and EL. SH analysed the data with the help  
619 of VEJJ, EL, MB and AS. SH and VEJJ led the writing of the manuscript with the help of RC and PK. All  
620 authors contributed critically to the drafts and gave final approval for publication.

621

622 **DATA AVAILABILITY**

623 Data are available from Figshare (10.6084/m9.figshare.c.5190902).

624

625 **REFERENCES**

626 Asao, M., & Madigan, M. T. (2010). Taxonomy, phylogeny, and ecology of the heliobacteria.

627 *Photosynthesis Research*, 104(2–3), 103–111. <https://doi.org/10.1007/s11120-009-9516-1>

628 Barlow, R. G., Cummings, D. G., & Gibb, S. W. (1997). Improved resolution of mono- and divinyl

629 chlorophylls a and b and zeaxanthin and lutein in phytoplankton extracts using reverse phase

630 C-8 HPLC. *Marine Ecology Progress Series*, 161, 303–307.

631 <https://doi.org/10.3354/meps161303>

632 Bar-On, Y. M., Phillips, R., & Milo, R. (2018). The biomass distribution on Earth. *Proceedings of the*

633 *National Academy of Sciences*, 115(25), 6506–6511.

634 <https://doi.org/10.1073/pnas.1711842115>

635 Basińska, A. M., Reczuga, M. K., Gąbka, M., Stróżecki, M., Łuców, D., Samson, M., Urbaniak, M.,

636 Leśny, J., Chojnicki, B. H., Gilbert, D., Sobczyński, T., Olejnik, J., Silvennoinen, H., Juszcak, R.,

637 & Lamentowicz, M. (2020). Experimental warming and precipitation reduction affect the

638 biomass of microbial communities in a Sphagnum peatland. *Ecological Indicators*, 112,  
639 106059. <https://doi.org/10.1016/j.ecolind.2019.106059>

640 Bates, S. T., Clemente, J. C., Flores, G. E., Walters, W. A., Parfrey, L. W., Knight, R., & Fierer, N. (2013).  
641 Global biogeography of highly diverse protistan communities in soil. *The ISME Journal*, 7(3),  
642 652–659. <https://doi.org/10.1038/ismej.2012.147>

643 Behrenfeld, M. J. (2014). Climate-mediated dance of the plankton. *Nature Climate Change*, 4(10),  
644 880–887. <https://doi.org/10.1038/nclimate2349>

645 Black, K., & Osborne, B. (2004). An assessment of photosynthetic downregulation in cyanobacteria  
646 from the Gunnera–Nostoc symbiosis. *New Phytologist*, 162(1), 125–132.  
647 <https://doi.org/10.1111/j.1469-8137.2004.01008.x>

648 Borsheim, K. Y., & Bratbak, G. (1987). Cell volume to cell carbon conversion factors for a  
649 bacterivorous *Monas* sp. enriched from seawater. *Marine Ecology Progress Series*, 36, 171–  
650 175.

651 Bragina, A., Berg, C., Cardinale, M., Shcherbakov, A., Chebotar, V., & Berg, G. (2012). *Sphagnum*  
652 mosses harbour highly specific bacterial diversity during their whole lifecycle. *The ISME*  
653 *Journal*, 6(4), 802–813. <https://doi.org/10.1038/ismej.2011.151>

654 Bragina, A., Oberauner-Wappis, L., Zachow, C., Halwachs, B., Thallinger, G. G., Müller, H., & Berg, G.  
655 (2014). The Sphagnum microbiome supports bog ecosystem functioning under extreme  
656 conditions. *Molecular Ecology*, 23(18), 4498–4510. <https://doi.org/10.1111/mec.12885>

657 Bridgman, S. D., Megonigal, J. P., Keller, J. K., Bliss, N. B., & Trettin, C. (2006). The carbon balance of  
658 North American wetlands. *Wetlands*, 26(4), 889–916. [https://doi.org/10.1672/0277-5212\(2006\)26\[889:TCBONA\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2006)26[889:TCBONA]2.0.CO;2)

660 Cano-Díaz, C., Maestre, F. T., Eldridge, D. J., Singh, B. K., Bardgett, R. D., Fierer, N., & Delgado-  
661 Baquerizo, M. (2019). Ecological niche differentiation in soil cyanobacterial communities  
662 across the globe. *BioRxiv*, 531145. <https://doi.org/10.1101/531145>

663 Capdeville, C., Pommier, T., Gervais, J., Fromard, F., Rols, J.-L., & Leflaive, J. (2019). Mangrove Facies  
664 Drives Resistance and Resilience of Sediment Microbes Exposed to Anthropogenic Disturbance.  
665 *Frontiers in Microbiology*, 9. <https://doi.org/10.3389/fmicb.2018.03337>

666 Caron, D. A., Alexander, H., Allen, A. E., Archibald, J. M., Armbrust, E. V., Bachy, C., Bell, C. J., Bharti,  
667 A., Dyhrman, S. T., Guida, S. M., Heidelberg, K. B., Kaye, J. Z., Metzner, J., Smith, S. R., &  
668 Worden, A. Z. (2017). Probing the evolution, ecology and physiology of marine protists using  
669 transcriptomics. *Nature Reviews Microbiology*, 15(1), 6–20.  
670 <https://doi.org/10.1038/nrmicro.2016.160>

671 Cermeño, P., Marañón, E., Harbour, D., & Harris, R. P. (2006). Invariant scaling of phytoplankton  
672 abundance and cell size in contrasting marine environments. *Ecology Letters*, 9(11), 1210–  
673 1215. <https://doi.org/10.1111/j.1461-0248.2006.00973.x>

674 Chavent, M., Kuentz, V., Liquet, B., & Saracco, J. (2011). Classification de variables : le package  
675 ClustOfVar. *43èmes Journées de Statistique (SFdS)*, 6 p. [https://hal.archives-ouvertes.fr/hal-](https://hal.archives-ouvertes.fr/hal-00601919)  
676 00601919

677 Ciais, P., Sabine, C., Govindasamy, B., Bopp, L., Brokvin, V., Canadell, J. G., Chhabra, A., DeFries, R.,  
678 Galloway, J., Heimann, M., Jones, C., Le Quéré, C., Myneni, R., Piao, S., & Thornton, P. (2013).  
679 Chapter 6: Carbon and Other Biogeochemical Cycles. In *Climate Change 2013: The Physical*  
680 *Science Basis* (Cambridge University Press). Stocker, T., Qin, D., and Plattner, G.-K.

681 Davies, L. O., Schäfer, H., Marshall, S., Bramke, I., Oliver, R. G., & Bending, G. D. (2013). Light  
682 Structures Phototroph, Bacterial and Fungal Communities at the Soil Surface. *PLOS ONE*, 8(7),  
683 e69048. <https://doi.org/10.1371/journal.pone.0069048>

684 Delgado-Baquerizo, M., Oliverio, A. M., Brewer, T. E., Benavent-González, A., Eldridge, D. J., Bardgett,  
685 R. D., Maestre, F. T., Singh, B. K., & Fierer, N. (2018). A global atlas of the dominant bacteria  
686 found in soil. *Science*, 359(6373), 320–325. <https://doi.org/10.1126/science.aap9516>

687 Dorrepaal, E., Toet, S., van Logtestijn, R. S. P., Swart, E., van de Weg, M. J., Callaghan, T. V., & Aerts,  
688 R. (2009). Carbon respiration from subsurface peat accelerated by climate warming in the  
689 subarctic. *Nature*, *460*(7255), 616–619. <https://doi.org/10.1038/nature08216>

690 Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andreae, M. O., & Pöschl, U. (2012).  
691 Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nature*  
692 *Geoscience*, *5*(7), 459–462. <https://doi.org/10.1038/ngeo1486>

693 Escudié, F., Auer, L., Bernard, M., Mariadassou, M., Cauquil, L., Vidal, K., Maman, S., Hernandez-  
694 Raquet, G., Combes, S., & Pascal, G. (2018). FROGS: Find, Rapidly, OTUs with Galaxy Solution.  
695 *Bioinformatics*, *34*(8), 1287–1294. <https://doi.org/10.1093/bioinformatics/btx791>

696 Falkowski, P. G., & Raven, J. A. (2013). *Aquatic Photosynthesis: Second Edition*. Princeton University  
697 Press.

698 Fierer, N. (2017). Embracing the unknown: disentangling the complexities of the soil microbiome.  
699 *Nature Reviews Microbiology*, *15*(10), 579–590. <https://doi.org/10.1038/nrmicro.2017.87>

700 Finkel, Z. V., Beardall, J., Flynn, K. J., Quigg, A., Rees, T. A. V., & Raven, J. A. (2010). Phytoplankton in a  
701 changing world: cell size and elemental stoichiometry. *Journal of Plankton Research*, *32*(1),  
702 119–137. <https://doi.org/10.1093/plankt/fbp098>

703 Galand, P. E., Fritze, H., Conrad, R., & Yrjälä, K. (2005). Pathways for Methanogenesis and Diversity of  
704 Methanogenic Archaea in Three Boreal Peatland Ecosystems. *Applied and Environmental*  
705 *Microbiology*, *71*(4), 2195–2198. <https://doi.org/10.1128/AEM.71.4.2195-2198.2005>

706 Geisen, S., Mitchell, E. A. D., Adl, S., Bonkowski, M., Dunthorn, M., Ekelund, F., Fernández, L. D.,  
707 Jousset, A., Krashevskaya, V., Singer, D., Spiegel, F. W., Walochnik, J., & Lara, E. (2018). Soil  
708 protists: a fertile frontier in soil biology research. *FEMS Microbiology Reviews*, *42*(3), 293–  
709 323. <https://doi.org/10.1093/femsre/fuy006>

710 Geisen, S., Tveit, A. T., Clark, I. M., Richter, A., Svenning, M. M., Bonkowski, M., & Urich, T. (2015).  
711 Metatranscriptomic census of active protists in soils. *The ISME Journal*, *9*(10), 2178–2190.  
712 <https://doi.org/10.1038/ismej.2015.30>

713 Gilbert, D., Amblard, C., Bourdier, G., & Francez, A.-J. (1998). The Microbial Loop at the Surface of a  
714 Peatland: Structure, Function, and Impact of Nutrient Input. *Microbial Ecology*, 35(1), 83–93.  
715 <https://doi.org/10.1007/s002489900062>

716 Gilbert, D., & Mitchell, E. A. D. (2006). Chapter 13 Microbial diversity in Sphagnum peatlands. In I. P.  
717 Martini, A. Martínez Cortizas, & W. Chesworth (Eds.), *Developments in Earth Surface*  
718 *Processes* (Vol. 9, pp. 287–318). Elsevier. [https://doi.org/10.1016/S0928-2025\(06\)09013-4](https://doi.org/10.1016/S0928-2025(06)09013-4)

719 Goldsborough, L., & Robinson, G. (1996). Patterns in wetlands. In *Algal ecology: freshwater benthic*  
720 *ecosystems* (Academic). Stevenson RJ, Bothwell ML, Lowe RL.

721 Graupner, N., Jensen, M., Bock, C., Marks, S., Rahmann, S., Beisser, D., & Boenigk, J. (2018). Evolution  
722 of heterotrophy in chrysophytes as reflected by comparative transcriptomics. *FEMS*  
723 *Microbiology Ecology*, 94(4). <https://doi.org/10.1093/femsec/fiy039>

724 Guillou, L., Bachar, D., Audic, S., Bass, D., Berney, C., Bittner, L., Boutte, C., Burgaud, G., de Vargas, C.,  
725 Decelle, J., del Campo, J., Dolan, J. R., Dunthorn, M., Edvardsen, B., Holzmann, M., Kooistra,  
726 W. H. C. F., Lara, E., Le Bescot, N., Logares, R., ... Christen, R. (2013). The Protist Ribosomal  
727 Reference database (PR2): a catalog of unicellular eukaryote Small Sub-Unit rRNA sequences  
728 with curated taxonomy. *Nucleic Acids Research*, 41(D1), D597–D604.  
729 <https://doi.org/10.1093/nar/gks1160>

730 Halsey, L. A., Vitt, D. H., & Gignac, L. D. (2000). Sphagnum-Dominated Peatlands in North America  
731 since the Last Glacial Maximum: Their Occurrence and Extent. *The Bryologist*, 103(2), 334–  
732 352. JSTOR.

733 Hamard, S., Robroek, B. J. M., Allard, P.-M., Signarbieux, C., Zhou, S., Saesong, T., de Baaker, F.,  
734 Buttler, A., Chiapusio, G., Wolfender, J.-L., Bragazza, L., & Jasey, V. E. J. (2019). Effects of  
735 Sphagnum Leachate on Competitive Sphagnum Microbiome Depend on Species and Time.  
736 *Frontiers in Microbiology*, 10. <https://doi.org/10.3389/fmicb.2019.02042>

737 Hansen, A. M., Kraus, T. E. C., Pellerin, B. A., Fleck, J. A., Downing, B. D., & Bergamaschi, B. A. (2016).  
738 Optical properties of dissolved organic matter (DOM): Effects of biological and photolytic

739 degradation. *Limnology and Oceanography*, 61(3), 1015–1032.

740 <https://doi.org/10.1002/lno.10270>

741 Heger, T. J., Giesbrecht, I. J. W., Gustavsen, J., Campo, J. del, Kellogg, C. T. E., Hoffman, K. M.,  
742 Lertzman, K., Mohn, W. W., & Keeling, P. J. (2018). High-throughput environmental  
743 sequencing reveals high diversity of litter and moss associated protist communities along a  
744 gradient of drainage and tree productivity. *Environmental Microbiology*, 20(3), 1185–1203.  
745 <https://doi.org/10.1111/1462-2920.14061>

746 Huete-Ortega, M., Cermeño, P., Calvo-Díaz, A., & Marañón, E. (2012). Isometric size-scaling of  
747 metabolic rate and the size abundance distribution of phytoplankton. *Proceedings of the*  
748 *Royal Society B: Biological Sciences*, 279(1734), 1815–1823.  
749 <https://doi.org/10.1098/rspb.2011.2257>

750 Hugelius, G., Loisel, J., Chadburn, S., Jackson, R. B., Jones, M., MacDonald, G., Marushchak, M.,  
751 Olefeldt, D., Packalen, M., Siewert, M. B., Treat, C., Turetsky, M., Voigt, C., & Yu, Z. (2020).  
752 Large stocks of peatland carbon and nitrogen are vulnerable to permafrost thaw.  
753 *Proceedings of the National Academy of Sciences*, 117(34), 20438–20446.  
754 <https://doi.org/10.1073/pnas.1916387117>

755 Jassey, V. E., Chiapusio, G., Binet, P., Buttler, A., Laggoun-Défarge, F., Delarue, F., Bernard, N.,  
756 Mitchell, E. A., Toussaint, M.-L., Francez, A.-J., & Gilbert, D. (2013). Above- and belowground  
757 linkages in Sphagnum peatland: climate warming affects plant-microbial interactions. *Global*  
758 *Change Biology*, 19(3), 811–823. <https://doi.org/10.1111/gcb.12075>

759 Jassey, V. E. J., Gilbert, D., Binet, P., Toussaint, M.-L., & Chiapusio, G. (2011). Effect of a temperature  
760 gradient on Sphagnum fallax and its associated living microbial communities: a study under  
761 controlled conditions. *Canadian Journal of Microbiology*, 57(3), 226–235.  
762 <https://doi.org/10.1139/W10-116>

763 Jassey, V. E. J., Reczuga, M. K., Zielińska, M., Słowińska, S., Robroek, B. J. M., Mariotte, P., Seppey, C.  
764 V. W., Lara, E., Barabach, J., Słowiński, M., Bragazza, L., Chojnicki, B. H., Lamentowicz, M.,

765 Mitchell, E. A. D., & Buttler, A. (2018). Tipping point in plant–fungal interactions under severe  
766 drought causes abrupt rise in peatland ecosystem respiration. *Global Change Biology*, 24(3),  
767 972–986. <https://doi.org/10.1111/gcb.13928>

768 Jassey, V. E. J., & Signarbieux, C. (2019). Effects of climate warming on Sphagnum photosynthesis in  
769 peatlands depend on peat moisture and species-specific anatomical traits. *Global Change*  
770 *Biology*, 25(11), 3859–3870. <https://doi.org/10.1111/gcb.14788>

771 Jassey, V. E. J., Signarbieux, C., Hättenschwiler, S., Bragazza, L., Buttler, A., Delarue, F., Fournier, B.,  
772 Gilbert, D., Laggoun-Défarge, F., Lara, E., T. E. Mills, R., Mitchell, E. A. D., Payne, R. J., &  
773 Robroek, B. J. M. (2015). An unexpected role for mixotrophs in the response of peatland  
774 carbon cycling to climate warming. *Scientific Reports*, 5, 16931.  
775 <https://doi.org/10.1038/srep16931>

776 Jeffrey, S. ., Mantoura, R. F. ., & Wright, S. . (1997). *Phytoplankton pigments in oceanography*.  
777 UNESCO Publishing.

778 Jia, L., Feng, X., Zheng, Z., Han, L., Hou, X., Lu, Z., & Lv, J. (2015). *Polymorphobacter fuscus* sp. nov.,  
779 isolated from permafrost soil, and emended description of the genus *Polymorphobacter*.  
780 *International Journal of Systematic and Evolutionary Microbiology*, 65(11), 3920–3925.  
781 <https://doi.org/10.1099/ijsem.0.000514>

782 Kalchev, R. K., Beshkova, M. B., Boumbarova, C. S., Tsvetkova, R. L., & Sais, D. (1996). Some allometric  
783 and non-allometric relationships between chlorophyll-a and abundance variables of  
784 phytoplankton. *Hydrobiologia*, 341(3), 235–245. <https://doi.org/10.1007/BF00014688>

785 Krumins, J. A., van Oevelen, D., Bezemer, T. M., De Deyn, G. B., Hol, W. H. G., van Donk, E., de Boer,  
786 W., de Ruiter, P. C., Middelburg, J. J., Monroy, F., Soetaert, K., Thébault, E., van de Koppel, J.,  
787 van Veen, J. A., Viketoft, M., & van der Putten, W. H. (2013). Soil and Freshwater and Marine  
788 Sediment Food Webs: Their Structure and Function. *BioScience*, 63(1), 35–42.  
789 <https://doi.org/10.1525/bio.2013.63.1.8>



790 Kulichevskaya, I. S., Danilova, O. V., Tereshina, V. M., Kevbrin, V. V., & Dedysh, S. N. (2014).  
791 Descriptions of *Roseiarcus fermentans* gen. nov., sp. nov., a bacteriochlorophyll a-containing  
792 fermentative bacterium related phylogenetically to alphaproteobacterial methanotrophs,  
793 and of the family Roseiarcaceae fam. nov. *International Journal of Systematic and*  
794 *Evolutionary Microbiology*, 64(Pt 8), 2558–2565. <https://doi.org/10.1099/ij.s.0.064576-0>

795 Lara, E., Mitchell, E. A. D., Moreira, D., & López García, P. (2011). Highly Diverse and Seasonally  
796 Dynamic Protist Community in a Pristine Peat Bog. *Protist*, 162(1), 14–32.  
797 <https://doi.org/10.1016/j.protis.2010.05.003>

798 Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology,  
799 evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573–579.  
800 <https://doi.org/10.1111/2041-210X.12512>

801 Leifeld, J., & Menichetti, L. (2018). The underappreciated potential of peatlands in global climate  
802 change mitigation strategies. *Nature Communications*, 9(1), 1071.  
803 <https://doi.org/10.1038/s41467-018-03406-6>

804 Li, A., Stoecker, D. K., & Adolf, J. E. (1999). Feeding, pigmentation, photosynthesis and growth of the  
805 mixotrophic dinoflagellate *Gyrodinium galatheanum*. *Aquatic Microbial Ecology*, 19(2), 163–  
806 176. <https://doi.org/10.3354/ame019163>

807 Liang, C., Schimel, J. P., & Jastrow, J. D. (2017). The importance of anabolism in microbial control over  
808 soil carbon storage. *Nature Microbiology*, 2(8), 1–6.  
809 <https://doi.org/10.1038/nmicrobiol.2017.105>

810 Lindo, Z., & Gonzalez, A. (2010). The Bryosphere: An Integral and Influential Component of the  
811 Earth's Biosphere. *Ecosystems*, 13(4), 612–627. <https://doi.org/10.1007/s10021-010-9336-3>

812 Lynn, T. M., Ge, T., Yuan, H., Wei, X., Wu, X., Xiao, K., Kumaresan, D., Yu, S. S., Wu, J., & Whiteley, A.  
813 S. (2017). Soil Carbon-Fixation Rates and Associated Bacterial Diversity and Abundance in  
814 Three Natural Ecosystems. *Microbial Ecology*, 73(3), 645–657.  
815 <https://doi.org/10.1007/s00248-016-0890-x>

816 Mahé, F., Rognes, T., Quince, C., Vargas, C. de, & Dunthorn, M. (2014). Swarm: robust and fast  
817 clustering method for amplicon-based studies. *PeerJ*, 2, e593.  
818 <https://doi.org/10.7717/peerj.593>

819 Maier, S., Tamm, A., Wu, D., Caesar, J., Grube, M., & Weber, B. (2018). Photoautotrophic organisms  
820 control microbial abundance, diversity, and physiology in different types of biological soil  
821 crusts. *The ISME Journal*, 12(4), 1032–1046. <https://doi.org/10.1038/s41396-018-0062-8>

822 McMurdie, P. J., & Holmes, S. (2013). phyloseq: An R Package for Reproducible Interactive Analysis  
823 and Graphics of Microbiome Census Data. *PLOS ONE*, 8(4), e61217.  
824 <https://doi.org/10.1371/journal.pone.0061217>

825 Mitchell, E. A. D., Gilbert, D., Buttler, A., Amblard, C., & Grosvernier, P. (2003). Structure of Microbial  
826 Communities in Sphagnum Peatlands and Effect of Atmospheric Carbon Dioxide Enrichment.  
827 *Microbial Ecology*, 46, 187–199.

828 Mitra, A., Flynn, K. J., Tillmann, U., Raven, J. A., Caron, D., Stoecker, D. K., Not, F., Hansen, P. J.,  
829 Hallegraeff, G., Sanders, R., Wilken, S., McManus, G., Johnson, M., Pitta, P., Våge, S., Berge,  
830 T., Calbet, A., Thingstad, F., Jeong, H. J., ... Lundgren, V. (2016). Defining Planktonic Protist  
831 Functional Groups on Mechanisms for Energy and Nutrient Acquisition: Incorporation of  
832 Diverse Mixotrophic Strategies. *Protist*, 167(2), 106–120.  
833 <https://doi.org/10.1016/j.protis.2016.01.003>

834 Myers, B., Webster, K. L., Mclaughlin, J. W., & Basiliko, N. (2012). Microbial activity across a boreal  
835 peatland nutrient gradient: the role of fungi and bacteria. *Wetlands Ecology and*  
836 *Management*, 20(2), 77–88. <https://doi.org/10.1007/s11273-011-9242-2>

837 Nichols, J. E., & Peteet, D. M. (2019). Rapid expansion of northern peatlands and doubled estimate of  
838 carbon storage. *Nature Geoscience*, 12(11), 917–921. [https://doi.org/10.1038/s41561-019-](https://doi.org/10.1038/s41561-019-0454-z)  
839 [0454-z](https://doi.org/10.1038/s41561-019-0454-z)

840 Ogawa, T., Misumi, M., & Sonoike, K. (2017). Estimation of photosynthesis in cyanobacteria by pulse-  
841 amplitude modulation chlorophyll fluorescence: problems and solutions. *Photosynthesis*  
842 *Research*, 133(1), 63–73. <https://doi.org/10.1007/s11120-017-0367-x>

843 Okamura, K., Hisada, T., Kanbe, T., & Hiraishi, A. (2009). Rhodovastum atsumiense gen. nov., sp. nov.,  
844 a phototrophic alphaproteobacterium isolated from paddy soil. *The Journal of General and*  
845 *Applied Microbiology*, 55(1), 43–50. <https://doi.org/10.2323/jgam.55.43>

846 Oliverio, A. M., Geisen, S., Delgado-Baquerizo, M., Maestre, F. T., Turner, B. L., & Fierer, N. (2020).  
847 The global-scale distributions of soil protists and their contributions to belowground systems.  
848 *Science Advances*, 6(4), eaax8787. <https://doi.org/10.1126/sciadv.aax8787>

849 Olson, R. J., Zettler, E. R., & Anderson, O. K. (1989). Discrimination of eukaryotic phytoplankton cell  
850 types from light scatter and autofluorescence properties measured by flow cytometry.  
851 *Cytometry*, 10(5), 636–643. <https://doi.org/10.1002/cyto.990100520>

852 Padfield, D., Buckling, A., Warfield, R., Lowe, C., & Yvon-Durocher, G. (2018). Linking phytoplankton  
853 community metabolism to the individual size distribution. *Ecology Letters*, 21(8), 1152–1161.  
854 <https://doi.org/10.1111/ele.13082>

855 Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., & Glöckner, F. O.  
856 (2013). The SILVA ribosomal RNA gene database project: improved data processing and web-  
857 based tools. *Nucleic Acids Research*, 41(D1), D590–D596.  
858 <https://doi.org/10.1093/nar/gks1219>

859 R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for  
860 *Statistical Computing*, Vienna, Austria. Available at: URL <http://www.R-project.org/>.

861 Reczuga, M. K., Lamentowicz, M., Mulot, M., Mitchell, E. A. D., Buttler, A., Chojnicki, B., Słowiński, M.,  
862 Binet, P., Chiapusio, G., Gilbert, D., Słowińska, S., & Jassey, V. E. J. (2018). Predator–prey  
863 mass ratio drives microbial activity under dry conditions in Sphagnum peatlands. *Ecology and*  
864 *Evolution*, 8(11), 5752–5764. <https://doi.org/10.1002/ece3.4114>

865 Reczuga, M. K., Seppey, C. V. W., Mulo, M., Jassey, V. E. J., Buttler, A., Słowińska, S., Słowiński, M.,  
866 Lara, E., Lamentowicz, M., & Mitchell, E. A. D. (2020). Assessing the responses of Sphagnum  
867 micro-eukaryotes to climate changes using high throughput sequencing. *PeerJ*, *8*, e9821.  
868 <https://doi.org/10.7717/peerj.9821>

869 Řeháková, K., Čapková, K., Dvorský, M., Kopecký, M., Altman, J., Šmilauer, P., & Doležal, J. (2017).  
870 Interactions between soil phototrophs and vascular plants in Himalayan cold deserts. *Soil*  
871 *Biology and Biochemistry*, *115*, 568–578. <https://doi.org/10.1016/j.soilbio.2017.05.020>

872 Rober, A. R., Wyatt, K. H., Stevenson, R. J., & Turetsky, M. R. (2014). Spatial and temporal variability  
873 of algal community dynamics and productivity in floodplain wetlands along the Tanana River,  
874 Alaska. *Freshwater Science*, *33*(3), 765–777. <https://doi.org/10.1086/676939>

875 Robroek, B. J. M., Jassey, V. E. J., Payne, R. J., Martí, M., Bragazza, L., Bleeker, A., Buttler, A., Caporn,  
876 S. J. M., Dise, N. B., Kattge, J., Zając, K., Svensson, B. H., van Ruijven, J., & Verhoeven, J. T. A.  
877 (2017). Taxonomic and functional turnover are decoupled in European peat bogs. *Nature*  
878 *Communications*, *8*(1), 1161. <https://doi.org/10.1038/s41467-017-01350-5>

879 Robroek, B. J. M., Schouten, M. G. C., Limpens, J., Berendse, F., & Poorter, H. (2009). Interactive  
880 effects of water table and precipitation on net CO<sub>2</sub> assimilation of three co-occurring  
881 Sphagnum mosses differing in distribution above the water table. *Global Change Biology*,  
882 *15*(3), 680–691. <https://doi.org/10.1111/j.1365-2486.2008.01724.x>

883 Rognes, T., Flouri, T., Nichols, B., Quince, C., & Mahé, F. (2016). VSEARCH: a versatile open source  
884 tool for metagenomics. *PeerJ*, *4*, e2584. <https://doi.org/10.7717/peerj.2584>

885 Rossi, F., Olguín, E. J., Diels, L., & De Philippis, R. (2015). Microbial fixation of CO<sub>2</sub> in water bodies and  
886 in drylands to combat climate change, soil loss and desertification. *New Biotechnology*, *32*(1),  
887 109–120. <https://doi.org/10.1016/j.nbt.2013.12.002>

888 Schuurmans, R. M., Alphen, P. van, Schuurmans, J. M., Matthijs, H. C. P., & Hellingwerf, K. J. (2015).  
889 Comparison of the Photosynthetic Yield of Cyanobacteria and Green Algae: Different

890 Methods Give Different Answers. *PLOS ONE*, 10(9), e0139061.  
891 <https://doi.org/10.1371/journal.pone.0139061>

892 Singh, B. K., Bardgett, R. D., Smith, P., & Reay, D. S. (2010). Microorganisms and climate change:  
893 terrestrial feedbacks and mitigation options. *Nature Reviews Microbiology*, 8(11), 779–790.  
894 <https://doi.org/10.1038/nrmicro2439>

895 Stoler, A. B., & Relyea, R. A. (2011). Living in the litter: the influence of tree leaf litter on wetland  
896 communities. *Oikos*, 120(6), 862–872. <https://doi.org/10.1111/j.1600-0706.2010.18625.x>

897 Sytiuk, A., Céréghino, R., Hamard, S., Delarue, F., Dorrepaal, E., Küttim, M., Lamentowicz, M.,  
898 Pourrut, B., Robroek, B. J., Tuittila, E.-S., & Jassey, V. E. J. (2020). *Morphological and*  
899 *biochemical responses of Sphagnum mosses to environmental changes* [Preprint]. *Ecology*.  
900 <https://doi.org/10.1101/2020.10.29.360388>

901 Sytiuk A., Céréghino R., Hamard S., Delarue F., et al. (2021) Predicting the structure and functions of  
902 peatland microbial communities from Sphagnum phylogeny, anatomical traits and  
903 metabolites. *Journal of Ecology*, under revision.

904 Tanabe, A. S., Nagai, S., Hida, K., Yasuike, M., Fujiwara, A., Nakamura, Y., Takano, Y., & Katakura, S.  
905 (2016). Comparative study of the validity of three regions of the 18S-rRNA gene for massively  
906 parallel sequencing-based monitoring of the planktonic eukaryote community. *Molecular*  
907 *Ecology Resources*, 16(2), 402–414. <https://doi.org/10.1111/1755-0998.12459>

908 Tang, K.-H., Tang, Y. J., & Blankenship, R. E. (2011). Carbon Metabolic Pathways in Phototrophic  
909 Bacteria and Their Broader Evolutionary Implications. *Frontiers in Microbiology*, 2.  
910 <https://doi.org/10.3389/fmicb.2011.00165>

911 Thormann, M. N. (2006). Diversity and function of fungi in peatlands: A carbon cycling perspective.  
912 *Canadian Journal of Soil Science*, 86(Special Issue), 281–293. [https://doi.org/10.4141/S05-](https://doi.org/10.4141/S05-082)  
913 082

914 Tian, W., Wang, H., Xiang, X., Wang, R., & Xu, Y. (2019). Structural Variations of Bacterial Community  
915 Driven by Sphagnum Microhabitat Differentiation in a Subalpine Peatland. *Frontiers in*  
916 *Microbiology*, *10*. <https://doi.org/10.3389/fmicb.2019.01661>

917 Turetsky, M. R. (2003). The Role of Bryophytes in Carbon and Nitrogen Cycling. *The Bryologist*,  
918 *106*(3), 395–409. JSTOR.

919 van Breemen, N. (1995). How Sphagnum bogs down other plants. *Trends in Ecology & Evolution*,  
920 *10*(7), 270–275. [https://doi.org/10.1016/0169-5347\(95\)90007-1](https://doi.org/10.1016/0169-5347(95)90007-1)

921 Wang, Y., & Qian, P.-Y. (2009). Conservative Fragments in Bacterial 16S rRNA Genes and Primer  
922 Design for 16S Ribosomal DNA Amplicons in Metagenomic Studies. *PLOS ONE*, *4*(10), e7401.  
923 <https://doi.org/10.1371/journal.pone.0007401>

924 Ward, B. A., & Follows, M. J. (2016). Marine mixotrophy increases trophic transfer efficiency, mean  
925 organism size, and vertical carbon flux. *Proceedings of the National Academy of Sciences*,  
926 *113*(11), 2958–2963. <https://doi.org/10.1073/pnas.1517118113>

927 Weisse, T., Müller, H., Pinto-Coelho, R. M., Schweizer, A., Springmann, D., & Baldringer, G. (1990).  
928 Response of the microbial loop to the phytoplankton spring bloom in a large prealpine lake.  
929 *Limnology and Oceanography*, *35*(4), 781–794. <https://doi.org/10.4319/lo.1990.35.4.0781>

930 Wilken, S., Huisman, J., Naus-Wiezer, S., & Donk, E. V. (2013). Mixotrophic organisms become more  
931 heterotrophic with rising temperature. *Ecology Letters*, *16*(2), 225–233.  
932 <https://doi.org/10.1111/ele.12033>

933 Worden, A. Z., Follows, M. J., Giovannoni, S. J., Wilken, S., Zimmerman, A. E., & Keeling, P. J. (2015).  
934 Rethinking the marine carbon cycle: Factoring in the multifarious lifestyles of microbes.  
935 *Science*, *347*(6223). <https://doi.org/10.1126/science.1257594>

936 Wyatt, K. H., Bange, J. S., Fitzgibbon, A. S., Bernot, M. J., & Rober, A. R. (2014). Nutrients and  
937 temperature interact to regulate algae and heterotrophic bacteria in an Alaskan poor fen  
938 peatland. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(3), 447–453.  
939 <https://doi.org/10.1139/cjfas-2014-0425>

940 Wyatt, K. H., & Turetsky, M. R. (2015). Algae alleviate carbon limitation of heterotrophic bacteria in a  
941 boreal peatland. *Journal of Ecology*, *103*(5), 1165–1171. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2745.12455)  
942 [2745.12455](https://doi.org/10.1111/1365-2745.12455)

943 Wyatt, K. H., Turetsky, M. R., Rober, A. R., Giroldo, D., Kane, E. S., & Stevenson, R. J. (2012).  
944 Contributions of algae to GPP and DOC production in an Alaskan fen: effects of historical  
945 water table manipulations on ecosystem responses to a natural flood. *Oecologia*, *169*(3),  
946 821–832. <https://doi.org/10.1007/s00442-011-2233-4>

947 Yu, Z. C. (2012). Northern peatland carbon stocks and dynamics: a review. *Biogeosciences*, *9*(10),  
948 4071–4085. <https://doi.org/10.5194/bg-9-4071-2012>

949 Yurkov, V., Gad'on, N., & Drews, G. (1993). The major part of polar carotenoids of the aerobic  
950 bacteria *Roseococcus thiosulfatophilus* RB3 and *Erythromicrobium ramosum* E5 is not bound  
951 to the bacteriochlorophyll a-complexes of the photosynthetic apparatus. *Archives of*  
952 *Microbiology*, *160*(5). <https://doi.org/10.1007/BF00252223>

953 Yvon-Durocher, G., Allen, A. P., Cellamare, M., Dossena, M., Gaston, K. J., Leitao, M., Montoya, J. M.,  
954 Reuman, D. C., Woodward, G., & Trimmer, M. (2015). Five Years of Experimental Warming  
955 Increases the Biodiversity and Productivity of Phytoplankton. *PLOS Biology*, *13*(12),  
956 e1002324. <https://doi.org/10.1371/journal.pbio.1002324>

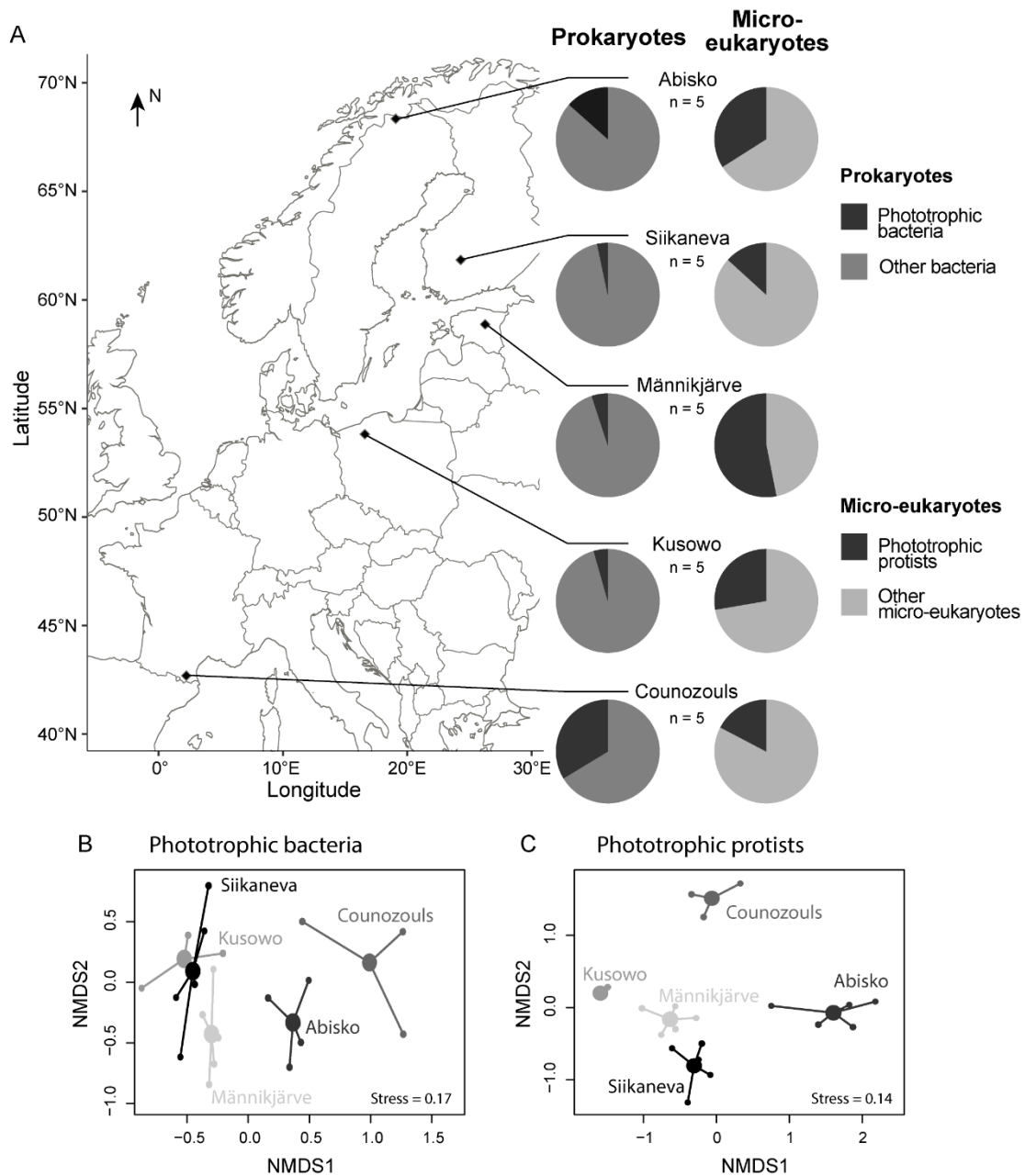
957 Zancan, S., Trevisan, R., & Paoletti, M. G. (2006). Soil algae composition under different agro-  
958 ecosystems in North-Eastern Italy. *Agriculture, Ecosystems & Environment*, *112*(1), 1–12.  
959 <https://doi.org/10.1016/j.agee.2005.06.018>

960 Zeng, Y., Feng, F., Medova, H., Dean, J., & Kobli ek, M. (2014). Functional type 2 photosynthetic  
961 reaction centers found in the rare bacterial phylum Gemmatimonadetes. *Proceedings of the*  
962 *National Academy of Sciences*, *111*(21), 7795–7800.  
963 <https://doi.org/10.1073/pnas.1400295111>

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965 **FIGURES**

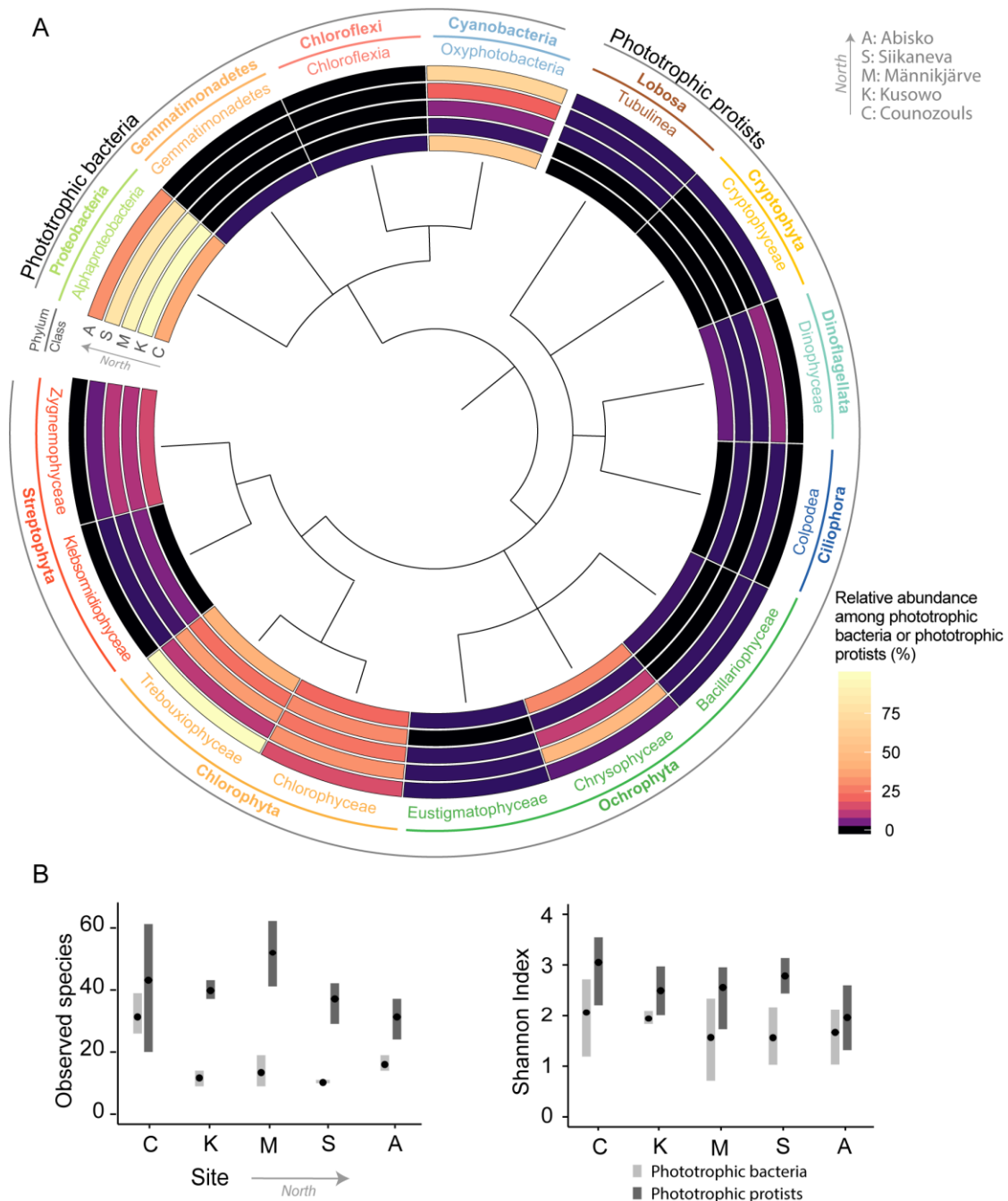
966 **Fig. 1:** Geographic locations of the five European peatlands and structure of microbial prokaryotic and  
 967 eukaryotic communities **(A)**. NMDS of the communities of phototrophic bacteria **(B)** and phototrophic  
 968 protists based on phototrophic OTUs **(C)**.



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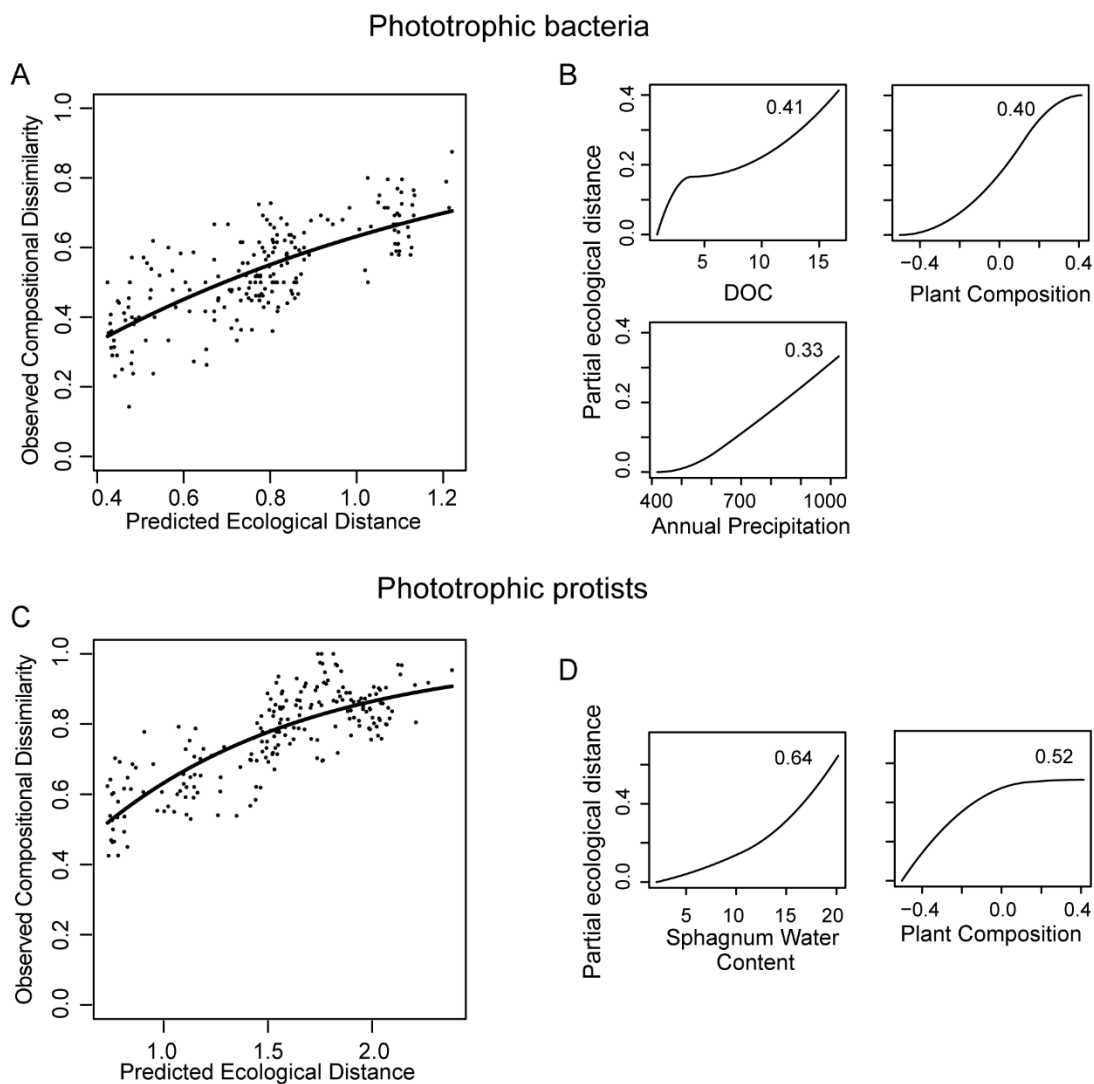


970 **Fig. 2:** Phylogenetic tree, relative abundance (A), and diversity (B) of the phototrophic OTUs identified  
 971 in the five peatland sites along the latitudinal gradient. Phototrophic OTUs include endosymbiotic  
 972 mixotrophs (e.g., *Hyalosphenia papilio*, Lobosa). Relative abundance of phototrophic OTUs is  
 973 calculated as a percentage of total phototrophic bacteria or total phototrophic protists. Alpha diversity  
 974 metrics include observed richness (OTU richness) and Shannon diversity index for both phototrophic  
 975 bacteria (light grey) and protists (dark grey). Bars range between the minimum and maximum values  
 976 (n = 5 replicates), while points represent the mean value in each site.



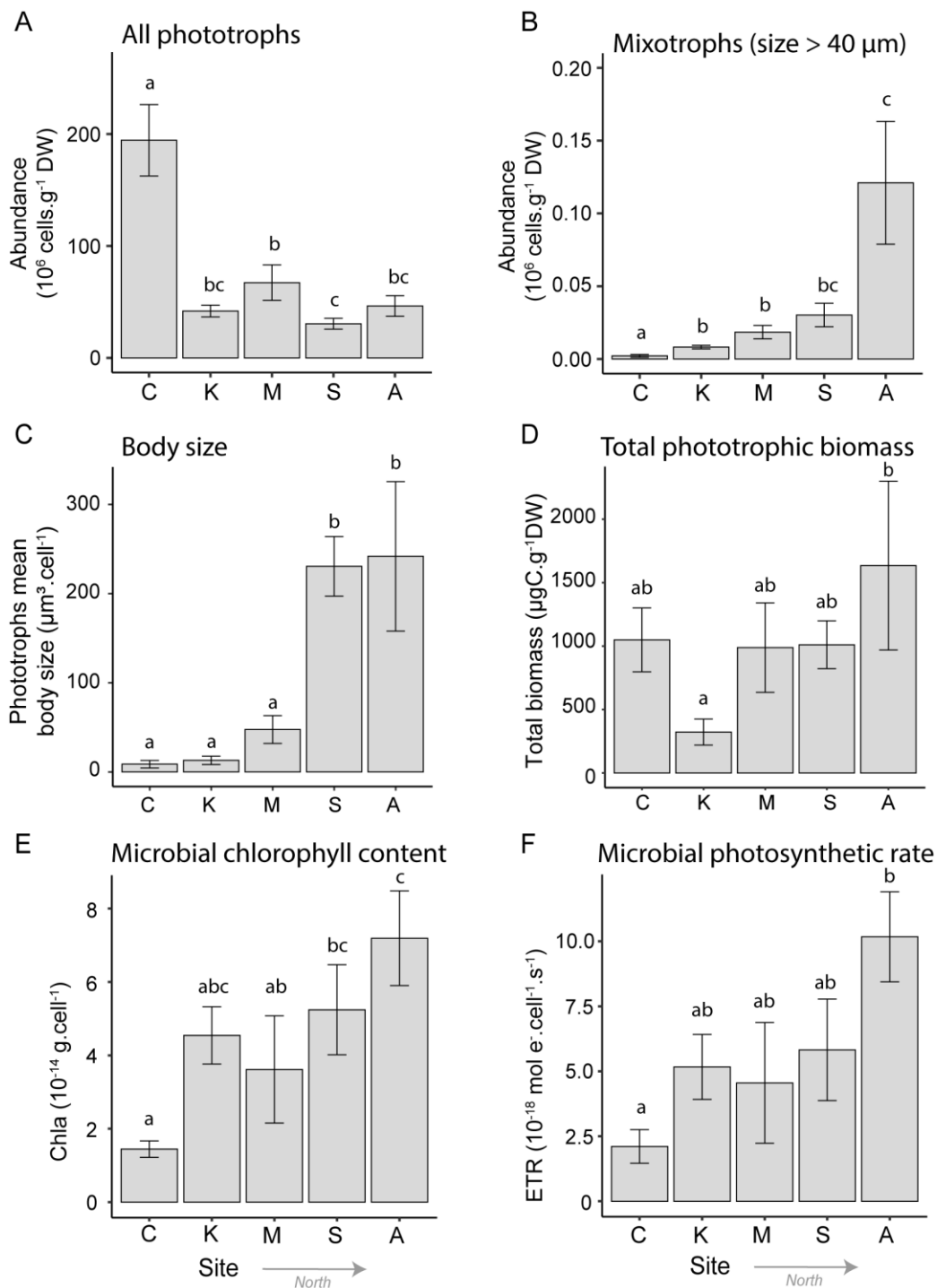
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978 **Fig. 3:** Generalised dissimilarity modelling and taxonomic turnover along environmental gradients.  
 979 Relationship between compositional dissimilarity between site pairs (species turnover or beta-  
 980 diversity) and their predicted environmental dissimilarity, for phototrophic bacteria communities **(A)**,  
 981 and for phototrophic protists communities **(C)**. Partial regression fits (Model-fitted-I-splines) for factors  
 982 significantly associated with phototrophic bacteria species turnover **(B)**, and phototrophic protist  
 983 species turnover **(D)**. Factors identified with a significant effect on species turnover were Plant  
 984 composition, *Sphagnum* Water Content, Dissolved Organic Carbon in *Sphagnum*-extractable water  
 985 (DOC) and Annual precipitation. The maximum height (inset number) reached by the I-spline curve  
 986 indicates the relative importance of that variable in explaining beta-diversity, keeping all other factors  
 987 constant.



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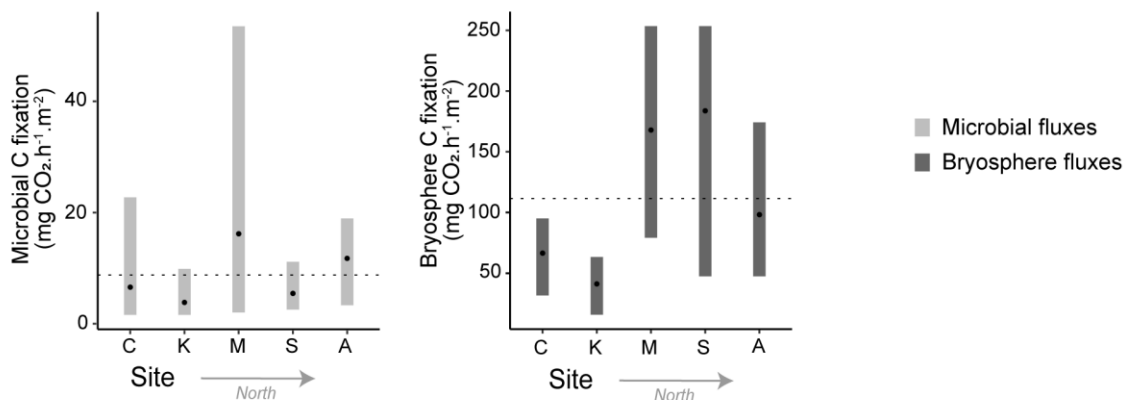
989 **Fig. 4:** Abundance of all phototrophs **(A)** and large mixotrophs (body size > 40  $\mu\text{m}$ ) **(B)** in the five  
 990 peatlands. Community-weighted mean body size of phototrophic microbes **(C)** and total phototrophic  
 991 biomass **(D)** in the five peatlands. Chlorophyll *a* cellular content of phototrophs in the five peatlands  
 992 **(E)**. Photosynthetic rates (electron transport rate -ETR- per cell) of phototrophs in the five peatlands  
 993 **(F)**. Error bars present standard error (n = 5 replicates). Significant differences ( $P < 0.05$ ) are indicated  
 994 by different letters above bars. C: Counozouls; K: Kusowo; M: Männikjärve; S: Siikaneva; A: Abisko.



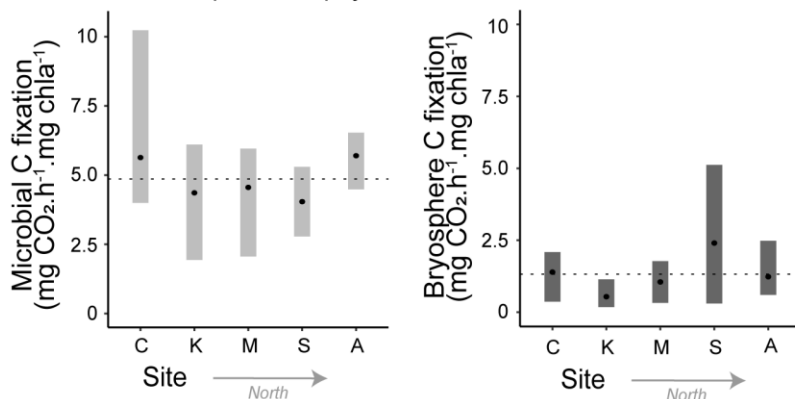
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996 **Fig. 5:** Microbial (light grey) and bryosphere (dark grey) C fixation rates, expressed per surface unit **(A)**  
 997 or normalised by the chlorophyll *a* content **(B)**; and contribution of microorganisms to bryosphere C  
 998 fixation **(C)** in the five peatlands. Bars range between minimum and maximum values (n = 5 replicates).  
 999 Points represent the mean values at each site, while the dotted line in panel **(C)** represent the mean  
 1000 values across sites. C: Counozouls; K: Kusowo; M: Männikjärve; S: Siikaneva; A: Abisko.

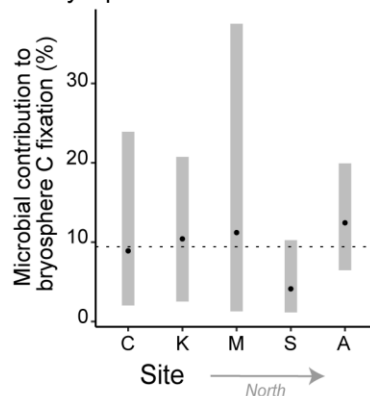
**A** Carbon fluxes per surface unit



**B** Carbon fluxes per chlorophyll content

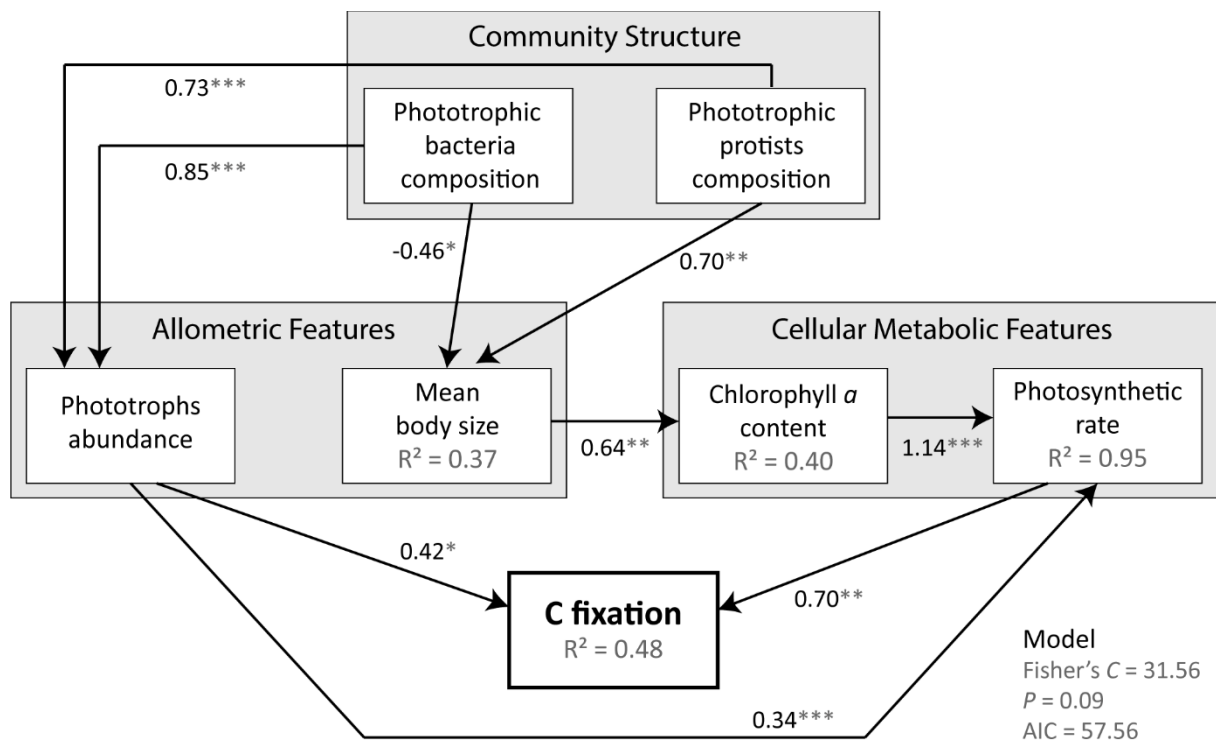


**C** Microbial contribution to bryosphere fluxes



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1002 **Fig. 6:** Structural equation model (SEM) of the correlations between the structure of phototrophic  
 1003 microbial communities, their allometric and metabolic features and microbial C fixation. Numbers in  
 1004 the boxes indicate the percentage of variance explained by the model (adjusted R-squared), while  
 1005 numbers along the arrows indicate the weight of the path relationship (\*  $0.01 < P < 0.05$ ; \*\*  
 1006  $0.001 < P < 0.01$ ; \*\*\*  $P < 0.001$ ).  
 1007



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