Predicting the structure and functions of peatland microbial communities from *Sphagnum* phylogeny, anatomical and morphological traits and metabolites

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Abstract

1. *Sphagnum* mosses are keystone species in northern peatlands. Notably, they play an important role in peatland carbon (C) cycling by regulating the composition and activity of microbial communities. However, it remains unclear whether information on *Sphagnum* phylogeny and/or traits-based composition (*i.e.* anatomical and morphological traits and metabolites) can be used to predict the structure of microbial communities and their functioning. Here we evaluated whether *Sphagnum* phylogeny and traits predict additional variation in peatland microbial community composition and functioning beyond what would be predicted from environmental characteristics (*i.e.* climatic and edaphic conditions).
2. We collected *Sphagnum* and microbial data from five European peatlands distributed along a latitudinal gradient from northern Sweden to southern France. This allowed us to assess *Sphagnum* anatomical and morphological traits and metabolites at different sites along changing environmental conditions. Using structural equation modelling (SEM) and phylogenetic distance analyses, we investigated the role of *Sphagnum* traits in shaping microbial community composition and functioning along with environmental conditions.
3. We show that microbial community composition and traits varied independently from both *Sphagnum* phylogeny and the latitudinal gradient. Specifically, the addition of *Sphagnum* traits to climatic and edaphic variables to the SEM allowed it to explain a larger proportion of the explained variance (R^2). This observation was most apparent for the biomass of decomposers (+42%) and phototrophs (+19%), as well as for growth yield microbial traits (+10%). As such, that *Sphagnum* metabolites were important drivers for microbial community structure and traits, while *Sphagnum* anatomical and morphological traits were poor predictors.

4. *Synthesis*. Our results highlight that *Sphagnum* metabolites are more to influence peatland microbial food web structure and functioning than *Sphagnum* anatomical and morphological traits. We provide further evidence that measurements of the plant metabolome, when combined with classical functional traits, improve our understanding of how the plants interact with their associated microbiomes.

Key-words: Functional traits, Latitudinal gradient, Metabolomics, Microbial traits, Peatlands, Plant and microbial communities, Plant–soil (below- ground) interactions, *Sphagnum*

Introduction

Soil microbial communities are highly diverse and make a significant contribution to many critical ecosystem functions (Crowther et al., 2019), such as the decomposition of plant litter (Geisen, 2020; Schlesinger & Andrews, 2000; Singh et al., 2010), nutrient cycling (Gui et al., 2017), and the mineralization and stabilization of soil organic matter (Liang et al., 2017, 2019). Moreover, soil microorganisms are interconnected with plants. By aiding plant nutrient acquisition (Averill et al., 2019) and drought resistance (Mariotte et al., 2015), soil microorganisms play a key role in shaping plant productivity and community dynamics (Mommer et al., 2018; Wardle et al., 2004). Plants, in turn, determine the composition of soil communities by regulating surface soil temperature and hydrology, as well as the chemical signature of organic carbon inputs (litter) and rhizodeposits (Bardgett & Wardle, 2010).

Biotic and abiotic factors influence the composition of soil microbial communities. Climatic (*e.g.* temperature, precipitation) and edaphic conditions (*e.g.* soil pH, moisture) are often seen as important determinants of microbial communities (Borowik & Wyszkowska, 2016; Singh et al., 2009; Wang et al., 2020) yet they cannot completely explain the full variation observed within microbial communities (De Gruyter et al., 2020). This suggests that biotic interactions also play an important role in shaping microbial communities (Geisen, 2020). Trophic and non-trophic (*e.g.* competition) interactions among microorganisms are important, but often neglected (Gralka et al., 2020). Recently, plant species identity (Burns et al., 2015), plant phylogeny (Barberán et al., 2015) and plant community composition (de Vries et al., 2012; Robroek et al., 2015) have also been identified as important drivers of microbial communities. However, disparity remains once individual plant leaf and root traits are taken into account (Leff et al., 2018), suggesting that plant traits are poor predictors of microbial communities and microbial processes (see Sweeney et al., 2020). Alternatively, the effect of plant species identity and/or community composition on microbial communities may mostly rely on chemical interactions between plant and soil

79 microbes (van Dam & Bouwmeester, 2016). Plants produce a plethora of biochemicals, and can release
80 over a hundred different metabolites in their surroundings that can attract, deter, or even kill
81 belowground microbes (Fernandez et al., 2016; Hamard et al., 2019; Hu et al., 2018; Pinton et al., 2001).
82 Elucidating which plant characteristics (phylogeny, morphological and anatomical traits and/or
83 metabolites) govern microbial communities, particularly in addition to microbial interactions and climatic
84 and edaphic conditions, is thus urgently needed to predict the structure of microbial communities, their
85 functioning and subsequent ramifications for biogeochemical cycles (Bardgett & Wardle, 2010).

86 We address this knowledge gap by examining the understudied linkages between peat mosses
87 (*i.e. Sphagnum* moss) and their associated microbiome. *Sphagnum*-dominated peatlands store more
88 carbon (C) than any other terrestrial ecosystem (Nichols & Peteet, 2019). Carbon accumulation in
89 *Sphagnum*-peatlands results from cold, acidic, nutrient-poor and water-saturated conditions that have
90 hindered microbial decomposition of litter over millennia (Rydin & Jeglum, 2006). *Sphagnum* mosses also
91 facilitate their own growth by creating unfavorable conditions for vascular plants, generating recalcitrant
92 litter and changing physical and chemical properties of the soil (Turetsky, 2003; van Breemen, 1995). As
93 *Sphagnum* do not possess roots, the leaf-associated microbiome comprises crucial functions, such as
94 defenses against pathogen and additional nutrient supply for *Sphagnum* growth and development (Opelt,
95 et al., 2007b). The association between *Sphagnum* moss and its microbiome, *i.e.* the bryosphere (*sensu*
96 Lindo & Gonzalez, (2010)), plays a key role in peatland C dynamics. These *Sphagnum*-associated microbial
97 communities include a core detrital network for C and nutrient cycling (Gilbert et al., 1998; Jassey et al.,
98 2015; Lindo & Gonzalez, 2010). Unique anatomical and morphological traits of *Sphagnum*, especially the
99 cell structure of leaves - with one layer of photosynthetically active cells (chlorocystes) and dead, water-
100 filled hyaline cells, create consistent microenvironments for the microbial communities (Bragina et al.,
101 2012a). Large hyaline cells can serve as less acidic 'oases' for microorganisms in the otherwise acidic
102 peatland pore water (Kostka et al., 2016). *Sphagnum* also actively excretes bioactive metabolites (*i.e.*

biochemicals) to their surroundings such as polyphenols (Rasmussen et al., 1995a; Rasmussen et al., 1995b; Rudolph & Samland, 1985; Schellekens et al., 2015), flavonoids (Sytiuk et al., 2020), carbohydrates (Hájek et al., 2011; Painter, 1991; Tetemadze et al., 2018; van Breemen, 1995), and tannins (Sytiuk et al., 2020; Verhoeven & Liefveld, 1997), that have been related to the functioning of peatlands (Verhoeven & Liefveld, 1997). Many of these metabolites show antimicrobial properties (Fudyma et al., 2019). For example, *Sphagnum* phenolics have been suggested to reduce vascular plant's mycorrhization (Binet et al. 2017; Chiapusio et al., 2018), and inhibit bacterial growth (Mellegård et al., 2009), decomposition (Freeman et al., 2001; Verhoeven & Liefveld, 1997; Verhoeven & Toth, 1995) and microbial respiration (Hamard et al., 2019). As *Sphagnum* species engineer their environment (van Breemen, 1995; Bengtsson et al., 2016; Bengtsson et al., 2018), both *Sphagnum* anatomical/morphological and biochemical traits may be expected to steer the structure and function of peatland microbial communities. A better identification and comprehension of these drivers are crucial for predicting the composition of the microbial community and its functioning in peatlands.

Here, we explore how and to what extent *Sphagnum* phylogeny, anatomical and morphological traits and metabolites drive the spatial variability of microbial community composition and functioning. To do so, we conducted an observational study in five European *Sphagnum*-dominated peatlands representing a wide range of climatic and edaphic conditions. Because *Sphagnum* microbial community composition can vary across space (Mitchell et al., 2003; Robroek et al., 2021), and according to the variation of edaphic factors such as pH and nutrient richness (Bragina et al., 2013a; Jassey et al., 2014; Opelt et al., 2007a), we hypothesized that (1) microbial community composition and functional traits will show distinct patterns among the five peatlands. We expected (2) that geographical variation in microbial community composition and microbial traits is driven by climatic/edaphic conditions as well as *Sphagnum* anatomical and morphological traits and metabolites. In particular, we hypothesized that (3) *Sphagnum* traits will explain a fraction of variation in microbial community composition and microbial traits that is

not explained by climatic and edaphic conditions. Among *Sphagnum* traits, we predicted that (4) *Sphagnum* metabolites have a stronger effect in shaping microbial properties than anatomical and morphological traits, since metabolites are released into *Sphagnum* surroundings and can directly influence microbial community composition and/or microbial traits. Finally, as *Sphagnum* traits do not exclusively vary with climatic and edaphic conditions (Sytiuk et al., 2020), but also according to phylogeny (Laine et al., 2021), we hypothesized that (5) *Sphagnum* phylogeny is an important determinants of microbial properties, in addition to climatic and edaphic conditions and *Sphagnum* traits.

Material and methods

Sites, sampling design and sample collection

We selected five *Sphagnum*-dominated peatlands along a latitudinal gradient from northern Sweden to southern France to represent a wide range of edaphic and climate conditions (Table 1, Table S1, S3). In each site, a preliminary vegetation survey (see Table S2) allowed us to select five homogeneous plots (50 x 30 cm each; 5 plots x 5 sites = 25 plots in total) dominated by a single *Sphagnum* species: *S. warnstorfii* (France, FR), *S. magellanicum* (Poland, PL), *S. rubellum* (Estonia, EST), *S. papillosum* (Finland, FI) and *S. balticum* (Sweden, SE). Dominant *Sphagnum* species were site specific, potentially creating a confounding effect with climate/edaphic conditions. To overcome this issue, we measured phylogenetic differences among *Sphagnum* species at five sites, and found that *Sphagnum* phylogeny did not covary with climatic variation (*i.e.* mean annual temperature, $F_{1,3} = 0.15$, $P = 0.72$, Fig. S1). Despite the absence of phylogeny-climate covariation, it remains true that species identity and site variation were still potentially confounding. We thus quantified metabolite plasticity (*i.e.,* water-soluble phenols) of the five *Sphagnum* species using a reciprocal transplantation along the latitudinal gradient to determine whether *Sphagnum* metabolite production is more sensitive to environmental variability than to taxonomy. We found that the concentration of water-soluble phenols increased for all *Sphagnum* species along the latitudinal gradient (Fig S2a, b), and more importantly that the variance of water-soluble phenol concentrations within the same species at different temperatures was higher than between the different species at the same temperature (Fig. S2c). Together, these findings show that water-soluble phenol concentrations in *Sphagnum* tissues vary independently of taxonomy. However, other metabolites may depend on taxonomy. To exclude this potential, we used unpublished data (Jassey, Allard and Robroek, unpublished data) on *Sphagnum* metabolomic profiling from 56 European ombrotrophic peatlands (see sites in Robroek et al., 2017). A PCoA analysis revealed that that the metabolomic composition of *Sphagnum*

157 species was strongly determined by local and regional conditions (site effect, $P < 0.05$), rather than by
158 taxonomy (species effect, $P = 0.46$; Fig. S3). Altogether, these additional analyses demonstrate that a
159 potential confounding effect of species and site was not an important issue when referring to *Sphagnum*
160 metabolites. However, we acknowledge that anatomical and morphological traits are used to identify
161 *Sphagnum* moss to species (Isoviita, 1966), and that in our study anatomical and morphological traits
162 cannot be disentangled from *Sphagnum* taxonomy. We therefore advise caution when using these data
163 to predict microbial communities and microbial activities.

164 In each plot, 15-20 *Sphagnum* shoots were sampled around ten marked spots (ca. 250 g fresh
165 weight of *Sphagnum* per plot). This sampling design allowed us to obtain a composite sample,
166 representative of the entire plot. Upon sampling, the living top of the *Sphagnum* shoots (0-3 cm) were cut
167 immediately, pooled, homogenized and then dispatched for the different lab analyses. Approximately 10
168 g of *Sphagnum* shoots were fixed in 20 mL of glutaraldehyde (2% final concentration) and stored at 4°C in
169 the dark for microbial biomass/abundance measurements. Approximately 20 g were frozen and
170 lyophilized for fungal and biochemical analyses. Another 10 g were frozen for analyses of microbial
171 enzymatic activities. The remaining 10 g were stored at 4°C and used for analyses of *Sphagnum* anatomical
172 and morphological traits. We collected *Sphagnum* samples in every site within the same week in early-
173 July 2018.

174 Characterizing climate and site conditions

175 For each site, we extracted bioclimatic data from WorldClim v2 (Fick & Hijmans, 2017): mean annual
176 temperature, temperature seasonality, annual precipitation, and precipitation seasonality averaged over
177 the 1960-2018 period (Table S1). Water-table depth (WTD) and pH were measured directly in the field
178 using a ruler and a portable multimeter Elmetron CX742, respectively (Table 1). Water-extractable organic
179 matter (WEOM) was extracted from the *Sphagnum* shoots (0-3 cm height) collected at the five sites

according to Jassey et al. (2018) (Table S3). Briefly, *Sphagnum* shoots were soaked in 30 mL of demineralized water and then shaken for 90 min at 150 rpm. *Sphagnum* shoots were then dried at 60°C for 48 hours and weighted to obtain dry mass (mg/g DW). The water extract was filtered with Whatman filter (1 µm pore size) and several physical-chemical parameters were analyzed: a TOC analyser (Shimadzu TOC-L) was used to quantify dissolved organic carbon, nitrogen and phosphate (WEOC, WEON and WEOP respectively). To measure dissolved organic matter aromatic content and molecular weight (WEOCq), we used absorbance measurements between 250 and 660 nm (15 wavelengths in total) in 200 µL sample aliquots in 96-well quartz microplate using a BioTek SynergyMX spectrofluorometer (Jaffrain et al., 2007). For a blank, we used demineralized water filtered through Whatman filter to correct our values for the potential C released from the filter. Spectral slopes ($S_{250-660}$, nm^{-1}) were calculated using linear least squares regressions with Ln-transformed absorptions. High $S_{250-660}$ values indicate low molecular weight material (Hansen et al., 2016).

We further performed a vegetation survey using two high-resolution images (25 x 15 cm) of each plot, according to Buttler et al. (2015). On each picture, we laid a grid of 336 points and identified species overlaying the grid intersects. This technique did not assess vertical biomass and could underestimate the relative abundance of certain species. However, the bias was alike in each plot, making species frequencies comparable among sites.

Sphagnum anatomical and morphological traits

We characterized a suite of four anatomical and morphological *Sphagnum* traits determining the capacity of *Sphagnum* moss to provide shelter for microbial communities following Jassey & Signarbieux (2019): volume of the capitulum (height x diameter of capitulum), water-holding capacity of the capitulum and shoot, number of hyaline cells per leaf area (*i.e.* dead cells storing water), the surface area of hyaline cell (length x width) and width of chlorocystes (photosynthetic cells surrounding hyaline cells). In total, 125

individuals (25 per site) were randomly collected to estimate the volume of the capitula (mm^3) by measuring their height and diameter using a precision ruler. Then, we used the same samples to quantify the net water content of the capitula and stem (first cm) at water saturation. Capitula and stems were submerged in water until their maximum water retention capacity was reached. Excess water was removed by allowing water to drain naturally for two minutes. Then, individual capitula and stems were weighed as water-saturated and subsequently dried for three days at 60°C. The net water content at water saturation of each individual was expressed in grams of water per gram of dry mass (g H_2O/g DW). For anatomical analyses, we carefully deconstructed five *Sphagnum* capitula in each plot (in total, 125 capitula) to isolate *Sphagnum* leaves. Then, we pooled all *Sphagnum* leaves, homogenized, and took three leaves from that pool to prepare microscope slides from each plot (375 leaves analyzed in total). We quantified the number of hyaline cells per leaf area (number of hyaline cells per mm^2), their surface (μm^2), as well as the width of chlorocystes (µm), using a light microscope connected to a camera (LEICA ICC50 HD) and the size analytic tools (LEICA suite software).

Sphagnum metabolic fingerprint

We assessed the metabolic fingerprint of *Sphagnum* mosses using two different approaches. First, we quantified a set of nine moss metabolites that can influence microbes. The different extractions pathways used for quantifying the various *Sphagnum* metabolites are detailed in Sytiuk et al. (2020). Briefly, *Sphagnum* mosses were frozen, lyophilized, ground and stored at -20°C prior to biochemical analysis. Then, we used (i) a 99.9% methanol extraction for quantifying *Sphagnum* pigments (chlorophyll a, b and total carotenoids), (ii) a 50% methanol extraction for quantifying total polyphenols, flavonoids, tannins and carbohydrates, (iii) a water extraction for quantifying water-extractable total polyphenols, (iv) a sulfosalicylic acid extraction for quantifying proline and (v) a dosage of proteins with bovine serum albumin (BSA). All metabolites were quantified using spectroscopy at different wavelengths. Secondly, we

characterized the polysaccharides, aromatic and aliphatics content of *Sphagnum* mosses using Fourier Transform Infrared Spectroscopy (FT–IR-ATR; (Hodgkins et al., 2014). 30 mg freeze-dried and ground *Sphagnum* was placed directly on a germanium crystal and pressed down with a flat tip to improve distribution and contact. Spectra were acquired by 64 scans at a 2 cm^{-1} resolution over the range 4000–600 cm^{-1}. All spectra were corrected for water vapor, CO_2 and for differences in depth of beam penetration at different wavelengths (ATR correction; Opus software). All spectra were then normalized. For each spectrum, normalization involved (i) a subtraction of the minimum absorption value applied to the whole spectrum followed by (ii) a multiplication - also applied on the whole spectra - to obtain a spectral maximal absorbance value of 1 for each *Sphagnum* sample. Six main absorption peaks were used as an indicator of *Sphagnum* polysaccharides, aromatics and aliphatics: 1) the 1064 cm^{-1} region (combination of C–O stretching and O-H deformation) is associated to polysaccharides; 2) the 1515 cm^{-1} region (C=C; aromatic compounds) is assigned to lignin/phenolic backbone; 3) the 1610 cm^{-1} region (C=C streching; aromatic compounds and/or asymmetric C-O stretch in COO-) is associated to lignin and other aromatics, or aromatic or aliphatic carboxylates; 4) the 1724 cm^{-1}-1710 cm^{-1} region (C=O stretch of COOH or COOR) corresponds to free organic acids, carboxylic acids, aromatic esters; 5) 2850 cm^{-1} region (symmetric CH_2) is associated to aliphatics; and 6) 2920 cm^{-1} region (antisymmetric CH_2) is associated to aliphatics. We used the ratio between the relative intensities of FT–IR absorption bands, where 1610 cm^{-1} region was used as denominator due to its highly recalcitrant nature, in order to evaluate *Sphagnum* fingerprints and their degree of degradability.

Microbial abundances and biomass

Microbial consumers (testate amoebae, ciliates, rotifers and nematodes), phototrophs (microalgae and cyanobacteria), and decomposers (fungi and bacteria) were extracted from *Sphagnum* following Jassey et al. (2011a). For bacterial counts, a 1-mL sub-sample was stained with SYBR Green (0.1x final

249 concentration) and incubated in the dark for 15 minutes. Then the sub-samples were run at a speed of 2
250 µL s^{-1} at a count rate not exceeding 1000 events s^{-1} in a cytometer (Guava® easyCyte). Epifluorescence
251 microscopy was used to determine the size of bacteria: 1 mL sub-samples were stained with DAPI (4,6-
252 diamino-2-phenylindole; 3 µg mL-1 final concentration), incubated in the dark for 15 minutes, filtered on
253 0.2 µm black membrane filters and examined by fluorescence microscopy at 1000x magnification.
254 Bacterial sizes were determined manually under the microscope following Jassey et al. (2011a). The
255 abundance of phototrophs and microbial consumers, as well as their identification to species level when
256 possible, was carried out using a 3-mL subsample and inverted microscopy (×400, Utermöhl method). The
257 abundance of bacteria, phototrophic and consumer species was then converted into biovolume (μm^3),
258 calculated based on geometrical shapes using dimensions measured under the microscope (length or
259 diameter; width, and height). Biovolumes were converted to biomass (µgC) using conversion factors as
260 given in Gilbert et al. (1998). The biomass data were expressed in micrograms of C per gram of *Sphagnum*
261 dry mass (µg C g^{-1} DM). The biomass of fungi was quantified using ergosterol quantification according to
262 the standard extraction procedure previously described in Gessner et al. (1991). Briefly, 50 mg of
263 lyophilized *Sphagnum* were incubated in glass vials with 5 mL of potassium hydroxide methanol (8 g L^{-1})
264 for 24h at 4°C. A control vial containing 100 µl of a 200-µg mL^{-1} solution of ergosterol was also incubated
265 in the same conditions to take into account the yield of the extraction. All vials were then heated at 80°C
266 for 30 min. After cooling, 1 mL of hydrochloric acid (0.65 mol L^{-1}) was added in each sample. 3mL of each
267 sample were filtered on Oasis HLB cartridges (60 mg sorbent, 30 µm particle size). Cartridges were
268 previously and successively conditioned with 1 mL of methanol and 1 mL of a mixture of 15%v methanol,
269 70%v potassium hydroxide methanol (8 g L^{-1}) and 15%v hydrochloric acid (0.65 mol L^{-1}). After sample
270 filtration, cartridges were washed with 1 mL of 5%v methanol diluted in autoclaved milli-Q water.
271 Cartridges were then dried under vacuum (-5 bar) for 1 h, after what they were eluted with 4*350 µl of
272 isopropanol. The concentration of ergosterol in eluates was assessed by HPLC, using a calibration curve.

The yield of the extraction was assessed by comparing the measured and theoretical concentration of ergosterol in the control vial. Ergosterol concentrations in samples were corrected from the yield of the reaction and were expressed in µg of ergosterol per g of *Sphagnum* dry weight.

Microbial traits

Following the revised life history theory for microbial traits (Malik et al., 2020), we collected microbial traits classified into three main microbial life history strategies: growth yield, resource acquisition and stress tolerance. We quantified nine traits in the growth yield strategy: biomass per cell, biovolume per cell, body size (length and width), the quantum yield of photosystem II for phototrophs, photosynthetic pigments content per cell for phototrophs, growth rate, reproduction rate, and respiration rate per cell. We classified 14 traits in the resource acquisition strategy: nine microbial enzyme activities, C uptake by phototrophs, predation rates, nitrogen fixation, methanotrophy and motility. Finally, three traits were assigned to the stress tolerance strategy: morphology, response to temperature increase, and tolerance to desiccation. A total of 26 microbial traits were either directly quantified or acquired from the literature (see Supplementary method on microbial traits for more details).

To describe the functional trait space in each site, we calculated community weighted means (CWM) of each trait calculated as the presence/absence weighted means of species trait values using the FD *R* package (Laliberté et al., 2015). We then created a functional distance matrix by applying Gower's distance on each pair of species described by their traits, and then computed a Principal Coordinate Analysis (PCoA) on it. Gower's distance allows mixing of different types of traits (*i.e.* qualitative and quantitative traits) while giving them equal weights. Then, the two first axes of the PCoA were selected as synthetic CWMs summarizing the microbial functional space in each site.

Numerical analyses

All statistical analyses were performed in *R* 3.5.3 (R Core Team, 2019) using packages, as specified below. Linear mixed effects models were used to assess the *Sphagnum* taxonomy effect (fixed effect) on the microbial biomass of each trophic group, CWM of each microbial trait and *Sphagnum* traits. The models were fitted with plot nested within *Sphagnum* taxonomy as a random effect on the intercept (Pinheiro & Bates, 2000). Tukey's multiple comparison test was used for *post hoc* analyses of differences among the levels of the fixed effects in the final model. Normality and homogeneity assumptions of the data, as well as model residuals, were assessed using a Shapiro test and diagnostic plots. Log_{10}-transformations of the data were applied if needed in order to meet these assumptions. To represent differences in microbial community composition, microbial trait composition and *Sphagnum* traits, we performed principal coordinate analysis (PCoA) using Gower's distance that allowed mixing of different types of data (*i.e.* qualitative and quantitative traits) while giving them equal weights. A standardization (*Sphagnum* anatomical and morphological traits and metabolites) or Hellinger transformation (microbial community composition and microbial traits) was applied on the matrices beforehand (Legendre & Legendre, 2012). We used Spearman correlations to test the potential relationships between microbial community composition, CWM of microbial traits and *Sphagnum* traits and/or climatic and edaphic factors.

We assessed the effect of *Sphagnum* phylogenetic distance on microbial biomass and microbial trait composition under the Brownian Motion model (BM). BM predicts that the variance in microbial properties increases at a constant rate proportionate to the evolutionary distance among *Sphagnum* species, with more closely related species having more similar values for microbial properties, and indicating that the variable has a phylogenetic signal (Felsenstein, 1985). We used Blomberg's K index (Münkemüller et al., 2012) to test for a *Sphagnum* phylogenetic signal among microbial variables with randomization and 1000 permutations (Table S4).

To assess whether differences in *Sphagnum* anatomical and morphological traits and metabolites predicted variation in microbial community composition and microbial traits beyond the explanatory power of climatic and edaphic conditions (Leff et al., 2018), we built a set of path diagrams subjected to structural equation modelling (Grace et al., 2010, 2014). We compared the explanatory power of the models, assessed through adjusted R^2 values and Akaike Information Criterion (AIC), by framing four types of models (Fig. 1). First, we tested the effects of climatic and edaphic conditions on each (hereafter 'single' SEM models) trophic group (*i.e.* the biomass of either decomposers, phototrophs, predators or the total microbial biomass) and microbial trait strategy (*i.e.* either growth yield, resource acquisition and stress tolerance strategies or the overall traits composition; Fig. 1a) separately. Second, we tested the effects of climatic and edaphic conditions on the interactions (hereafter 'interactions' SEM model) among/within microbial community composition and microbial trait strategies (Fig. 1b). Third, we tested the effect of *Sphagnum* anatomical and morphological traits and metabolites (*i.e. Sphagnum* traits; in addition to climatic and edaphic conditions as in the first model) on each trophic group and microbial trait strategy separately (Fig. 1c) and in interaction (Fig. 1d). The benefits gained (ΔR^2) by including *Sphagnum* anatomical and morphological traits and metabolites into the models were calculated as follows:

$$\Delta R^2 = (R^2_{SEM\ with\ Sphagnum\ traits} - R^2_{SEM\ without\ Sphagnum\ traits}) * 100\%$$

We further compared AIC values between models with and without *Sphagnum* traits to check for potential overfitting (Burnham & Anderson, 2004). In these models, we used annual precipitation and mean temperature of the wettest quarter as climate variables, selected beforehand using a principal component analysis (PCA) applied on all bioclimatic variables. For edaphic peatland conditions, we used *Sphagnum* water content and the first axis of a PCA applied on WEON, WEOC, WEOP and $S_{260\text{-}660}$. For microbial trait strategies, we used the first axis of three PCoAs applied on the CWM of traits of each trait strategy, respectively. The paths of the SEM were fitted as previously described for ANOVAs using *piecewiseSEM*

340 package (Lefcheck, 2016). We selected this approach as it allowed using the Shipley's test of d-separation
341 to assess whether direct or indirect paths are missing from the *a priori* mode. The adequacy of the model
342 was evaluated via several tests including non-significant *Fisher's C* statistic (P >0.05), and low Akaike
343 information criterion (AIC) (Grace et al., 2010).

344 We used two strategies to validate our SEM models and generate statistics of the models'
345 predictive power. The first strategy was inspired by 'null-model' analyses in ecology (Gotelli & Ulrich,
346 2012), and tests the assumption that the effects of *Sphagnum* traits in predicting microbial community
347 composition and microbial traits are not random and driven by changes in *Sphagnum* traits. To test this
348 assumption, we randomized *Sphagnum* trait matrices to break any structure in the data. We iteratively
349 and randomly shuffled the *Sphagnum* trait matrices ten times before running the SEM models. The second
350 strategy focused on the size of the data set as it can strongly influence SEM modelling (Grabowski & Porto,
351 2017; Grace et al., 2010). To do so, we iteratively reduced our entire data set by 20% by randomly
352 removing one replicate from the dataset. In other words, we retained four out of five replicates before
353 running the SEM models. We repeated this step five times, until all possible combinations were covered.
354 For each SEM model we extracted the data relative to the adequacy of the model (*Fisher's C* statistic and
355 *P*-value) and AIC values (see model outputs in Fig. S7 and Tables S11, S12). The sensitivity analyses were
356 performed on the most relevant SEM models, where the benefits gained (ΔR^2) by including *Sphagnum*
357 traits into the models was more that 10%: decomposers single, decomposers interactions, phototrophs
358 single, and yield single.

359

Results

Throughout this section we refer to changes in sites (see Table 1 for sites' acronyms), which nevertheless are confounded with *Sphagnum* species identity. Thus, we advise to check the Materials and methods section and Supplementary materials (Fig S1, S2, S3) where we demonstrate that a potential confounding effect of species and site was not an important issue.

Sphagnum morphological and anatomical traits and metabolites

PCoA analysis revealed that *Sphagnum* trait composition (anatomical and morphological traits and metabolites) differed among the five sites (Fig. 2a). Three distinct groups emerged from the first PCoA axis: a first group composed of *Sphagnum* from FI, a second group composed of EST and SE and a third group with FR and PL. On the second PCoA axis, there was a gradient ranging from FI to FR/PL and then SE/EST. This gradient was not related to any particular climatic and/or edaphic trend. Instead, it showed a clear trend as *Sphagnum* from FI, PL and FR had higher capitulum sizes, water holding-capacity and/or metabolites concentrations (Fig. S4, S5, Table S5), as compared to SE and EST. Specific *Sphagnum* anatomical and morphological traits and metabolites varied between five *Sphagnum* species from three phyla (Fig. 2b; Fig. S4, S5). We found that *Sphagnum* from FR and PL produced more total and water-soluble phenols, total flavonoids and tannins than SE and FI (Fig. 2b). However, *Sphagnum* from SE, FI and EST produced more polysaccharides, organic acids, symmetric and antisymmetric CH_2 than FR and PL. In terms of anatomical and morphological traits, *Sphagnum* sampled from PL and FI possessed higher capitulum diameter, height and volume than EST and FR. Water holding capacities, hyaline cell surface and chlorocyste width were highest for *Sphagnum* from FI and FR. Even though *Sphagnum* from EST had highest number of hyaline cells per leaf area, its surface of hyaline cells was smallest.

Microbial community composition and trait composition

Microbial community composition and microbial traits differed significantly among the five sites (Fig. 3; Fig. S6-S9, Tables S5), and similar to the *Sphagnum* traits composition, no particular climatic and/or edaphic trend was found neither in microbial community composition nor microbial traits (Fig. 3). The first PCoA axis showed three distinct groups of microbial community composition with FR and SE aside and a third group composed of PL, FI and EST (Fig. 3c). On the second axis, there was a clear separation between SE and the four other sites. Microbial trait composition differed markedly across the five sites (Fig. 3d). While no particular variation was observed on the second PCoA axis, sites were well separated along the first PCoA axis (Fig. 3d). Overall biomass differed with *Sphagnum* phylogeny. Specifically, the highest biomass of consumers and decomposers was observed in SE and FR (Fig. 3a, Fig. S6). Conversely, PL and EST were characterized by low biomass of most microbial groups (Fig. 3a, Fig. S6). For community weighted mean (CWM) microbial traits, we found that the microbial traits related to the growth yield strategy were the most abundant in FI and SE, and the least abundant in EST (Fig. 3b, Fig. S7). Microbial traits related to resource acquisition peaked in FI and EST, while stress tolerance traits were the most abundant in SE (Fig. 3b, Fig. S8, S9). Despite such differences in microbial biomass and CWMs of traits among sites, *Sphagnum* phylogenetic distances were weakly related to differences in microbial biomasses ($P > 0.1$ in most cases) and in microbial trait composition ($P > 0.1$ in all cases; Table S4). Only the biomass of flagellates ($K = 1.1$, $P = 0.03$; Table S4) was significantly related to *Sphagnum* phylogenetic distances.

Predictors of microbial community and microbial traits

Differences in microbial community composition and microbial traits were related to both climatic and edaphic conditions and *Sphagnum* traits (Fig. 4). As *Sphagnum* trait composition was also correlated with climatic and edaphic conditions (*i.e.* annual precipitation and WEOM chemistry, Fig. 4), we ran structural equation models with and without *Sphagnum* anatomical and morphological traits and metabolites to

tease apart the effects attributable to *Sphagnum* traits and metabolites on microbial properties (Fig. 5, Table S6-S10). Shifts in microbial community composition and microbial traits across *Sphagnum* species were correlated with multiple climatic and edaphic variables, which together explained 27%-86% of the variation of the biomass of decomposers, phototrophs and consumers, as well as of microbial trait composition (Table S6). When *Sphagnum* anatomical and morphological traits and metabolites were added to the SEM models, prediction accuracies for most microbial biomass and trait compositions increased by 42% (Fig. 5), notably for decomposer biomass (+42%), phototrophs (+19%) and traits related to growth yield (+10%). Rigorous sensitivity analyses on SEM models revealed that R^2 improvements provided by the addition of *Sphagnum* traits in SEMs were robust and without bias due to possible randomness in the estimations (Fig. S7, S11) or the size of the dataset (Fig. S7, Table S12). Our sensitivity analyses hence indicated that microbial properties can be reasonably predicted from *Sphagnum* traits, and most importantly, that such effects are complementary to environmental (*i.e.* climatic and edaphic conditions) variation.

More precisely, most *Sphagnum* metabolites were related to microbial biomasses and/or microbial trait strategies (Fig. 6). The biomass of cyanobacteria, some decomposers (*i.e.* fungi and bacteria) and rotifers was positively related to water-soluble phenolic compounds, whereas microalgae and testate amoebae tended to be negatively correlated to phenols (Fig. 6). *Sphagnum* anatomical and morphological traits, such as the width of chlorocystes and water-holding capacity, were positively correlated with the biomass of nematodes and some growth yield traits (*i.e.* respiration, biomass, biovolume) and some enzymes. However, methanotrophs were negatively correlated to the same *Sphagnum* traits. Most of the individual microbial traits, especially those related to growth yields (microbial pigments, respiration, size), were negatively correlated to water-soluble phenols, total tannins, phenols, proteins, carbohydrates and pigments while also being positively correlated to polysaccharides,

427 phenols/lignins, CH_2 compounds. Opposite trends were observed for some resource acquisition traits

428 (mostly enzymes; Fig. 6).

429

Discussion

Here we tested whether *Sphagnum* phylogeny, anatomical and morphological traits and metabolites are important determinants of peatland microbial community composition and functional traits. Contrary to our expectations which were based on earlier observations suggesting a high degree of similarity in microbial composition among closely related *Sphagnum* species (Bragina et al., 2013b; Bragina et al., 2012b; Putkinen et al., 2012), we found here that microbial community and trait composition did not vary with *Sphagnum* phylogenetic distance. Our findings may indicate that certain microbial taxa and traits are strongly related with particular *Sphagnum* anatomical and morphological traits and metabolites, while other microbial taxa and traits are more generalist and mostly influenced by environmental (climatic and edaphic) conditions. Hence, *Sphagnum* interspecific trait plasticity may drive microbial community composition and functional diversity in addition to climatic and local condition variables. Our results, however, need to be interpreted cautiously as *Sphagnum* species and sampling site co-varied in our study. Moreover, our observations were undertaken at a single date, thereby ignoring potential seasonality. Nevertheless, our study represents an important and necessary step in understanding which traits from diverse *Sphagnum* species are key in shaping the *Sphagnum* microbiome along an environmental gradient.

In contrast to peatland plant species richness and functional diversity (Robroek et al., 2017), no notable latitudinal trends, neither in microbial community composition nor trait composition, were observed. Instead, climatic (*i.e.* the mean temperature of the wettest quarter and annual precipitation) and edaphic (*i.e.* water table depth, *Sphagnum* water content, and nutrient availability) variables were identified as important drivers of microbial community and traits. This corroborates previous studies showing that global and local peatland conditions play deterministic roles in shaping microbial communities and functioning (Elliott et al., 2015; Jassey et al., 2014; Urbanová & Bárta, 2016). However, we show that *Sphagnum* traits, mostly metabolites, were as important as climatic and edaphic conditions

453 in driving microbial community composition and functioning (Fig. 4). Our analysis revealed that microbial
454 consumers, as well as growth yield and resource acquisition traits, generally decreased with frequent
455 rainfall, high *Sphagnum* water content, and low nutrient content. Phototrophs and decomposers,
456 however, showed opposite trends. In addition, *Sphagnum* traits were negatively correlated to
457 decomposers, but positively to growth yield and resource acquisition. While correlations between
458 microbial traits, *Sphagnum* traits and climatic and edaphic factors enabled us to assess the direction of
459 these relationships, the underlying mechanisms remain unknown, since here *Sphagnum* metabolites were
460 also driven by climatic and edaphic conditions. Using the SEM approach and taking into account the
461 response of *Sphagnum* traits to climatic and edaphic conditions, our multi-model comparisons revealed
462 that the addition of *Sphagnum* traits generally did increase the predictive power of SEMs, especially for
463 the biomass of decomposers, phototrophs, and growth yield traits, while avoiding overfitting the models.
464 This suggests that *Sphagnum* anatomical and morphological traits and metabolites are important
465 regulators of *Sphagnum*-microbial interactions.

466 Overall, *Sphagnum* anatomical and morphological traits were poor predictors of microbial
467 communities. Nevertheless, we found that the biomass of cyanobacteria, large consumers, such as
468 nematodes, and microbial traits related to growth yield (*i.e.* respiration, size and volume) and resource
469 acquisition (*i.e.* some extracellular enzymes) were positively correlated to *Sphagnum* species with high
470 capitulum size, and, hence, high water-holding capacities, and width of chlorocystes (Fig. 6). Water held
471 between leaves and hyaline cells of the capitulum provides a habitat for many microorganisms (Vitt,
472 2000), and allows them to move freely with water exchange between hyaline cells and adjacent
473 photosynthetic cells (Kostka et al., 2016). However, large *Sphagnum* species are known to maintain a more
474 stable water content under unfavorable conditions thanks to the high water-holding capacity traits of
475 their capitula (Jassey & Signarbieux, 2019). Consequently, our findings suggest that microbial communities
476 associated with *Sphagnum* species with high water-holding capacity are better protected from desiccation

than for those living in smaller *Sphagnum* species, while the hunting space for large consumers is less limited. Indeed, habitat-size is an important factor structuring microbial communities. For example, Sweeney et al (2020) found that increased root surface area improved opportunities for mycorrhizal fungi colonization in grasslands. Moreover, Delgado-Baquerizo et al. (2018) highlighted habitat-size as a crucial driver of soil bacterial biodiversity and functional diversity.

Comparative effects between *Sphagnum* anatomical and morphological traits and metabolites provide evidence that *Sphagnum* metabolites play a central role in structuring microbial communities and their traits. We found that the biomass of cyanobacteria, fungi, and bacteria, as well as a number of resource acquisition traits, such as extracellular enzymes, were positively correlated to many metabolites, including total carbohydrates, proteins, *Sphagnum* pigments, total phenols and/or tannins (Fig. 6). In contrast, the biomass of microalgae and nematodes, and most of microbial growth yield traits (*i.e.* microbial pigments, respiration, biomass, volume and size), were negatively correlated to *Sphagnum* metabolites (Fig. 6). Our findings suggest that *Sphagnum* metabolites have diverse effects on microbial communities and their traits, supporting observations that the degree of host specificity varies despite *Sphagnum* phylogenetic distances (Bragina et al., 2012b). The positive links between decomposers and resource acquisition traits (mostly enzyme activities), and *Sphagnum* pigments, proteins and carbohydrates suggest that the activity of these microorganisms benefit *Sphagnum* growth (Kostka et al., 2016). Alternatively, *Sphagnum* also releases easy-degradable carbohydrates (*i.e.* glucose) that can stimulate decomposers' nutrient mineralization, which directly and positively feeds back to *Sphagnum* growth, the 'host'. However, such beneficial interactions between microbes and plants often involve specific metabolites (Hiruma, 2019). Our findings indeed suggest that *Sphagnum* use an array of specific metabolites to regulate microbial communities and their functions. Polyphenols (*e.g. Sphagnum* acids) are released by *Sphagnum* to interact with *Sphagnum* associated microbial communities (Hamard et al., 2019; van Breemen, 1995; Verhoeven & Liefveld, 1997). Polyphenols can be associated with *Sphagnum*

cell walls and prohibit microbial breakdown of *Sphagnum* litter (Freeman et al., 2001; van Breemen, 1995; Verhoeven & Liefveld, 1997; Verhoeven & Toth, 1995) or can be released into the environment to deter or kill microorganisms (Fudyma et al., 2019; Hamard et al., 2019; Mellegård et al., 2009; Opelt et al., 2007b). This likely explains the negative link between phenols and most of the microbial growth traits. Cell-wall carbohydrates (*e.g.* sphagnan) are released slowly into the environment and thus inhibit microbial activity (Stalheim et al., 2009; van Breemen, 1995) either directly by inactivation of extracellular enzymes or indirectly by limiting C and N mineralization and thus microbial growth (Balance et al., 2007; Hájek et al., 2011). However, additional chemical analyses as well as targeted experiments are required to justify this assumption for such *Sphagnum*-microbial interactions.

Our findings demonstrate how soil microbial communities can be structured by *Sphagnum* metabolites. Also, our findings highlight the need for more targeted *Sphagnum* metabolomic analyses to identify the specific compounds involved in *Sphagnum*-microbial relationships (Chiapusio et al., 2018; Fudyma et al., 2019). *Sphagnum* leachates are composed of thousands of compounds (Fudyma et al., 2019; Hamard et al., 2019), and contain not only *Sphagnum* compounds but also microbial derivative compounds (Hamard et al., 2019). We found that *Sphagnum* organic acids, symmetric and asymmetric CH_2 (lipids and fatty acids) were positively related to microbial phototrophic traits such as microbial photosynthetic pigments, photosynthesis efficiency, and C fixation. Microbial phototrophs are highly diverse and abundant in *Sphagnum* mosses (Jassey et al., 2015), and are an important source of lipids (Griffiths & Harrison, 2009). Hence, these findings suggest that free lipids biomarkers within the *Sphagnum* surface may indicate the activity of photosynthetic microbes associated with *Sphagnum*, which is in line with previous findings on the occurrence of cyanobacterial lipids in peat deposits (Huang et al., 2012). In addition, phototrophic lipids also possess antimicrobial properties (Leflaive & Ten-Hage, 2007), which could explain the negative relationships between lipids and microbial enzyme activities. Further studies are clearly needed to assess how well molecular-derived *Sphagnum* and microbial metabolites can

525 determine microbial community and trait assemblages. In particular, more attention should be given to
526 how to extract and quantify *Sphagnum* metabolites to be able to distinguish the effects of strictly
527 *Sphagnum*-derived metabolites from microbial metabolites on microbial community composition and
528 functioning.

529 Our study showcases the key role of *Sphagnum* interspecific trait variations in driving microbial
530 community composition and microbial traits in addition to climatic and edaphic variables. Despite the
531 importance of these findings, some limitations have to be acknowledged and considered for further
532 experiments. Firstly, the confounding effect between dominant *Sphagnum* species and climate (sampled
533 one species per site), did not allow us to test for species identity and climatic effects separately. However,
534 our additional analyses showed that such a potential confounding effect was not an issue for *Sphagnum*
535 metabolites, and thus did not prevent us from assessing the direct and indirect effects of *Sphagnum* traits
536 and phylogeny in driving microbial community composition and microbial traits. Secondly, despite the
537 limited size of our dataset, sensitivity analyses showed that reducing sample size by 20 % did not
538 influenced our SEM model outputs, providing our findings with robustness and confidence.

539 In summary, our findings show that Sphagnum metabolites prevail over *Sphagnum* morphological
540 and anatomical traits as predictors of microbial community composition and functioning in peatlands.
541 They further reveal the possible pathways by which *Sphagnum* interacts with its microbiome. Despite the
542 importance of anatomical and morphological traits for determining *Sphagnum* ecophysiology (Oke et al.,
543 2020; Såstad & Flatberg, 1993; Såstad et al., 1999) and peatland functioning (Bengtsson et al., 2016; Laing
544 et al., 2014; Turetsky et al., 2008), we show that *Sphagnum* anatomical and morphological traits are poor
545 predictors of microbial processes compared to *Sphagnum* metabolites. This finding echoes previous work
546 in grasslands, where classical plant leaf and root traits leave a large fraction of variation in microbial
547 communities unexplained (Leff et al., 2018; but see Sweeney et al., 2020), suggesting a limited role for

548 classic morphological traits in explaining plant-microbial interactions. This can potentially be explained by
549 the fact that *Sphagnum* mosses grow in clumps, where they maintain uniform growth and
550 anatomical/morphological characteristics (Oke et al., 2020) whilst their metabolome can vary according
551 to surrounding conditions (Chiapusio et al., 2018). In addition, changes among *Sphagnum* anatomical and
552 morphological traits can take weeks or years to become apparent (Jassey & Signarbieux, 2019; Oke et al.,
553 2020), whereas changes in *Sphagnum* metabolite concentrations occur more quickly after an
554 environmental stimulus (Bakhtiari et al., 2020; Callis-Duehl et al., 2017; Defossez et al., 2021; Jassey et al.,
555 2011b) – a timescale that corresponds to microbial growth rates. As such, while the effects of climatic and
556 edaphic factors on *Sphagnum* health can be missed in anatomical/morphological traits, they can be
557 detectable in the *Sphagnum* metabolome.

558 The exact mechanisms by which *Sphagnum* mosses shape their microbiome are as yet unknown,
559 but differences in the metabolite cocktails that *Sphagnum* release into their surrounding are likely to be
560 an important factor. Interestingly to mention, a recent study found that repeated litter inputs resulted in
561 directional shifts in the composition of the soil microbiome, especially fungal communities (Veen et al.,
562 2021). The addition of grass litter to tree soils resulted in the convergence of fungal communities to those
563 found in grass soils incubated with grass litter and vice versa. Such steering effects are more likely driven
564 by different chemical composition of plant litter, suggesting that microbial communities can be selected
565 by adding particular litter, and therefore particular plant metabolite cocktails (van Dam & Bouwmeester,
566 2016; Veen et al., 2021). These results support our findings and highlight the urgent need in new
567 experiments to test whether plants select particular soil microbiome. The use of deeper plant
568 metabolomic analyses would certainly shine more light into the 'black box' of plant-microbial interactions.

569

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Author contribution

VEJJ conceived the ideas and designed methodology with the help of AS and RC. VEJJ chose the sites with the help of BJMR, ML, MK, EST and ED. VEJJ and SH collected samples with the help of MK. AS, SH and VEJJ proceeded to laboratory work with the help of BP. AS analysed the data with the help of VEJJ, JMB and BJMR. AS and VEJJ led the writing of the manuscript with the help of RC, JMB and BJMR. All authors contributed to the drafts and gave final approval for publication.

Data availability

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data and *R* codes related to this paper will be publicly available from Figshare (10.6084/m9.figshare.c.5191493).

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Tables

Table 1. Site conditions and climatic data of the study sites

Site	location	Longitude	Latitude	Altitude	Mean annual temperature	Annual precipitation	pH (pore water)*	Water table depth*	Trophic state	Dominant *Sphagnum* on the site
FR	Counozouls (France)	2°14'02.4"	42°41'19.7"	1374 m	7.9 °C	1027 mm	4.90	16.5 cm	poor fen	*Sphagnum warnstorfii*
PL	Kusowo (Poland)	16°35'12.1"	53°48'47.9"	145 m	7.3 °C	656 mm	3.56	60 cm	bog	*Sphagnum magellanicum*
EST	Männikjärve (Estonia)	26°15'03.6"	58°52'26.4"	82 m	4.9 °C	623 mm	4.11	20 cm	bog	*Sphagnum rubellum*
FI	Siikaneva (Finland)	24°17'17.5"	61°50'41.6"	160 m	2.9 °C	611 mm	3.86	8 cm	poor fen	*Sphagnum papillosum*
SE	Abisko (Sweden)	19°03'58.7"	68°20'43.1"	281 m	- 0.1 °C	418 mm	3.83	10 cm	bog	*Sphagnum balticum*

*Measured in early July 2018

Figure captions

Figure 1. *A priori* conceptual structural equation model (SEM) depicting pathways by which climate and edaphic conditions (standardized data of annual precipitation (clim1), mean temperature of the wettest quarter (clim2), *Sphagnum* water content (local1), PC1 of WEOM chemistry (local2), PCoA1 of *Sphagnum* anatomical and morphological traits (anatom) and metabolites(metab) can affect microbial community composition (PcoA1 of tot.biom=total microbial biomass; Hellinger transformation of decomp.=decomposers, consum.=consumers, phototr.=phototrophs) and traits (PCoA 1 of tot.traits=total traits, yield=growth yield, res.acq.=resource acquisition, stress=stress tolerance). (A) a single model, (B) an interaction model, (C) a single model with *Sphagnum* traits (D) an interaction model with *Sphagnum* traits. Thin lines indicate a single path, while thicker lines indicate that any climatic/edaphic parameter affected each representative of microbial community composition (or the sum of them) and/or microbial trait composition (or the sum of them).

Figure 2. *Sphagnum* anatomical and morphological traits and metabolites data. A) Principal coordinates analysis (PCoA) on the Gower dissimilarity matrix of *Sphagnum* anatomical and morphological traits and metabolites for five dominant species collected along a gradient. Groups are colored according to *Sphagnum* species sampled in sites spanning from south to north. B) *Sphagnum* phylogenetic tree and normalized means of *Sphagnum* anatomical and morphological traits and metabolites. The square shape represents mean values of anatomical and morphological traits, while circle shape – mean values of metabolites. The size of mean is represented from the smallest (the smallest circle/square) to the highest (the highest circle/square) values of anatomical and morphological traits and metabolites.

Figure 3. Microbial community composition and traits composition. Upper panels: *Sphagnum* phylogenetic tree with the corresponding heatmap showing the dissimilarities in (A) the composition of each trophic group components in which colors represent the standardized value calculated from

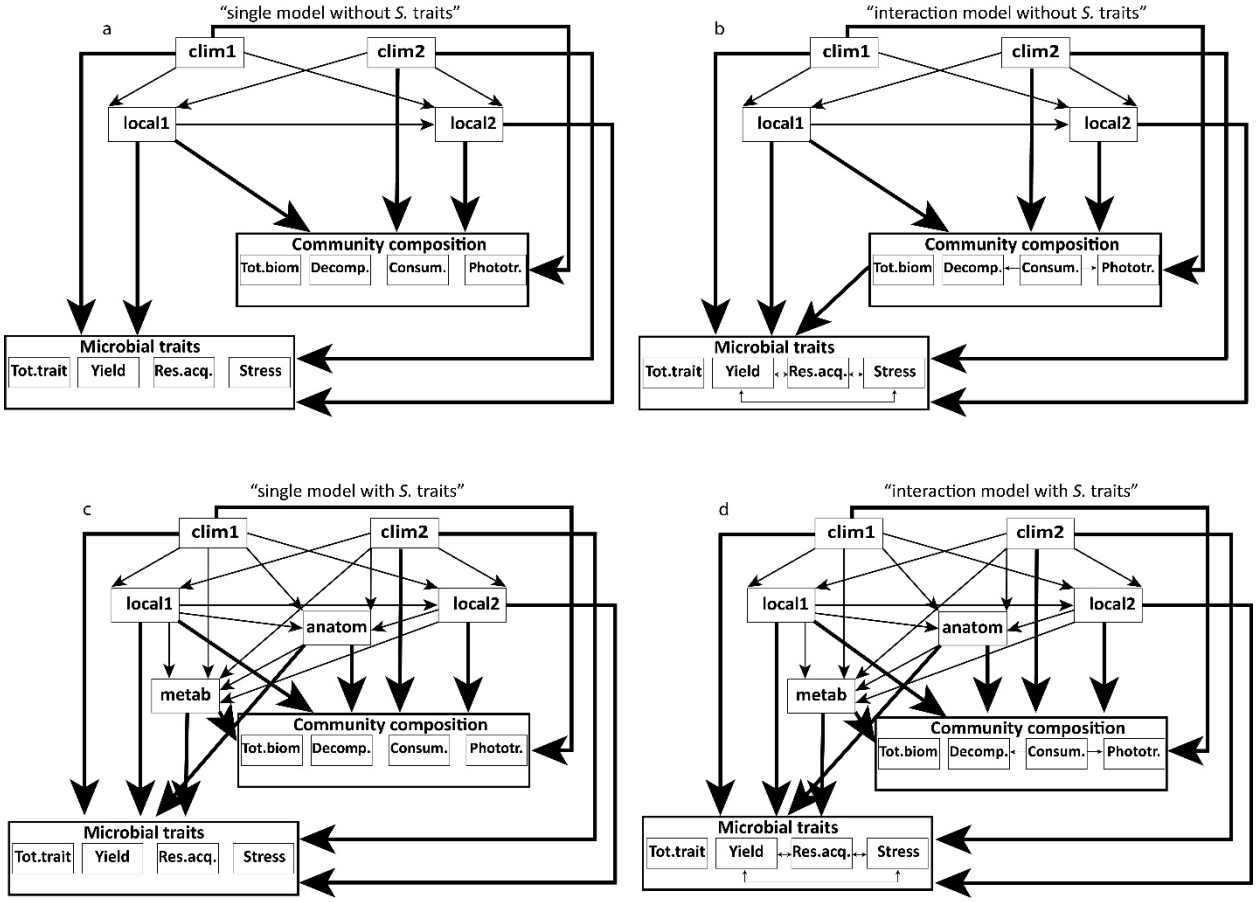
standardized means of microbial biomass, and (B) the microbial traits composition in which colors represent the standardized value calculated from the first PCoA on the Gower dissimilarity matrix of microbial trait composition. Lower panels: Principal coordinates analysis (PCoA) on the Gower dissimilarity matrix of (C) the microbial community composition based on the abundance of all microbes (micro-eukaryotic species cyanobacteria, fungi and non-photosynthetic bacteria) and (D) the microbial traits composition. Groups are colored according to *Sphagnum* species sampled in sites spanning from south to north.

Figure 4. Correlation table on the relationships between climatic and edaphic conditions (standardized data of annual precipitation (an. precip.), the mean temperature of the wettest quarter (war. temp.), PC1 of WEOM chemistry (WEOM. chem.), *Sphagnum* water content (*S.*wat.cont.), PCoA1 of *Sphagnum* anatomical and morphological traits and metabolites (*S*. traits) and microbial community composition and traits (PCoA1). Correlations with $P<0.05$ only are shown.

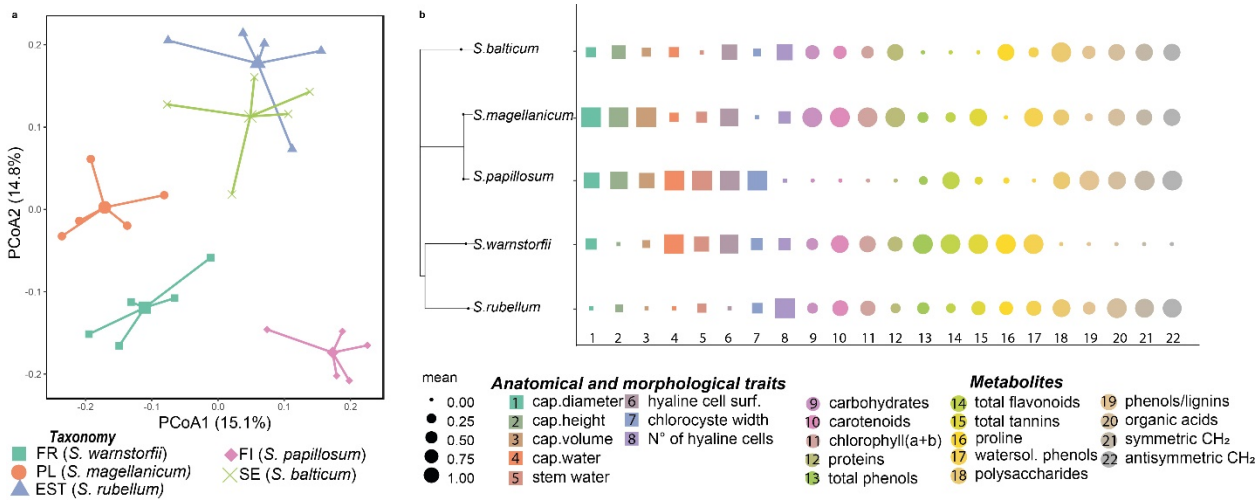
Figure 5. Outputs of the SEMs when *Sphagnum* traits were included in SEMs for microbial community composition and microbial traits composition: (A) the benefits gained (ΔR^2) and (B) Akaike Information Criteria (AIC) values. *Full summed models= Full model with PCoA1 for total microbial biomass and PCoA1 for total microbial traits. All details about SEMs including R^2, *P*-values, *Fisher's C,* path explanations are provided in Tables S6-S10.

Figure 6. The relationship between differences in the microbial community composition (sum of Hellinger-transformed microbial biomass per trophic group) and their traits (PCoA1 axes) and individual *Sphagnum* traits. Points represent Spearman correlation coefficients (Rho) and their significance ($P<0.05$).

Figure 1


a
"single model without S. traits"
clim1
clim2
local1
local2
Community composition
Tot.biom
Decomp.
Consum.
Phototr.
Microbial traits
Tot.trait
Yield
Res.acq.
Stress
b
"interaction model without S. traits"
c
"single model with S. traits"
anatom
metab
d
"interaction model with S. traits"

940 Figure 2



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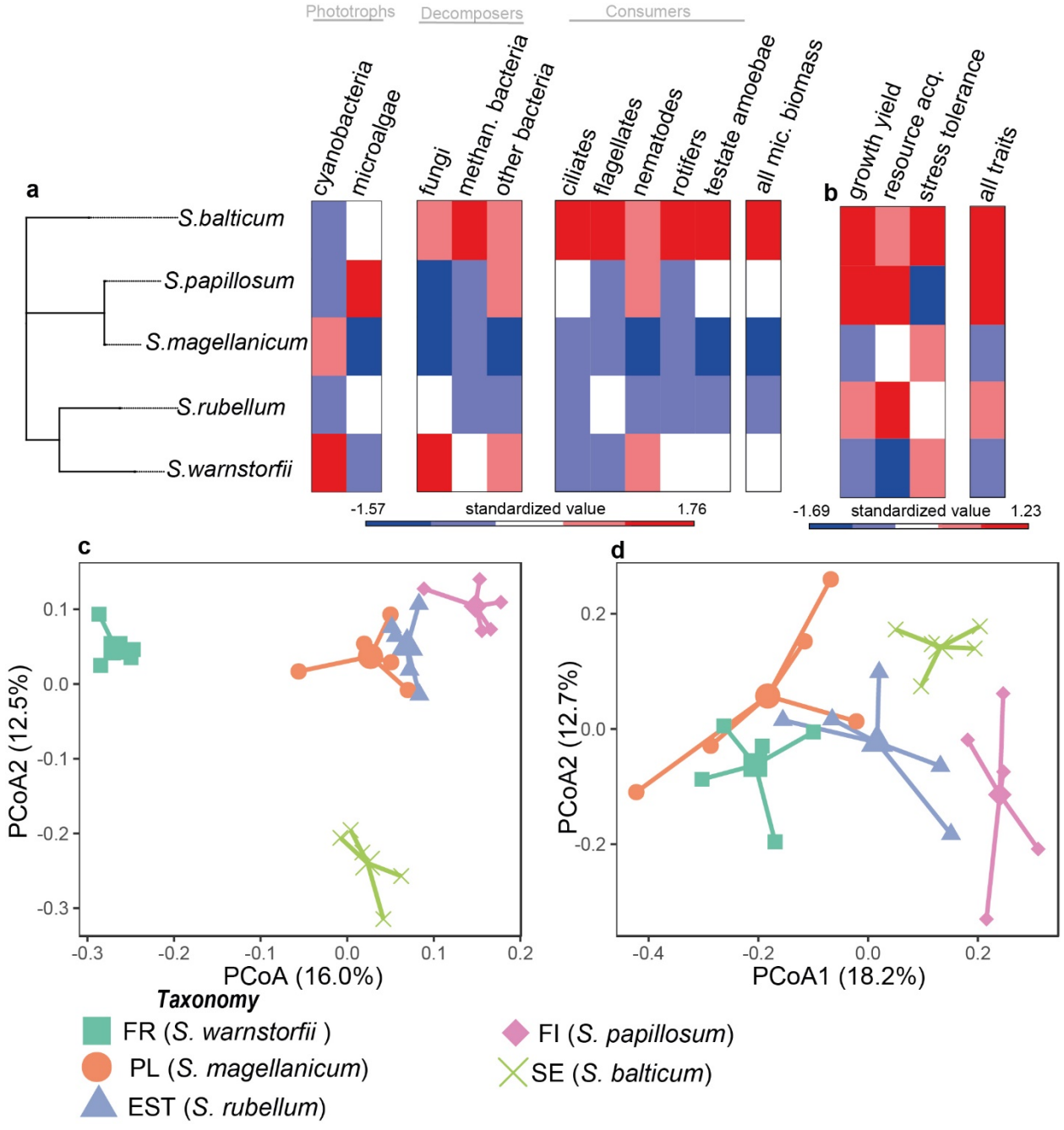
943 Figure 3



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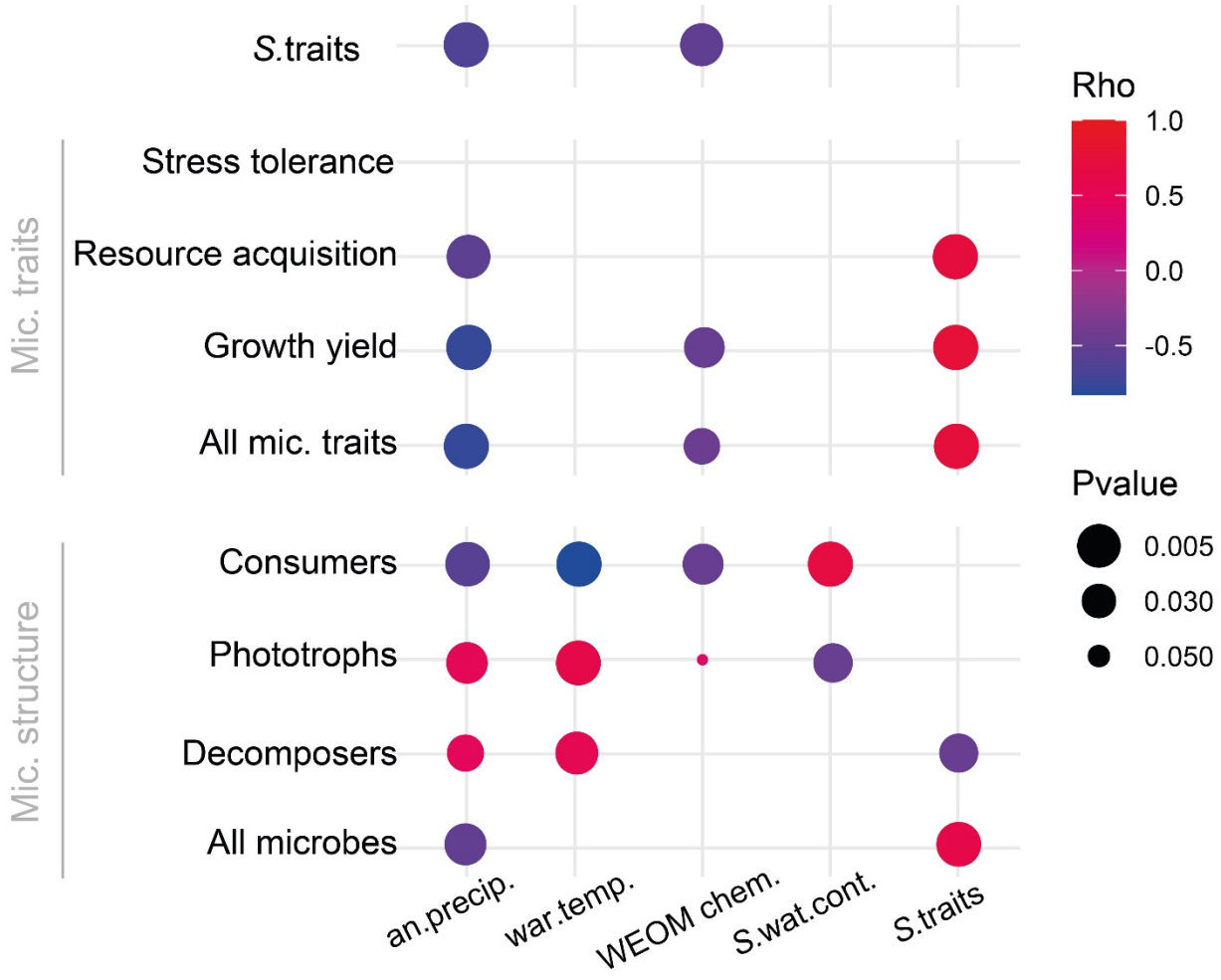
946 Figure 4



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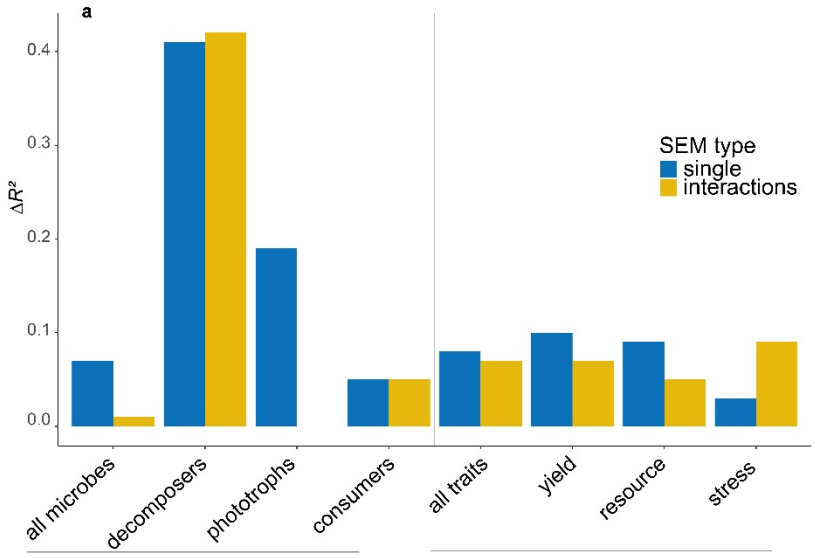
948

949 Figure 5



b

	AIC with *Sphagnum* traits	AIC without *Sphagnum* traits
single SEM		
Decomposers	51.75	57.05
Phototrophs	68.56	65.79
Consumers	56.44	51.32
Growth yield	51.51	50.51
Ressource acquisition	54.85	56.41
Stress tolerance	55.74	51.34
All microbes	62.19	60.13
All traits	52.43	51.95
interactions SEM		
Full model	185.51	220.80
Full summed model*	90.49	81.21

950
951

952 Figure 6

953