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Contribution of phototrophic microbes to peatland carbon uptake in a changing climate

Samuel Hamard

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Samuel Hamard. Contribution of phototrophic microbes to peatland carbon uptake in a changing climate. Global Changes. Université Paul Sabatier - Toulouse III, 2022. English. NNT: 2022TOU30062 . tel-04057192

HAL Id: tel-04057192

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THÈSE

**En vue de l'obtention du
DOCTORAT DE L'UNIVERSITÉ DE TOULOUSE
Délivré par l'Université Toulouse 3 - Paul Sabatier**

**Présentée et soutenue par
Samuel HAMARD**

Le 11 mai 2022

**Contribution des microbes phototrophiques à la fixation de
carbone des tourbières dans un contexte de changement
climatique.**

Ecole doctorale : **SDU2E - Sciences de l'Univers, de l'Environnement et de
l'Espace**

Spécialité : **Ecologie fonctionnelle**

Unité de recherche :

Laboratoire écologie fonctionnelle et environnement

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Au grand-père d'un arcandier

« J'en avais rencontré quelques-uns de ces calculateurs. Ils baguaient les colibris et éventraient des goélands pour prélever des échantillons de bile. Ils mettaient le réel en équation. Les chiffres s'additionnaient »

Sylvain Tesson
La Panthère des neiges

Foreword

This work has been funded by the French ministry of higher education, research and innovation. I obtained the thesis grant from a specific allocation attributed to the students of the Ecole Normale Supérieure. The field work and analyses inherent to the functioning of this work have been funded by the French Agence Nationale de la Recherche (ANR) in the framework of the MIXOPEAT project attributed to Vincent Jassey.



This work has been realized in the Laboratoire écologie fonctionnelle et environnement:

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Acknowledgment

I thank my PhD supervisors, Vincent Jassey and Regis Céréghino for making this work possible. I am profoundly grateful for all the time, advice, investment and availability they gave to me. I sincerely thank Béatrice Lauga and Téléspore Sime Ngando who accepted to be rapporteurs of this thesis, and also Julien Cucherousset, Cécile Lepère and Lucie Zinger who accepted to examine my work. I thank the members of my PhD committee: Jean-François Carrias, Antoine Lecerf and Bjorn Robroek. I also thank the colleagues from the Mixopeat project for their help in the field or for their advice for data analyses: Maialen Barret, Enrique Lara, Martin Küttim, Ellen Dorrepaal and Mariusz Lamentowicz. Of course, I thank Anna Sytiuk, also involved in the Mixopeat project and PhD twin. I thank the two interns who helped me for lab work, Chloé Argouet and Lucas Deramond. I am grateful to Jessica Ferriol, Didier Lambrigot and Frederique Julien for their time and help for lab analyses. I want to thank Yann Morell, who solved my computer problems. I also thank these people for all what they bring to me aside of work. Finally, I am thankful to many more people. They know who they are, and I know what I owe them.

Scientific valorisation

Publications

Published

Hamard S., Küttim M., Céréghino R., *et al.* Peatland microhabitat heterogeneity drives phototrophic microbe distribution and photosynthetic activity. (2021). *Journal of Ecology*, doi: 10.1111/1462-2920.15779

Hamard S., Céréghino R., Barret M., *et al.* Contribution of microbial photosynthesis to peatland carbon uptake along a latitudinal gradient. (2021). *Journal of Ecology*, doi: 10.1111/1365-2745.13732

Sytiuk A., Céréghino R., **Hamard S.**, *et al.* Predicting the structure and functions of peatland microbial communities from *Sphagnum* phylogeny, anatomical and morphological traits and metabolites. (2021). *Journal of Ecology*, doi: 10.1111/1365-2745.13728

Barel J., Moulia V., **Hamard S.**, *et al.* Come rain, come shine: peatland carbon dynamics shift under extreme precipitation. (2021). *Frontiers in Environmental Science*, doi: 10.3389/fenvs.2021.659953

Hamard S., Robroek B.M.J., Allard P.M., *et al.* Effects of *Sphagnum* leachate on competitive *Sphagnum* microbiome depend on species and time. (2019). *Frontiers in Microbiology*, doi: 10.3389/fmicb.2019.02042

Robroek B., Albrecht R., **Hamard S.**, *et al.* Peatland vascular plant functional types affect dissolved organic matter chemistry. (2016). *Plant and Soil*, doi: 10.1007/s11104-015-2710-3

In press

Garnica S., Liao Z., **Hamard S.**, *et al.* Environmental stress determines the colonization and impact of an endophytic fungus on invasive Knotweed. (2022). *Biological Invasions*, in press.

Jassey V.E.J., Walcker R., Kardol P., *et al.* Contribution of soil algae to the global carbon cycle. (2022). *New Phytologist*, in press.

Sytiuk A., Céréghino R. **Hamard S.**, *et al.* Biochemical traits enhance the trait concept in *Sphagnum* ecology. (2022). *Oikos*, in press.

Submitted

Hamard S.*, Jassey V.E.J*, Lepère C., *et al.* Photoautotrophic microbes from terrestrial bryospheres contribute to ecosystem carbon uptake. *Microbial Ecology*. *co-first author

In preparation

Hamard S., Sytiuk A., Céréghino R., *et al.* Temperature and *Sphagnum* water content mediate microbial photosynthesis response to climate change in European peatlands.

Communications

Talks in an international congress:

Talk at the BES-SFE² meeting, 2019

Hamard S., Robroek B.J.M, Allard P.M., Jassey V.E.J. Effects of *Sphagnum* leachate on competitive *Sphagnum* microbiome depend on species and time.

Talk at the ECOVEG meeting, 14th edition, 2019

Hamard S., Robroek B.J.M, Jassey V.E.J. La guerre chimique entre sphaignes: que le meilleur gagne !

Poster in an international congress:

Poster at the POPBIO meeting, 30th edition, 2017

Hamard S., Liao Z., Garnica S., Parepa M. Environmental stress determines the colonization and impact of an endophytic fungus on invasive Knotweed.

Talk for popularisation of science:

Talk at the Rencontre des Naturalistes de l'Aude, 2019

Hamard S., Jassey V. Les microorganismes des tourbières, un grand rôle pour de petites créatures.

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CONTEXTE en français

La vie est apparue sur Terre durant l'Archéen, il y a plus de 3.8 milliards d'années, sous la forme de microorganismes aussi appelés microbes (Javaux, 2006). De par leurs métabolismes, les microbes ont interagi avec leur environnement chimique et ont altéré la spéciation de presque tous les éléments à la surface de la Terre (Falkowski et al., 2008). Ceci a permis à la vie de prospérer et de se diversifier (Knoll, 2003). De nos jours, les microbes sont représentés dans les trois domaines du vivant (i.e. Bactéries, Archées et Eucaryotes) et revêtent une multitude de formes, de tailles ou de traits fonctionnels. En particulier, le métabolisme des microbes couvre tous les types trophiques existants, ce qui signifie que les microbes peuvent acquérir de l'énergie et de la matière organique par le biais de divers mécanismes. Ils peuvent combiner l'utilisation de carbone (C) organique ou inorganique comme source de C, l'utilisation d'énergie lumineuse ou chimique, et l'utilisation de donneurs d'électrons organiques ou inorganiques pour assimiler la source de C (Table 0.1). Cette diversité de mécanismes permet aux microbes de coloniser des environnements extrêmement divers (Seckbach, 1999). Les microbes sont par conséquent omniprésents à la surface du globe, et malgré leur petite taille ont la biomasse totale la plus élevée après les plantes (Bar-On et al., 2018). Cette diversité et abondance confère aussi aux microbes un rôle clé et dominant dans les cycles biogéochimiques de la Terre (Bertrand et al., 2015; Falkowski, 2012; Madsen, 2011). Par exemple, les microbes jouent un rôle majeur dans le cycle du C à l'échelle globale (e.g. Caron et al., 2017; Fierer, 2017; Singh et al., 2010). La contribution microbienne aux flux de C est habituellement séparée entre leurs activités autotrophes et hétérotrophes. Les microbes autotrophes ont des activités anaboliques. Ils fournissent du C organique aux écosystèmes via une conversion de C inorganique en composés organiques et en

biomasse. Par exemple, le phytoplancton contribue à plus d'un tiers à la fixation photosynthétique de CO₂ terrestre (Ciais et al., 2013). A l'opposé, les microbes hétérotrophiques favorisent le relargage de C depuis les écosystèmes via leurs activités cataboliques et la minéralisation de C organique (Schimel & Schaeffer, 2012). Les microbes hétérotrophiques sont responsables de l'émission importante de gaz à effet de serre (Gougoulas et al., 2014; Shao et al., 2013). Etant donné leur importance pour le fonctionnement des écosystèmes et leur sensibilité aux changements environnementaux (Graham et al., 2016; Liu et al., 2010; Schimel et al., 2007), les microbes auto- et hétérotrophiques jouent un rôle clé dans la réponse des écosystèmes aux changements globaux (Dutta & Dutta, 2016; Hutchins et al., 2019; Waldrop & Firestone, 2006).

Table 0.1: Les différents types trophiques microbiens sur Terre.

Source d'énergie	Donneur d'électron	Source de C	Nom
Lumière	Organique	Organique	Photoorganohétérotrophe
		Inorganique	Photoorganautotrophe
	Inorganique	Organique	Photolithohétérotrophe
		Inorganique	Photolithoautotrophe
Composés chimiques	Organique	Organique	Chemoorganohétérotrophe
		Inorganique	Chemoorganautotrophe
	Inorganique	Organique	Chemolithohétérotrophe
		Inorganique	Chemolithoautotrophe

Dans les écosystèmes terrestres, les microbes sont souvent étudiés d'un point de vue hétérotrophique. L'impact du changement climatique sur les microbes du sol et sur les fonctions écosystémiques qu'ils génèrent est principalement explorée au regard de leurs activités cataboliques (Bardgett et al., 2008; Jansson & Hofmockel, 2020). Deux raisons peuvent expliquer cela. Premièrement, les microbes hétérotrophe sont à la base des écosystèmes terrestres car ils recyclent les éléments essentiels (e.g. Bates et al., 2013; Karimi et al., 2018; Tedersoo et al., 2014), ce qui permet l'établissement de vie plus complexe et l'émergence de réseaux trophiques (e.g. Alongi, 1994; Singh et al., 1989; Vitousek & Sanford, 1986). Deuxièmement, la source de C organique dans les écosystèmes terrestres est souvent attribuée aux plantes (Krumins et al., 2013; Liang et al., 2017), ce qui cache le

rôle invisible des microbes photoautotrophiques. De fait, la production primaire microbienne des sols a été essentiellement étudiée dans les systèmes avec peu ou pas de plantes, où les microbes photoautotrophiques colonisent des habitats inhospitaliers tels la roche nue, la glace ou la neige (Anesio *et al.*, 2009; Maier *et al.*, 2018; Chen *et al.*, 2020). Cependant, les microbes photoautotrophiques sont omniprésents et abondants dans tous les écosystèmes terrestres (Cano-Díaz *et al.*, 2020; Jassey *et al.*, 2022; Oliverio *et al.*, 2020). Au travers de leurs activités photosynthétiques, ils contrebalancent les flux cataboliques de C et participent aussi activement au cycle global du C (Elbert *et al.*, 2012a; Jassey *et al.*, 2022). Ils contribuent à la réponse des écosystèmes terrestres aux changements globaux, et peuvent avoir une rétroaction négative sur le réchauffement climatique via leurs activités anaboliques (Rossi *et al.*, 2015).

Une étude récente sur de larges jeux de données a montré que l'abondance des microbes photoautotrophiques est plutôt maximale dans les écosystèmes couverts de plantes, plus particulièrement dans ceux qui sont humides et acides tels les zones humides ou les forêts tempérées ou boréales (Jassey *et al.*, 2022). Les microbes photoautotrophiques pourraient ainsi contribuer significativement à la production primaire de ces écosystèmes, mais leur rôle fonctionnel reste sous-évalué. Cette absence de connaissance est particulièrement alarmante pour les écosystèmes qui stockent du C, telles les tourbières, au regard de leur rôle important dans la régulation du climat. Les tourbières constituent en effet de larges réservoirs de C, où une portion de la matière organique produite par les organismes autotrophes n'est pas décomposée. Cette portion s'accumule sous forme de tourbe au cours des temps géologiques, et les tourbières stockent de nos jours plus de 30% du C total des sols (Harris *et al.*, 2021; Yu, 2012). Dans les tourbières Nordiques, l'activité autotrophique est attribuée aux plantes, principalement à des mousses appelées sphagnes. Dans ce schéma, le rôle des microbes photoautotrophiques n'est pas pris en compte (Fig. 0.1A). Par conséquent, leur contribution à la production primaire des tourbières et à la dynamique du C reste quasiment inconnue, alors même que ces microbes sont abondants, atteignant plusieurs millions de cellules par litre d'eau (Gilbert & Mitchell, 2006a). Ce manque de connaissance suggère que notre compréhension du cycle du C des tourbières est incomplète et qu'il manque une pièce dans nos prédictions sur le devenir des flux de C des tourbières face aux changements climatiques. Le devenir des tourbières dans le futur est une source de grande inquiétude parce que les tourbières pourraient relâcher une grande majorité de C au cours de ce siècle (Crowther *et al.*, 2016). Malheureusement, les prédictions actuelles de la production

primaire sont uniquement basées sur la réponse des sphaignes et des plantes vasculaires (e.g. Dieleman et al., 2015; Gavazov et al., 2018; Jassey & Signarbieux, 2019; Mäkiranta et al., 2018; McPartland et al., 2020; Zhang et al., 2020). Les microbes photoautotrophiques ont des cycles de reproduction courts, une croissance et un renouvellement rapide, et peuvent répondre rapidement aux changements environnementaux puisque des variations phénotypiques peuvent être sélectionnées rapidement (e.g. Collins & Bell, 2004). Leur réponse aux changements climatique pourraient donc suivre une autre direction que celle des sphaignes ou des plantes, et ainsi, leur contribution à la production primaire des tourbières pourrait évoluer rapidement sous de futurs climats. Cela pourrait entraîner des conséquences dramatiques pour le fonctionnement des tourbières.

Par conséquent, pour mieux comprendre la dynamique du C des tourbières et ses rétroactions possibles au climat, il est important d'étudier le compartiment inconnu des microbes photoautotrophiques. Dans ce projet, financé par l'ANR MIXOPEAT, j'ai cherché à estimer :

- 1) L'importance des microbes photoautotrophiques dans les tourbières nordiques, et leur contribution à la production primaire.
- 2) La réponse des microbes photoautotrophiques et de leur photosynthèse aux changements climatiques.

J'ai émis l'hypothèse que les microbes photoautotrophiques contribuent significativement à la production primaire des tourbières nordiques (Fig. 0.1.B). J'ai aussi émis l'hypothèse que le changement climatique et plus particulièrement que le réchauffement climatique allait affecter la photosynthèse microbienne (Fig. 0.1.C), en l'augmentant potentiellement via des modifications de la structure, de l'abondance ou de la physiologie des communautés de microbes photoautotrophiques, comme cela peut être observé dans les environnements océaniques (Winder & Sommer, 2012). Pour répondre à ces hypothèses, j'ai utilisé différentes approches complémentaires :

- une étude de terrain exploratoire cherchant à mieux connaître les communautés de microbes photoautotrophiques dans les tourbières nordiques et leurs différents habitats, à estimer leur photosynthèse et leur contribution à la production primaire (chapitre II et chapitre III).
- une expérience de laboratoire utilisant des communautés microbiennes naturelles dans des conditions contrôlées pour déchiffrer la place de certains microbes photoautotrophiques dans les

réseaux trophiques microbiens, et comment cette place est conditionnée par les espèces hôtes de sphaignes (chapitre IV).

- une transplantation réciproque en conditions naturelles, utilisant une substitution d'espace à la place du temps pour simuler un changement climatique et estimer ses effets sur les communautés microbiennes photoautotrophiques et leur photosynthèse au cours d'une saison de végétation (chapitre V).

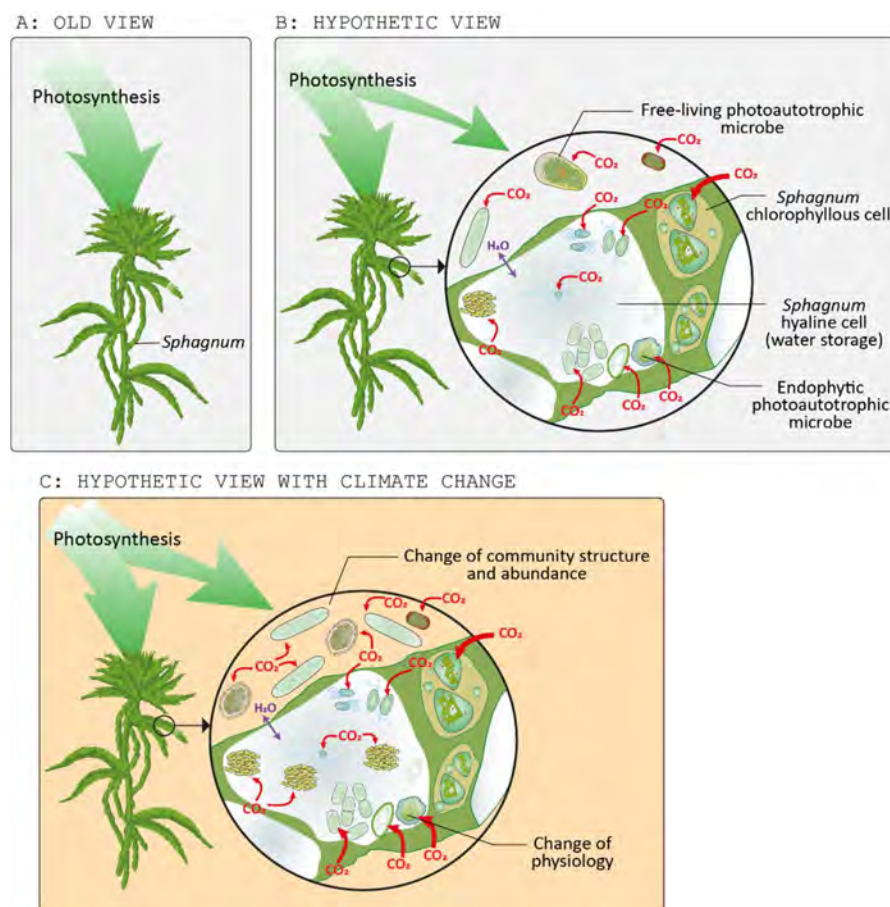


Figure 0.1: Dans la vue classique des tourbières nordiques, la production primaire est réalisée par les plantes, en particulier par les sphaignes (A). J'émetts l'hypothèse que les microbes photoautotrophiques contribuent de manière significative à cette production primaire (B). J'émetts aussi l'hypothèse que le changement climatique va affecter cette contribution via une altération de la structure des communautés, de l'abondance ou de la physiologie des microbes photoautotrophiques (C).

CONTEXT in English

Life has been present on Earth since more than 3.8 billion years ago, appearing during the Archean under the form of microorganisms—or microbes (Javaux, 2006). By their metabolic processes, microbes interacted with their chemical environment and altered the speciation of almost all elements at the Earth surface (Falkowski et al., 2008), allowing life to thrive and to diversify (Knoll, 2003). Nowadays, microbes are found in the three domains of the tree of life (i.e. Bacteria, Archaea and Eukarya) and take on a tremendous range of life forms, sizes and styles. In particular, the metabolisms of microbes cover all the existing primary nutritional groups, meaning that they can acquire organic matter and energy through very diverse pathways. Microbes can combine the use of organic or inorganic carbon (C) as a C source, the use of chemical or light energy, and the use of organic or inorganic electron donors to assimilate the C source (Table 0.1). This lifestyle diversity allows microbes to colonize extremely diverse and extreme environments (Seckbach, 1999). Therefore, microbes are omnipresent at the globe surface, and despite their unseen size, they are the most abundant taxa by their biomass after plants (Bar-On et al., 2018). This diversity and abundance also gives to microbes a dominating and key role in the biogeochemical cycles of the Earth (Bertrand et al., 2015; Falkowski, 2012; Madsen, 2011). For instance, microbes play a massive role in the C cycle, driving some of the main fluxes at the global scale (e.g. Caron et al., 2017; Fierer, 2017; Singh et al., 2010). The microbial contribution to C fluxes is usually classified between the dichotomous roles of autotrophic and heterotrophic activity. Autotrophic microbes have anabolic activities. They provide organic C to ecosystems through the conversion of inorganic C into organic compounds and living biomass. For instance, oceanic phytoplankton contributes to more than one third of the global photosynthetic CO₂ fixation (Ciais et al., 2013). At the opposite, heterotrophic microbes promote the release of C from ecosystems through

their catabolic activities and the mineralization of organic C (Schimel & Schaeffer, 2012). Heterotrophic microbes are a major component of the greenhouse gases emissions (Gougoulas et al., 2014; Shao et al., 2013). Further, given their importance for ecosystem functioning and their sensitivity to the environment (Graham et al., 2016; Liu et al., 2010; Schimel et al., 2007), auto- and heterotrophic microbes play a key role in the response of ecosystems to global change (Dutta & Dutta, 2016; Hutchins et al., 2019; Waldrop & Firestone, 2006).

Table 0.1: The different primary nutritional groups of microbes on Earth.

Energy source	Electron donor	C source	Name
Sun light	Organic	Organic	Photoorganoheterotroph
		Inorganic	Photoorganotroph
	Inorganic	Organic	Photolithoheterotroph
		Inorganic	Photolithotroph
Chemical compounds	Organic	Organic	Chemoorganoheterotroph
		Inorganic	Chemoorganotroph
	Inorganic	Organic	Chemolithoheterotroph
		Inorganic	Chemolithotroph

In terrestrial ecosystems, microbes are often seen through heterotrophic lens. The impact of climate change on soil microbiome and the ecosystem function they provide is mainly studied regarding their catabolic activities (Bardgett et al., 2008; Jansson & Hofmockel, 2020). Two reasons can explain this. First, heterotrophic microbes are a foundation of terrestrial ecosystems as they both mineralize soil organic C and stabilize soil C inputs into organic forms. They recycle essential elements (e.g. Bates et al., 2013; Karimi et al., 2018; Tedersoo et al., 2014), which allows the establishment of more complex life forms and the emergence of complex food webs (e.g. Alongi, 1994; Singh et al., 1989; Vitousek & Sanford, 1986). Second, the source of organic C in terrestrial ecosystems is usually dominated and attributed to plants (Krumins et al., 2013; Liang et al., 2017), obscuring the interest for the unseen photoautotrophic microbes. Hence, microbial primary production in soils has been mainly studied in systems with few or no plants, where photoautotrophic microbes colonize inhospitable habitats such as exposed rocks, ice and snow (Anesio *et al.*, 2009; Maier *et al.*, 2018; Chen *et al.*, 2020).

Yet, photoautotrophic microbes are widely distributed and abundant in every terrestrial ecosystems (Cano-Díaz et al., 2020; Jassey et al., 2022; Oliverio et al., 2020). Through their photosynthetic activities, they balance the catabolic fluxes of C and actively take part in the global C cycle too (Elbert et al., 2012a; Jassey et al., 2022). They contribute to the response of terrestrial ecosystems to global changes and could have a negative feedback on climate warming through their anabolic activities (Rossi et al., 2015).

Recent research on extensive dataset shows that photoautotrophic microbial abundance rather peaks in vegetated ecosystems, especially in the moist and acidic ones such as wetlands or northern forests (Jassey et al., 2022). Photoautotrophic microbes could thus significantly contribute to the primary production of these ecosystems, but their functional role remains unexplored. This absence of knowledge is particularly striking for C-accreting systems such as peatlands, regarding their important role in climate regulation. Peatlands are indeed large C sinks, where a fraction of the organic matter produced by autotrophic organisms is not decomposed. This fraction accumulates through geological timescales under the form of peat and peatlands store nowadays more than 30% of the total soil C (Harris et al., 2021; Yu, 2012). In northern peatlands, autotrophic activities are attributed to plants, and especially to mosses from the *Sphagnum* genus. In this schema, the role of photoautotrophic microbes is not taken into consideration (Fig. 0.1A). Therefore, the contribution of photoautotrophic microbes to peatland primary production and C dynamic remains virtually unknown although these organisms are abundant, often reaching several millions of cells per liter of water (Gilbert & Mitchell, 2006a). This lack of knowledge suggests that our understanding of the peatland C cycle is incomplete and that our prediction of the peatland C fluxes under future global changes might miss an important piece. The becoming of peatlands in the future is indeed a source of high concerns because peatlands could contribute to the majority of warming-induced soil C loss over the next century (Crowther et al., 2016). Yet, the current predictions of peatland primary production evolution under global changes are based on *Sphagnum* and vascular plants only (e.g. Dieleman et al., 2015; Gavazov et al., 2018; Jassey & Signarbieux, 2019; Mäkiranta et al., 2018; McPartland et al., 2020; Zhang et al., 2020). Photoautotrophic microbes have short generation times, fast growth and turnover, and might quickly respond to environmental changes, as adapted phenotypes can be rapidly selected (e.g. Collins & Bell, 2004). Then, their response to climate change might follow a different direction than

the one of *Sphagnum* or vascular plants, and their contribution to peatland primary production might rapidly change under future climates. The consequences for peatland functioning could be dramatic.

It is therefore primordial to study the unknown compartment of photoautotrophic microbes in peatlands to better understand the peatland C dynamic and its possible feedbacks to climate change.

Therefore, in this project funded by the ANR MIXOPEAT, I aim to estimate:

- 1) The importance of photoautotrophic microbes in peatlands and their contribution to peatland primary production.
- 2) The response of photoautotrophic microbes and their photosynthesis to climate changes.

I hypothesize that photoautotrophic microbes significantly contribute to primary production of northern peatlands (Fig. 0.1.B). I also hypothesize that climate change and especially climate warming will affect microbial primary production (Fig. 0.1.C), potentially increasing its rate through an alteration of community structure, physiology or abundance as it can be observed in oceanic environments (Winder & Sommer, 2012). To explore these hypotheses and bring response elements, I used different complementary experiments:

- an exploratory field study, aiming to better know the photoautotrophic microbial communities in peatlands, to estimate their photosynthesis and their contribution to the peatland primary production in different habitats (chapter II and chapter III).
- a lab experiment using natural microbial communities in controlled conditions, aiming to decipher the place of specific photoautotrophs in microbial food webs, and how this place is dependent on the host *Sphagnum* species (chapter IV).
- a reciprocal transplantation in natural conditions, using a space for time substitution to mimic climate change and to estimate its effects on photoautotrophic microbial communities and photosynthesis throughout a growing season (chapter V).

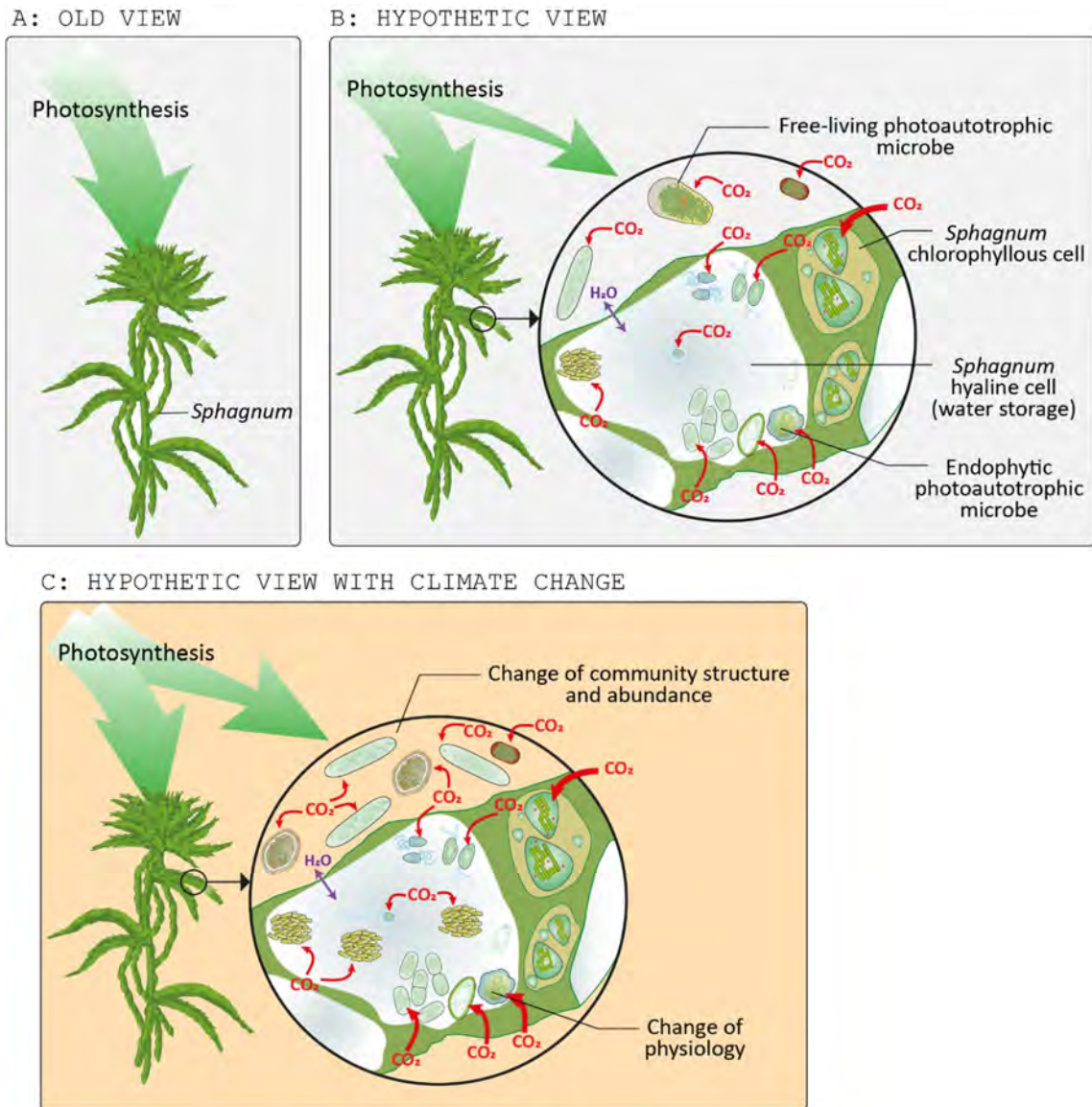


Figure 0.1: In the classic view of northern peatlands, primary production is performed by plants and especially by *Sphagnum* mosses (A). We hypothesise that photoautotrophic microbes significantly contribute to this primary production (B). We also hypothesise that climate change will affect this contribution through an alteration of community structure, physiology or abundance of photoautotrophic microbes (C).



Chapter I

Introduction

1. The microbial primary producers on Earth

All life on Earth depends on carbon (C) fixation, in which autotrophic organisms convert inorganic C into organic compounds and living biomass. To perform this conversion, autotrophic organisms need an energy source that can derive from sun light or from chemical compounds (Srinivasan et al., 2012). In the first case, autotrophic organisms are called photoautotrophs and perform photosynthesis, while in the second case they are called chemoautotrophs. In this work, I only focus on photoautotrophic organisms, to which I also refer as primary producers or phototrophic organisms.

1.1. Diversity of microbial primary producers

Photosynthesis arose early in Earth's history, probably around 3.8 billion years ago (Olson, 2006) and evolved since then through several revolutions, such as the apparition of oxygenic photosynthesis 2.4 billion years ago, and through several mechanisms, such as gene transfer or endosymbiotic events. Along with these metabolism changes, phototrophic organisms also diversified and nowadays they encompass myriads of different species. A common and easy view differentiates plants from phototrophic microorganisms. The first ones are highly represented in terrestrial ecosystems, while the seconds are mostly known for their importance in oceanic and lacustrine environments, as phytoplankton. These two groups are not comparable in terms of diversity. All plants belong to only one clade, the Embryophyte one (belonging to Archaeplastida, Fig. 1.1). This low phylogenetic diversity contrasts with that of phototrophic microbes, which are highly polyphyletic (Baldauf, 2003; Cardona, 2015) and gather a multitude of prokaryotic and micro-eukaryotic species (Fig. 1.1). Among prokaryotes, species containing a photosynthetic machinery have been reported in seven out of more than 60 formally described bacterial phyla (Bryant & Frigaard, 2006; Raymond, 2008; Zeng et al., 2014). These phyla gather Cyanobacteria (also called blue-green algae), Proteobacteria (including purple sulphur and non-sulfur bacteria), Chlorobi (green sulphur bacteria), Chloroflexi (filamentous anoxic phototrophs or green non-sulphur bacteria), Firmicutes (Heliobacteria), Acidobacteria (or Chloroacidobacteria), and the more recently discovered phylum Gemmatimonadetes. These phyla also include many heterotrophic species, underlining the fact that photosynthesis is not an evolutionary constant. To date, photosynthetic reaction centres have not been detected in any archaea (Bryant &

Frigaard, 2006), although the existence of photoautotrophic pathways is still under question (Kono et al., 2017; Pan et al., 2020). Among micro-eukaryotes, phototrophic microbes are spread across at least six of the eight major groups of eukaryotes (Baldauf, 2003; Burki et al., 2020; P. G. Falkowski et al., 2004; Gilbert & Mitchell, 2006a). These groups include Archaeplastida in which are found green algae (Chlorophyta and Streptophyta), and red algae (Rhodophyta). They also include Excavates (Euglenophyta), Cryptista (Cryptophyta), Haptista (Haptophyta) and TSAR, i.e. telonemids, stramenopiles, alveolates, and rhizaria (Dynophyta, Ciliophora, Cercozoa, and Ochrophyta including brown algae). Some Amorphea species (Amoebozoa) are also capable of endosymbiosis, thus being photosynthetic by their associated symbionts (Gomaa et al., 2014).

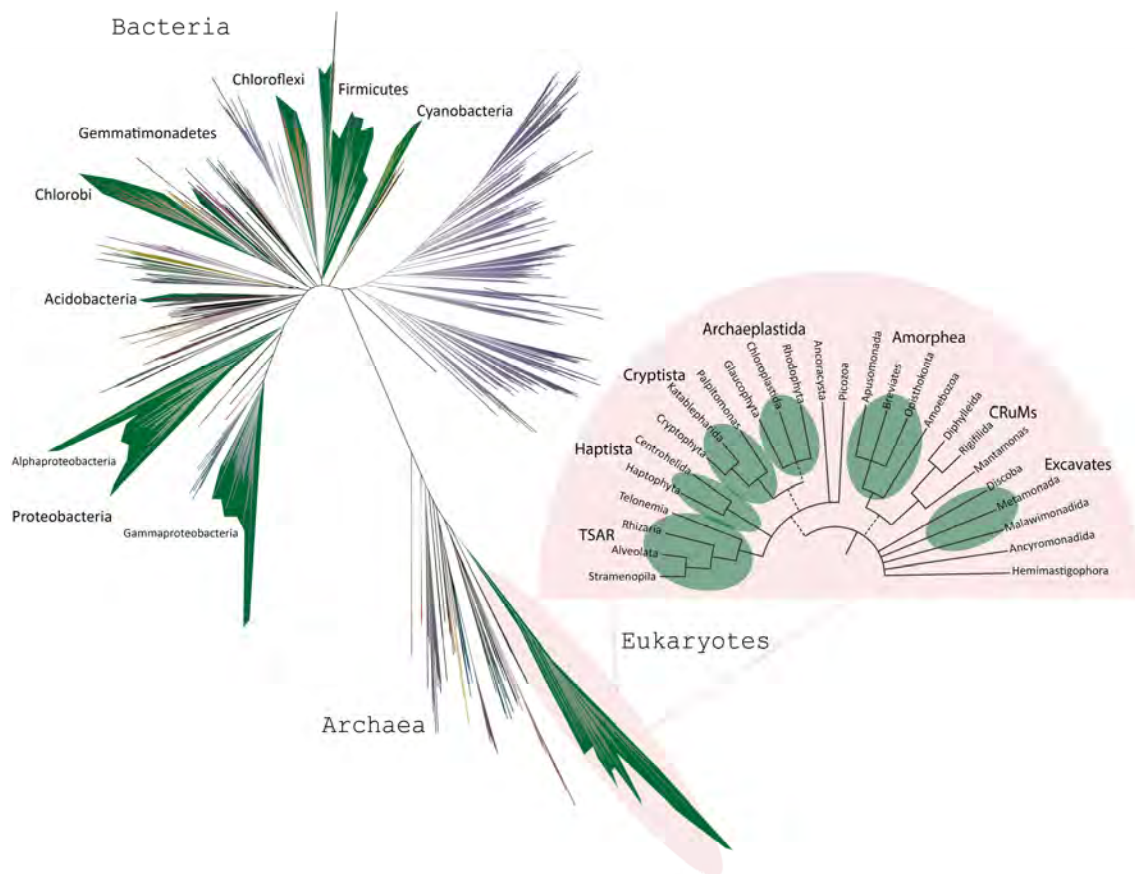


Figure I.1: Tree of life showing in green the major microbial groups in which photosynthetic microbes have been identified. By comparison, all photosynthetic plants belong to Archaeplastida (adapted from Burki et al., 2020 and Hug et al., 2016).

1.2. The diverse photosynthetic pathways of microbial primary producers

Along with the phylogenetic diversity of microbial primary producers, the complicated evolution of photosynthesis multiplied the photosynthetic pathways and the modes of C fixation (Hohmann-Marriott & Blankenship, 2011). The only common characteristic between the different types of microbial photosynthesis is that they produce organic matter from inorganic C (atmospheric CO₂), using light energy. The photosynthetic reaction can be summarized as: CO₂ + light + electron donor → organic matter + byproducts. Photosynthesis is performed in two phases, one in which photosynthetic pigments capture light to produce chemical energy, and the other in which this chemical energy is used to assimilate CO₂. While plants mainly perform one type of photosynthesis (oxygenic one, similar to green algae), phototrophic microbes can use different photosynthetic pathways according to the nature of their photosynthetic pigments, electron carriers, or modes of CO₂ assimilation (Table I.1). The most important scission is done between oxygenic and anoxygenic photosynthesis, according to the nature of the electron donor in the photosynthetic reaction. In oxygenic photosynthesis, water (H₂O) is used as electron donor, and dioxygen (O₂) is released as byproduct. In anoxygenic photosynthesis, the electron donor is most often dihydrogen sulphur (H₂S), but it can also be dihydrogen (H₂), iron (Fe²⁺), arsenic (As³⁺) or even organic compounds. This photosynthetic pathway does not produce O₂ as byproduct. Micro-eukaryotes as well as Cyanobacteria perform the oxygenic photosynthesis, while the other photosynthetic bacterial phyla perform the anoxygenic photosynthesis (Table I.1). In link with these different photosynthetic pathways, the photosynthetic pigments used by phototrophic microbes to collect light differ (Table I.1). In particular, the main pigments used by micro-eukaryotes and Cyanobacteria are chlorophylls (Chl), while the other photosynthetic bacterial phyla use bacteriochlorophylls (BChl) (Kirchman, 2018; Raymond, 2008). Chlorophyll *a* is nevertheless used in small amounts by anoxygenic photosynthetic bacteria such as Chlorobi or Firmicutes (Bryant & Frigaard, 2006; Raymond, 2008). Further, other pigments associated with Chl or BChl can harvest light, such as carotenoids or phycobiliproteins (P. G. Falkowski et al., 2004; Hohmann-Marriott & Blankenship, 2011). Yet, Chl *a* and Bchl play a more important role because they act as electron donor, initiating electron transports and redox reactions necessary to the photosynthesis. According to their environmental requirement and especially to the necessity of dioxygen presence or absence, phototrophic microbes are classified between aerobic or anaerobic

organisms (Table I.1). At last, the second phase of the photosynthesis, in which occurs C fixation, differs between the different phototrophic taxa (Thauer, 2007). Briefly and without going into details, micro-eukaryotes, Cyanobacteria and Proteobacteria use the Calvin-Benson cycle, while Chlorobi use the reverse tricarboxylic acid cycle and Chloroflexi use the hydroxypropionate cycle (Hohmann-Marriott & Blankenship, 2011; Thauer, 2007).

Table I.1: Characteristics of the main photosynthetic microbial groups. Plants have the same characteristics than phototrophic micro-eukaryotes.

Photosynthetic microbial group	Type of photosynthesis	Aerobic status	Main pigments
Phototrophic micro-eukaryotes <i>Green, brown, red algae</i>	Oxygenic	Aerobic	Chl <i>a, b, c, d</i>
Cyanobacteria <i>Blue-green algae</i>	Oxygenic	Aerobic	Chl <i>a, b, c, d</i>
Alphaproteobacteria <i>Purple non-sulphur bacteria</i>	Anoxygenic	Aerobic	Bchl <i>a, b</i>
Gammaproteobacteria <i>Purple sulphur bacteria</i>	Anoxygenic	Anaerobic	Bchl <i>a, b</i>
Chloroflexi <i>Filamentous green non-sulfur bacteria</i>	Anoxygenic	Aerobic	Bchl <i>a, c</i>
Chlorobi <i>Green sulfur bacteria</i>	Anoxygenic	Anaerobic	Bchl <i>a, c, d, e, Chl a</i>
Firmicutes <i>Heliobacteria</i>	Anoxygenic	Anaerobic	Bchl <i>g, Chl a</i>
Acidobacteria	Anoxygenic	Aerobic	Bchl <i>a, c</i>
Gemmatimonadetes	Anoxygenic	Aerobic	Bchl <i>a</i>

Photosynthesis and C assimilation are part of phototrophic microbial metabolism. Historically, living organisms have been classified depending on their metabolism and trophic strategy, either as autotrophs or as heterotrophs. Yet, recent research shows that microbes can combine autotrophy and heterotrophy, a phenomenon called mixotrophy in its broad sense. Thus, the C source of phototrophic microbes can be constituted by a mix balanced between fully inorganic (strict autotrophy) and fully organic C (strict heterotrophy). Mixotrophy has been classified in different categories (e.g. Mitra et al., 2016; Selosse et al., 2017; Stoecker et al., 2017), whose denomination depends on the authors. The first category is absorbotrophic mixotrophy or osmo-mixotrophy, in which mixotrophs acquire soluble organic matter in addition to photosynthesis. The second category, photoheterotrophy, is another form of mixotrophy (Stoecker et al., 2017) that uses light energy to increase metabolism, but that

needs organic C for growth. Recent studies suggest that some phototrophic microbes are essentially heterotrophic but that they might be capable of CO₂ fixation (Tang et al., 2021; Tang et al., 2011), potentially contributing to the global carbon cycle (Graham et al., 2018). It is for instance the case of some anoxygenic phototrophic bacteria such as Acidobacteria or Gemmatimonadetes (Garcia Costas et al., 2012; Zeng et al., 2014). The first two mechanisms are sometimes not considered as mixotrophy in its restrictive definition. Some scientists indeed prefer to restrict mixotrophy to the following strategies: constitutive and non-constitutive mixotrophy. Constitutive or necrotrophic or phago-mixotrophy acquires organic matter by predation on other organisms in addition to photosynthesis. It is particularly well developed among nanoflagellates (mainly belonging to TSAR; Faure et al., 2019). At the opposite, non-constitutive or biotrophic mixotrophy acquires organic matter through the interaction with phototrophic organisms, in addition to phagotrophy. The interactions can be symbiotic (as in some TSAR or Amorphea species), or can result from the appropriation of chloroplasts from photosynthetic preys (as in some TSAR species).

As a conclusion, numerous and very diverse pathways are gathered under the name of microbial photosynthesis. Microbial CO₂ fixation is not only performed by strict photoautotrophic microbes but rather by various taxa forming a continuum towards photoheterotrophy. In link with this diversity of mechanisms, phototrophic microbes are found in all the major aquatic and terrestrial biomes of the planet (Kirchman, 2018), being even able to colonise hostile environments with for instance extreme temperatures, pH, or salt concentrations (Seckbach & Oren, 2007). It shows the complexity of microbial primary producers but also their omnipresence, and questions their respective contribution to the global C cycle.

1.3. Microbial primary production in terrestrial ecosystems

In terrestrial ecosystems, phototrophic microbes constitute a small proportion of the soil microbial biomass (Jassey et al., 2013; Mitchell et al., 2003), and an even smaller proportion of the primary producer biomass, as plants develop a high biomass (Bar-On et al., 2018). Soil phototrophic microbes are therefore often seen as insignificant for C uptake. They were rather studied for other characteristics and function, especially for their diverse taxonomy (Hokmollahi et al., 2016; Starks et al., 1981; Zancan et al., 2006), for their prey role driving food web structure (Lukešová & Frouz, 2007;

Shachak & Steinberger, 1980), of for their role in nutrient cycles, some taxa being able to fix large amounts of nitrogen (Isichei, 1990; Mandal et al., 1999). The microbial primary production has historically been studied in systems with few or no plants, where phototrophic biocrusts constitute the main source of C for the soil system (Anesio et al., 2009; Chen et al., 2020; Maier et al., 2018a). From these studies arose the idea that phototrophic microbes could contribute to the global C cycle (Anesio et al., 2009; Elbert et al., 2012a), and more generally to all soil C fluxes. Many phototrophic microbes are indeed able of C fixation in soils (Miltner et al., 2004; Oliverio et al., 2020), and recent global studies have shown their omnipresence (Bay et al., 2021; Cano-Díaz et al., 2020; Jassey et al., 2022; Oliverio et al., 2020). Jassey et al. (2022) estimated that 5.5×10^6 phototrophic microbial cells inhabit each gram of surface soil on average, and that this abundance unexpectedly peaks in vegetated soils, especially in the moist and acidic ones such as forests or grasslands. A global estimation showed that soil phototrophic microbes could have on average a primary production of $30 \text{ g C.m}^{-2}.\text{yr}^{-1}$ (Fig. 1.2), fixing 3.6 Pg C per year and contributing approximately to 6% of the terrestrial primary production (Jassey et al., 2022). These global estimates however lack precision, and several ecosystems are not or only partially studied. It is the case of northern peatlands, which cover less than 2.5% of continental surfaces (Hugelius et al., 2020; Leifeld & Menichetti, 2018a) and are therefore little represented in these studies. Thus, the role of phototrophic microbes in the primary production and the C dynamic of northern peatland remains virtually unknown. A piece is potentially missing in the comprehension of these peculiar environments, where a slight and fragile unbalance between primary production and decomposition leads to a fascinating C storage. Regarding the global importance of phototrophic microbes in the primary production of numerous terrestrial ecosystems, we believe important to extend this knowledge to northern peatlands.

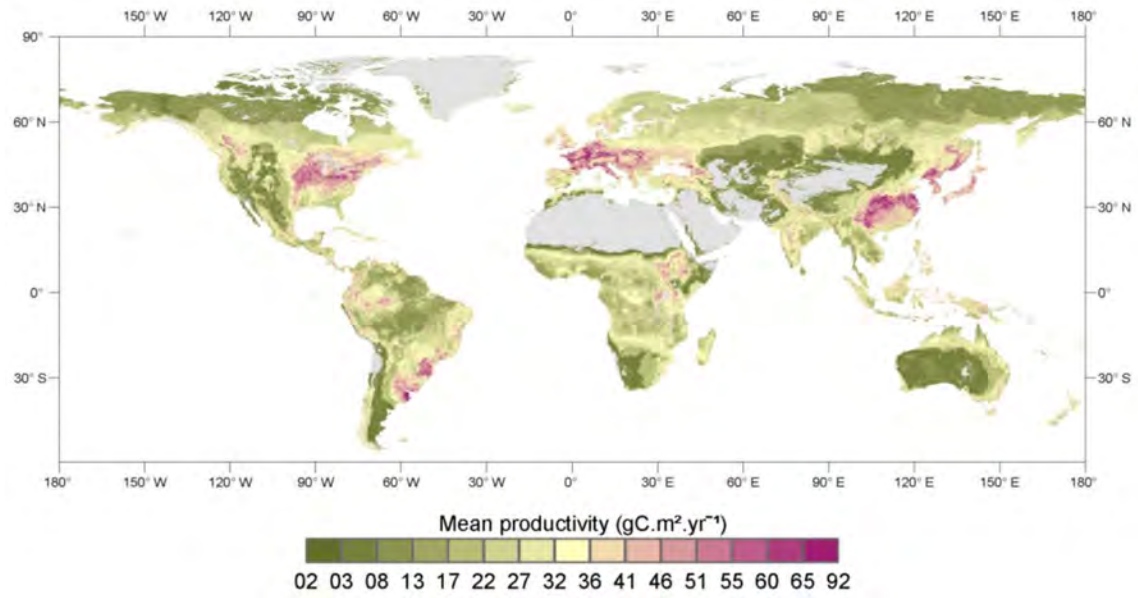


Fig. I.2: Global map of microbial phototrophic primary production in soils, extrapolated from 203 points at the Earth surface (from Jasey et al., 2022).

2. Northern peatland ecosystems

2.1. Functioning of northern peatlands

Northern peatlands are particular ecosystems, where waterlogged, anoxic nutrient-poor and most often acidic conditions reign. They developed and expanded after the postglacial period, mainly over the past 5000 years (Belyea & Baird, 2006; Gajewski et al., 2001), and they currently cover a large part of boreal latitudes (Fig. I.3). Northern peatlands have a particular functioning in which C uptake through photosynthesis exceeds C losses through respiration, decomposition and export. Some estimates show that 2 to 16% of the C fixed by photosynthesis is not decomposed (Päivänen & Vasander, 1994), which results in the accumulation of organic C at a rate of $18.5 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ on average (Yu, 2012). The corresponding organic matter stays in peatlands under the form of peat, which accumulates for thousands of years and forms large layers from few dozens of centimetres to several meters (Manneville et al., 1999). Peatlands are consequently large repositories for terrestrial C. They store more than 500 Gt C at the global scale, which represents a third of the total soil C on Earth (Clymo et al., 1998; Yu, 2011, 2012). Through their fixation of C, peatlands play a major role in global C cycle and climate cooling (Harris et al., 2021). Their activities during the Holocene for instance contributed to decrease atmospheric CO_2 concentrations by 35 ppmv (Frolking & Roulet, 2007).

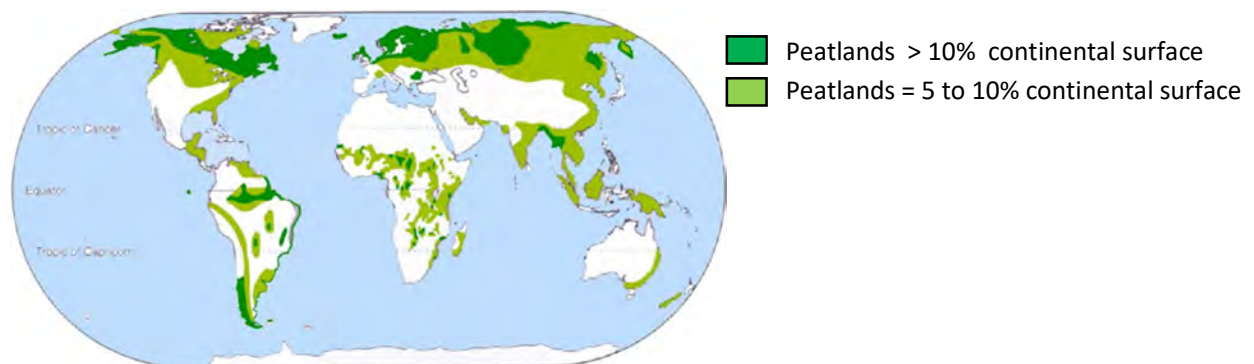


Figure I.3: Repartition of peatlands (from Charman, 2002). Most of peatlands are present in northern latitudes where they developed after Würm glaciation.

The functioning of northern peatlands is fascinating and relatively unique. The imbalance between C uptake and C release is due to several mechanisms. The environmental conditions found in northern peatlands are shown to hamper microbial heterotrophy and decomposition. Microbial communities indeed face physical, chemical and energetic constraints limiting their catabolic activities. For instance, the cold, acidic and nutrient-poor (oligotrophic) conditions found in peatlands slow down enzymatic activities. These conditions can also physically affect the growth of some decomposers, limiting for instance the hyphal growth of specific fungal species (Andersen et al., 2013). Further, waterlogged conditions favour anaerobic environments, restricting aerobic decomposition to the oxic upper layers of peatlands, called acrotelm. More deeply in the catotelm, the absence of dioxygen (O₂) and more globally of other electron acceptors (Artz, 2009) requires the presence of specialist microbial species for the decay process (Andersen et al., 2013; Artz et al., 2006; Thormann et al., 2003). In addition to environmental conditions, decomposition activities highly depend on primary production and on the release of organic C in ecosystems. Primary production is indeed the grounds of energy and material flows in all ecosystems, supporting food chains by the organic matter it produces, and initiating C and nutrient cycles. More precisely, the rate and quality of organic matter production drive decomposition rates and C accumulation in northern peatlands (Andersen et al., 2013). In other words, the nature and the activity of primary producers is crucial for the functioning of northern peatlands. Only an exhaustive understanding of these producers can help to depict a relevant view of peatland C dynamic.

2.2. The primary producers of northern peatlands

2.2.a. *Sphagnum*

Sphagnum are non-vascular peat mosses without roots and lignin (Fig. 1.4). They belong to the bryophyte group, and several hundreds of different species exist, of which 60 are present in Europe (Laine et al., 2018; Michaelis, 2019). Among the different primary producers in northern peatlands, *Sphagnum* mosses are the most important. They can reach a cover of 80-100% (Robroek et al., 2007), dominating the ecosystem. *Sphagnum* mosses are keystone species in peatlands because they shape their habitat in a way that supports peatland development (Hayward & Clymo, 1982; Rydin et al., 2013; van Breemen, 1995). *Sphagnum* do not have a high energetic efficiency, but they use nutrients quite efficiently, which allows them to have a net production comprised between 150 and 800 g C.m⁻².yr⁻¹

(Clymo & Hayward, 1982; van Breemen, 1995). In particular, *Sphagnum* acquire nutrients through a powerful exchange of cation with H^+ , thus impoverishing and acidifying their environment (Lamers et al., 2000; Limpens et al., 2011). Further, *Sphagnum* form dense mats which compete with other plants for space, nutrients or light (Malmer et al., 2003; van Breemen, 1995). The *Sphagnum* mats are efficient in keeping moist conditions, favouring waterlogged conditions, although the mats are highly permeable, also allowing the water level to fluctuate. More particularly, when drought occurs and the water table drops, *Sphagnum* can still get water by their high capillarity, storing it in large dead cells called hyaline cells. If the drought is too intense, *Sphagnum* species can support desiccation as poikilohydric organisms, and can stop or reduce their photosynthetic activity (Jassey & Signarbieux, 2019), which plays an important role in the seasonality of the primary production and the nutrient cycle (Rydin et al., 2006). *Sphagnum* have a continuous growth, growing from the top called capitulum, while the oldest parts at the opposite of their stems become senescent and die (Fig I.4). Thus, a large part of the freshly dead *Sphagnum* organic matter is directly located in deep horizons, close to the slowly permeable and anoxic catotelm. In addition to these specificities allowing *Sphagnum* to dominate northern peatlands and to build a favourable environment for peat accumulation, *Sphagnum* play another key role for the C sequestration by the compounds they produce, illustrating the interactions existing between organic matter input and decomposition. In particular, *Sphagnum* species produce a recalcitrant matter, partly composed by polyphenols (Verhoeven & Liefveld, 1997) and that is extremely resistant to microbial decomposition (Hájek et al., 2011). Peat is thus mainly composed by *Sphagnum* residues (Williams & Yavitt, 2003). *Sphagnum* also release allelochemicals that have antimicrobial properties (Verhoeven & Liefveld, 1997), hampering microbial catabolic activities (Freeman et al., 2001). Through all these aspects, *Sphagnum* are fundamental photosynthetic organisms playing a key role in the peatland functioning. Yet, peatland ecosystems shelter other primary producers such as vascular plants and microbes.

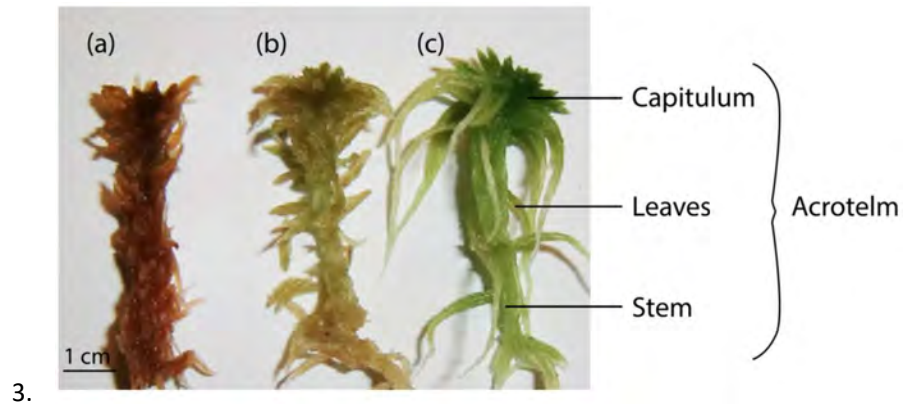


Figure 1.4: Example of different *Sphagnum* species found in European peatlands, and their morphologies (from Granath et al., 2012): *S. fuscum* (a), *S. balticum* (b) and *S. fallax* (c).

2.2.b. Vascular plants

In addition to *Sphagnum* mosses, northern peatlands show a diverse vegetation composed by vascular plants including graminoids, herbs, shrubs or even tree species (Rydin et al., 2013; Fig. 1.5). Vascular plants compete with *Sphagnum* mosses for light, water and nutrients (Malmer et al., 2003), but they can also facilitate *Sphagnum* growth when their cover remains low. The root system of vascular plants makes a frame for *Sphagnum* shoots, while vascular plants can create stable microclimates improving microhabitat conditions (Pouliot et al., 2011; Rydin et al., 2013; Tuittila et al., 2000).



Figure 1.5: Different vascular plant species found in European peatlands, including graminoids (*Eriophorum angustifolium* (a)), ericoids (*Andromeda polifolia* (b)), and herbs (*Drosera rotundifolia* (c) and *Rubus chamaemorus* (d)).

Further, as primary producers, vascular plants also have an important role in the fixation and the dynamic of C in peatlands. Vascular plants have globally a higher photosynthetic efficiency than *Sphagnum* species (Armstrong et al., 2015; Ward et al., 2009), but their lower cover implies that they contribute less to the total peatland C fixation (Rydin et al., 2013). Nevertheless, when vascular plant cover is high, as it is for instance the case with dense shrub layers, vascular plants can contribute to about 50% to peatland gross photosynthesis (Gavazov et al., 2018), having a production comprised between 60 and 760 g C.m⁻².yr⁻¹. The primary production of vascular plants is important in peatlands because it is more stable than *Sphagnum* production throughout the growing season. In particular, vascular plants allow a maintenance of high levels of CO₂ fixation during warm and dry conditions, when *Sphagnum* are less productive due to desiccation (Gavazov et al., 2018; Kuiper et al., 2014; Laine et al., 2012). Similar to *Sphagnum*, vascular plant organic matter fuels heterotrophic microbial communities. However, vascular plant litter has different chemical properties than the *Sphagnum* one; hence, it has a different effect on microbial decomposition. In particular, the litter of vascular plants is more labile and decomposes faster than the *Sphagnum* litter (Bragazza et al., 2007; Mao et al., 2018; Mastný et al., 2018). It further provides decomposers extra-energy to invest in the decomposition of more recalcitrant organic matter (Basiliko et al., 2012; Hardie et al., 2009; Walker et al., 2016). Therefore, vascular plants can destabilise the peatland C dynamic through the input of fresh and labile organic matter, and they can lead to an increase of C release toward the atmosphere (Robroek et al., 2016).

Altogether, these result highlights that the community composition of primary producers can affect the decomposition processes in peatlands, with cascading effects on C sequestration or release (Fig. I.6) (Del Giudice & Lindo, 2017). It illustrates the necessity of knowing the community composition of primary producers in peatlands to understand plainly the C dynamic. Yet, among the peatland primary producers, there is one whose functional role is totally neglected: phototrophic microbes (Fig. I.6).

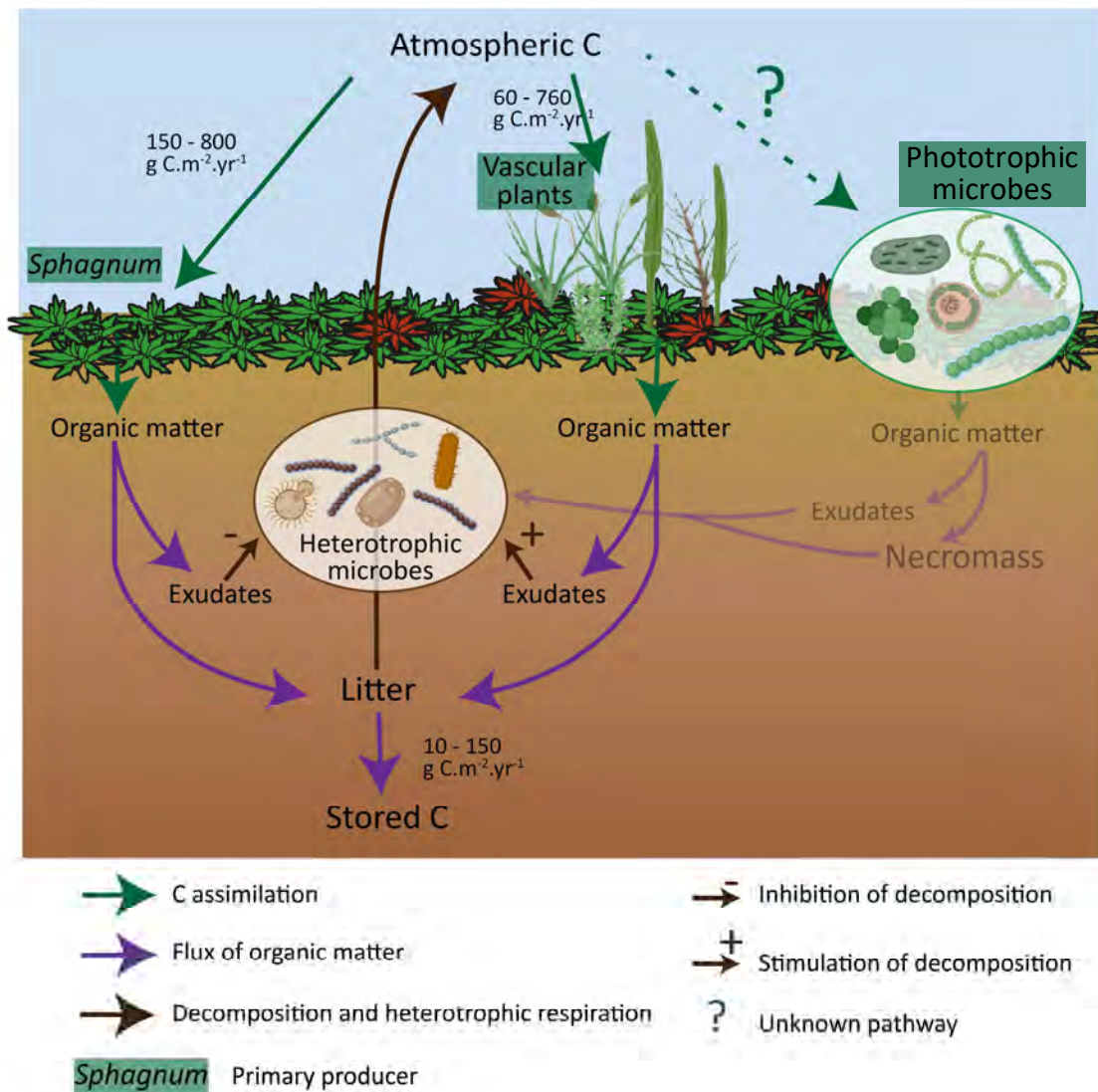


Figure I.6: Simplified view of the peatland C fluxes, and role of the primary producers. In the current view, the role of phototrophic microbes is neglected.

2.2.c. Phototrophic microbes

In northern peatlands, *Sphagnum* shape an inhospitable environment but also shelter a diverse microbial community living inside or at the surface of their leaves. *Sphagnum* have a particular cellular structure, in which large dead cells called hyalocists store water with an elevated pH compared to the acidic peatland (Turetsky et al., 2012). Hyalocists are therefore seen as oases in which microbial

communities can thrive and develop (Fig. I.7; Kostka et al., 2016). Consequently, a close link exists between *Sphagnum* species and microbial communities, which are considered as the *Sphagnum* microbiome. This means that the diversity and function of microbial groups is specific to *Sphagnum* species (Bragina et al., 2012; Kostka et al., 2016), and that the microbial community benefits the peat moss host, correlating with its fitness and health (Bragina et al., 2014). This close association between *Sphagnum* and their microbiome is called the bryosphere (Lindo & Gonzalez, 2010). The highest abundance and diversity of microbes is found in *Sphagnum* capitula, probably because of their light and aerobic conditions (Searles et al., 1999). Phototrophic microbes are part of the *Sphagnum* microbiome, and together with the other heterotrophic microbes, they form a complex food web (Lindo & Gonzalez, 2010) composed by a dominance of prokaryotes, essentially bacteria but only few archaea (Bragina et al., 2014), and by micro-eukaryotes. The microbial food web comprises primary producers (phototrophic microbes), decomposers (heterotrophic bacteria and fungi), and predators (heterotrophic protists and micro-metazoa). A strong top-down control drives the structure of the microbial food web, due to the presence of testate amoebae, which are unicellular eukaryotes from diverse body size (20 – 200 μm). Testate amoebae can ingest very diverse preys including phototrophic microbes, bacteria, fungi, or heterotrophic protists (Gilbert et al., 2000, 2003; Jassey et al., 2012b). They establish thus a key trophic link between organic matter cycling, decomposers, micro-eukaryotes and plants (Jassey et al., 2016; Wilkinson & Mitchell, 2010).

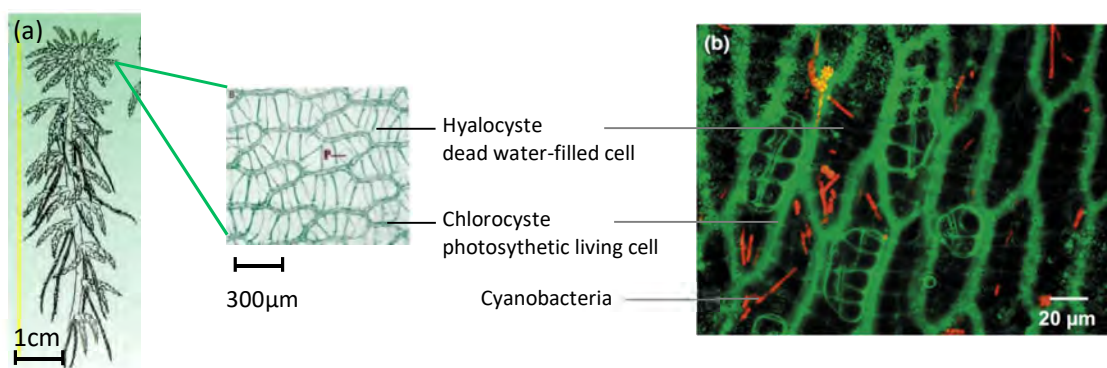


Figure I.7: Cellular structure of *Sphagnum* (a, from Manneville et al., 1999), with their hyalocysts sheltering microbes, here Cyanobacteria (b, from Kostka et al., 2016).

From a taxonomic standpoint, phototrophic microbes are extremely diverse (Fig. 1.8) to the point of being considered as the most diverse group of microbes in peatlands (Gilbert & Mitchell, 2006a). The six major micro-eukaryote groups in which photosynthesis has been identified on Earth are present in peatlands (Gilbert & Mitchell, 2006a; Jassey et al., 2011b; Reczuga et al., 2020; Singer et al., 2019). Further, the phototrophic prokaryotic groups Cyanobacteria, purple bacteria (Proteobacteria) and green sulphur bacteria (Chlorobi) have been reported in peatlands (Bragina et al., 2012, 2014; Kamal & Varma, 2008; Urbanová & Bárta, 2014, 2016). Acidobacteria and Chloroflexi have also been reported, but without knowing if they were phototrophic or heterotrophic taxa (Bragina et al., 2012, 2014). In terms of species, more than 400 phototrophic microbes can be identified in a single peatland, but most often, around 200 species are found (Gilbert & Mitchell, 2006a). This diversity is in link with more recent studies that use metabarcoding technics. Up to 110 operational taxonomic units (OTUs) of phototrophic protists were indeed identified in a Canadian peatland (Heger et al., 2018a). A higher diversity was found in a Polish peatland, with 216 OTUs of photoautotrophic and 52 OTUs of mixotrophic micro-eukaryotes (Reczuga et al., 2020). In terms of abundance, numerous individuals of phototrophic microbes thrive in peatlands, with a number of cell ranging between 10^3 and 10^7 cell.l⁻¹ of pore water or between 10^2 and 10^7 cell.g⁻¹ of *Sphagnum* dry weight (Gilbert & Mitchell, 2006a; Jassey et al., 2015). Among phototrophic microbes, green algae (Archaeplastida, essentially Chlorophyta) are the most diverse and abundant group, as they can represent 45% of the species (Gilbert & Mitchell, 2006a) and 65% of the cell density (DeColibus et al., 2017). The study of DeColibus et al. (2017), lead in an Alaskan peatland (though not in a *Sphagnum*-dominated peatland), further shows that Cyanobacteria are the second most important group by their abundance, representing between 20% and 40% of the phototrophic microbial community. Then, diatoms, dynophytes, chrysophytes (TSAR group) and euglenoids (Discoba group) are less abundant, representing less than 10% of the total cell density of phototrophic microbes. This study slightly differed from the biomass observations made in a French *Sphagnum*-dominated peatland (Jassey et al., 2011b), where Chlorophyta dominated, with the presence of the class Chlorophyceae (e.g. *Cylindrocystis* sp. and *Penium* sp.), followed by Ochrophyta, with the class Bacillariophyceae (e.g. *Pinnularia viridis*). In these observations, Cyanobacteria were also dominant, representing on average a quarter of the phototrophic microbial biomass, with the presence of the order Chroococcales (e.g. *Chroococcus giga*) and Nostocales (e.g. *Anabaenae cylindrical*, *Aphanothece nidulans*). Mixotrophic species are also well represented in

Sphagnum-dominated peatlands with for instance the presence of the mixotrophic ciliate *Paramecium bursaria*, or the mixotrophic testate amoeba *Hyalosphenia papilio*, *Archerella flavum*, or *Heleopera sphagni* (Gilbert et al., 2000; Jassey et al., 2012b, 2016; Mieczan, 2009a).

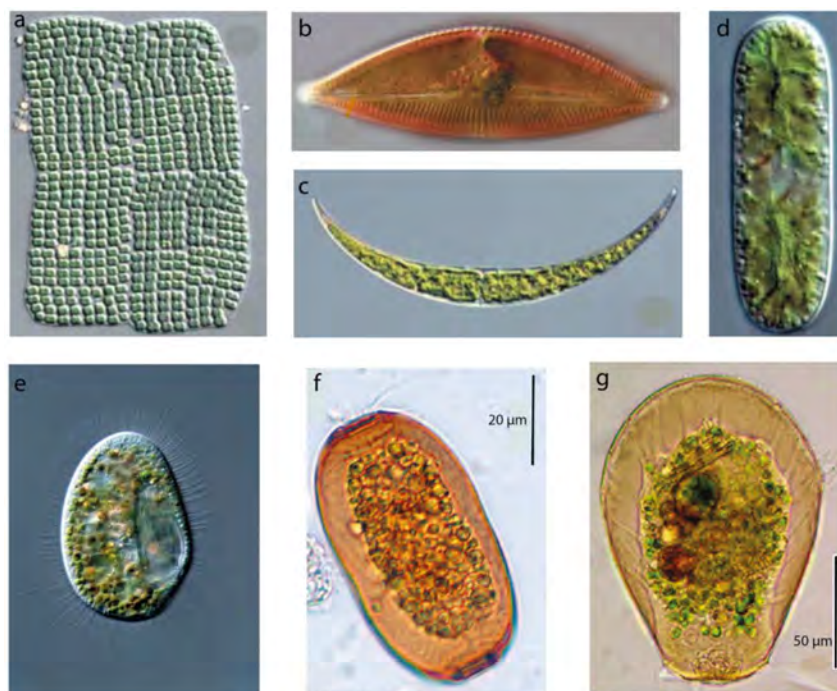


Figure I.8: Picture of some phototrophic microbes encountered in northern *Sphagnum*-dominated peatlands: a: *Merismopedia sp.*, b: *Cymbella ehrenbergii*, c: *Closterium diana*e, d: *Cylindrocystis brebissonii*, e: *Histiobalantium natans*, f: *Archerella flavum*, g: *Hyalosphenia papilio*. From Kreutz & Foissner, 2006 (a-e), Vincent Jassey (f) and Edward Mitchell (g).

Phototrophic microbes are a non-negligible component of the *Sphagnum* microbiome as they can represent 35% (Gilbert et al., 1998a) or even 50% (Gilbert et al., 1998b; Gilbert & Mitchell, 2006a) of the total microbial biomass. The relative importance of the different microbial groups is however strongly variable according to the environmental conditions (Gilbert & Mitchell, 2006a), and phototrophic microbes can have a lower importance, between 10% and 25% of the total biomass (Basińska et al., 2020; Jassey et al., 2011b). Some estimates gave a phototrophic microbial biomass around 0.2 mg C.g⁻¹ of *Sphagnum* dry weight (DW), and an heterotrophic microbial biomass around 2 mg C.g⁻¹ DW (heterotrophic bacteria: 1 mg C.g⁻¹ DW, fungi: 0.5 mg C.g⁻¹ DW, predators: 0.5 mg C.g⁻¹ DW; Basińska et al., 2020; Gilbert & Mitchell, 2006; Jassey et al., 2011b; Mitchell et al., 2003). Yet, the

estimation of phototrophic biomass often does not take into account mixotrophic species that are abundant in northern peatlands. Mixotrophs can represent a high biomass due to their large body size. It is especially the case of mixotrophic testate amoeba whose biomass has been shown to reach 20% of the total microbial biomass (0.4 over 1.9 mg C.g⁻¹ DW) in a *Sphagnum*-dominated peatland (Jassey et al., 2015). In that case, the biomass of mixotrophic testate amoebae exceeded the one of all other phototrophic microbes. This high biomass, in addition to their peculiar feeding habit between autotrophy and top-predators, confers to mixotrophic testate amoebae a key role in the functioning of microbial communities in peatlands (Jassey et al., 2015). Globally, the relative importance of phototrophic microbes in terms of biomass joins the relative importance in terms of sequences found in metabarcoding surveys. For instance, phototrophic microbes have been found to represent between 10% and 50% of the microeukaryotic sequences in a *Sphagnum*-dominated Polish peatland (Reczuga et al., 2020). Another study have shown that Chlorophyta only (Archaeplastida) can represent between 10% and 40% of the total protist sequences in a Canadian peatland (Heger et al., 2018a). Concerning prokaryotes, Cyanobacteria seem to be less represented among bacteria, as they have been shown to represent around 1% of the prokaryotic sequences in an Austrian *Sphagnum*-dominated peatland (Bragina et al., 2012, 2014).

Despite a high abundance and proportion in the microbial community, the functional role of phototrophic microbes is little explored regarding their role of C fixation. Yet, as primary producers, phototrophic microbes constitute a source of organic C that can be used by heterotrophic communities and more generally by the microbial food web of *Sphagnum*. The flow of matter, nutrients and energy transits through the food chain and initiate a microbial loop (organic matter -> decomposers -> micro-predators; Gilbert et al., 1998). This flow is necessary in peatlands because it allows a recycling of C and nutrients, redistributing them at every level of the food chain. For instance, the production of labile exudates by phototrophic microbes can stimulate and promote heterotrophic bacteria in graminoid-dominated peatlands (Wyatt & Rober, 2020; Wyatt & Turetsky, 2015a). An important gap remains on the importance of this phenomenon, since the levels of microbial primary production in *Sphagnum*-dominated peatlands are little studied. A first estimation has been made in 1998 by Gilbert et al. (1998a), evaluating the microbial production at about 3 g C.m⁻².yr⁻¹ in a *Sphagnum*-dominated peatland, i.e. less than 1% of plant production (Gilbert et al., 1998a). This estimation was however limited in time and space, and it is challenged by the recent global estimates of phototrophic microbes

importance in terrestrial ecosystems (Jassey et al., 2022). It is also challenged by other measurements done in graminoid-dominated peatlands, where phototrophic microbes could contribute up to 10% of ecosystem primary production. Further, a mesocosm experiment showed that the primary production of *Sphagnum*-dominated peatlands is correlated with the abundance of phototrophic microbes and especially of mixotrophic testate amoebae (Jassey et al., 2015), suggesting an unexpected role of phototrophic microbes in peatland primary production.

Phototrophic microbes are abundant in *Sphagnum*-dominated peatlands, but their primary production remain unexplored despite its potential importance for the peatland C dynamic. We thus believe crucial to re-evaluate the microbial C fixation in *Sphagnum*-dominated peatlands and its contribution to the total C uptake of the ecosystem. In particular, we believe important to study the spatial and temporal patterns of microbial primary production and to identify the environmental drivers that could affect the levels of microbial photosynthesis.

3. Environmental variations in peatland ecosystems and possible consequences for phototrophic microbes

Until now, our presentation of northern *Sphagnum*-dominated peatlands depicts them as even environments, with a common ecosystem structure and functioning. Yet, they spread over a large part of the northern hemisphere, from mid to high latitudes (above 40°N). Northern peatlands therefore expand from oceanic to arctic climates. In these latitudes, peatlands are subject to a seasonality in their functioning, with an alternation of growing seasons and more or less harsh winters. Further, peatlands also experience global change, and especially climate change that is predicted to be more intense in high latitudes. All these environmental variations affect northern peatlands with consequences on their structure (for instance affecting the composition of plant community) and on their functioning (for instance affecting the photosynthetic rates of primary producers). How these environmental changes affect microbial photosynthesis and its contribution to ecosystem primary production remains however unknown and need to be studied (Fig. I.9).

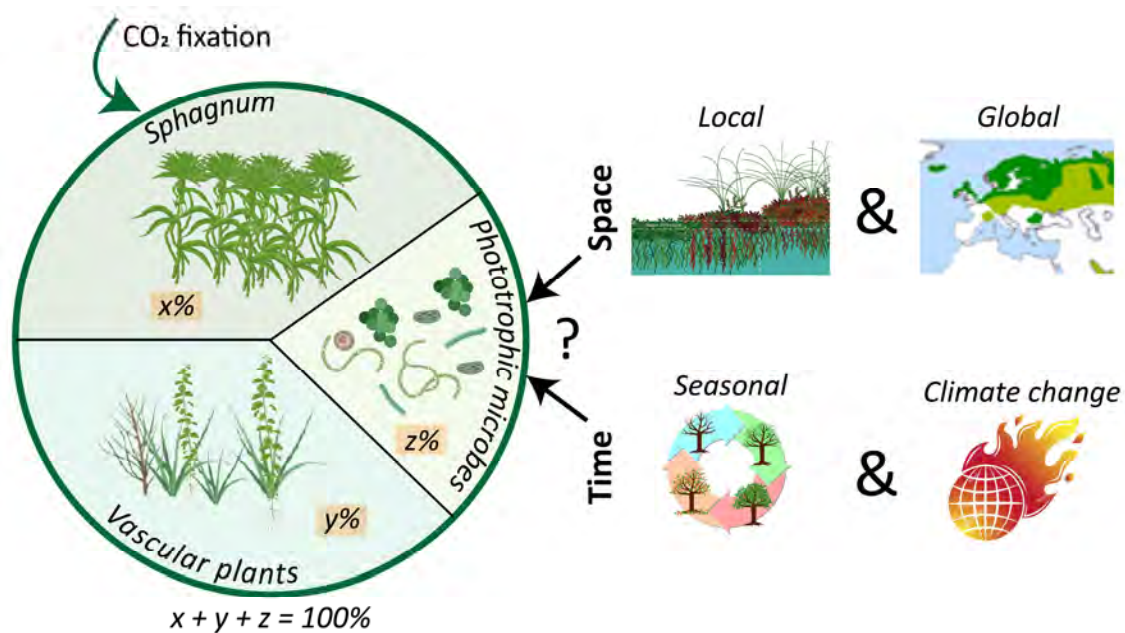


Figure I.9: Overview of the spatiotemporal factors that could affect the contribution of phototrophic microbes to peatland primary production.

3.1. Spatial variation in peatland ecosystems

Northern peatlands show very diverse habitats and microhabitats characterised by different vegetation communities in terms of *Sphagnum* and vascular plant species (Kvillner & Sonesson, 1980). The vegetation changes are underpinned by different environmental factors both at a global scale where climate play a major role (Robroek et al., 2017b), and at a local scale where the effects of water table depth or nutrient availability are more important (Rydin et al., 2013) (Fig. I.10; Fig. I.11). For instance, at a global scale, mean annual temperature and precipitation drive the taxonomic turnover of *Sphagnum* and vascular plant species (Robroek et al., 2017b). At a local scale, northern peatlands exhibit a mosaic of various microhabitats, principally distinguished along microtopographic gradients including hollows, lawns or hummocks as the distance to the water table increases (Fig. I.10). Plant community changes along this gradient, with for instance a vascular plants shift from graminoids in lawns to shrubs in hummocks (Payette & Rochefort, 2001), or with *Sphagnum* shifts, from species more adapted to waterlogged conditions in hollows (e.g. *Sphagnum fallax*, *S. cuspidatum*), to species more adapted to droughts in hummocks (e.g. *S. fuscum*, *S. divinum*, *S. rubellum*) (Gunnarsson, 2005; Hayward & Clymo, 1982; Kvillner & Sonesson, 1980). A distinction is also done among *Sphagnum*-dominated peatlands between bogs and fens. Bogs are ombrotrophic, i.e. they receive only rain water, while fens are more minerotrophic, being closer to the water table, and being supplied by mineral-rich soil waters. Different plant species are found in fens and bogs (Rydin et al., 2013; Sjörs, 1959; Vitt & Slack, 1975).

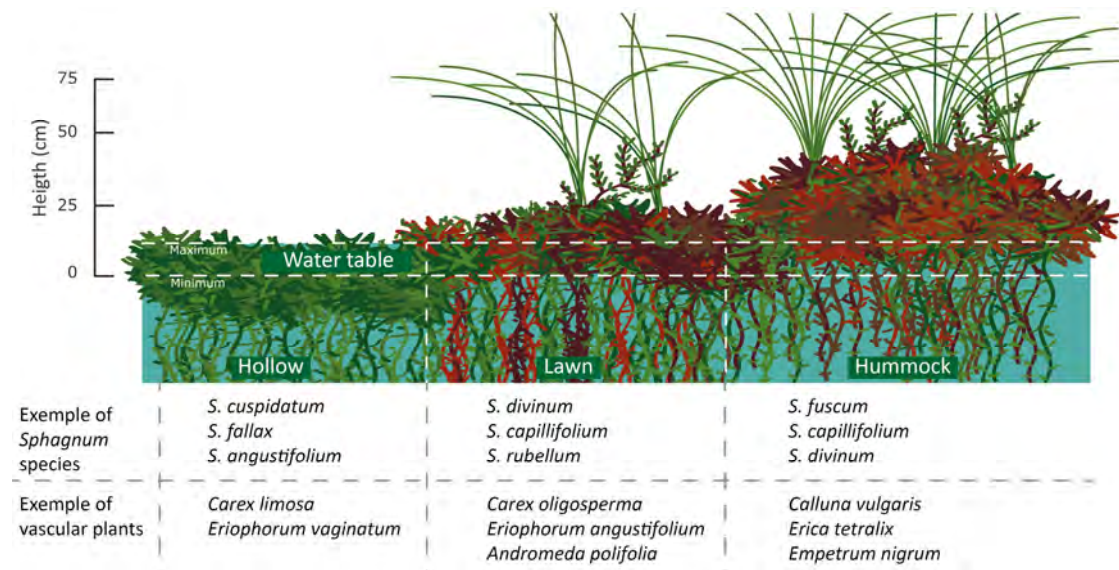


Figure I.10: Schematic view of microhabitats encountered along microtopographic gradients, and of their plant communities (from Vincent Jassey).

Peatland microbial communities are affected by these environmental changes all the more that they are sensitive to plant diversity and community composition (Jassey et al., 2014; Robroek et al., 2015a). A high spatial heterogeneity of microbial communities is found in the different peatlands habitats (e.g. Oloo et al., 2016; Küttim et al., 2017; Heger et al., 2018; Chroňáková et al., 2019), modulating microbial processes, C-related multifunctionality (Robroek et al., 2017a, 2016) and eventually ecosystem functioning (e.g. Robroek et al., 2015). Phototrophic microbes are not immune to these environmental changes, and their community structure varies spatially. Phototrophic microbial assemblages and turnovers depend on microhabitat, but also on geographic distance (Jassey et al., 2011a; Machová-Černá & Neustupa, 2009). Abiotic factors such as conductivity, moisture or pH can affect the repartition of phototrophic microbes (Machová-Černá & Neustupa, 2009), as it is for instance the case of diatoms (L. Küttim et al., 2017) or mixotrophic ciliates (Mieczan, 2009a). Biotic factors are also known to drive the community composition of phototrophic microbes in peatlands. In particular, several species of diatoms or desmids are specific of their *Sphagnum* host (Mutinová et al., 2016). Plant community composition can affect bacterial communities including phototrophic taxa such as Cyanobacteria, Chlorobi or Chloroflexi (Chroňáková et al., 2019). Further, different plant communities produce a different shade according to the vascular plant cover, which can affect the composition of phototrophic microbial communities (L. Küttim et al., 2017).

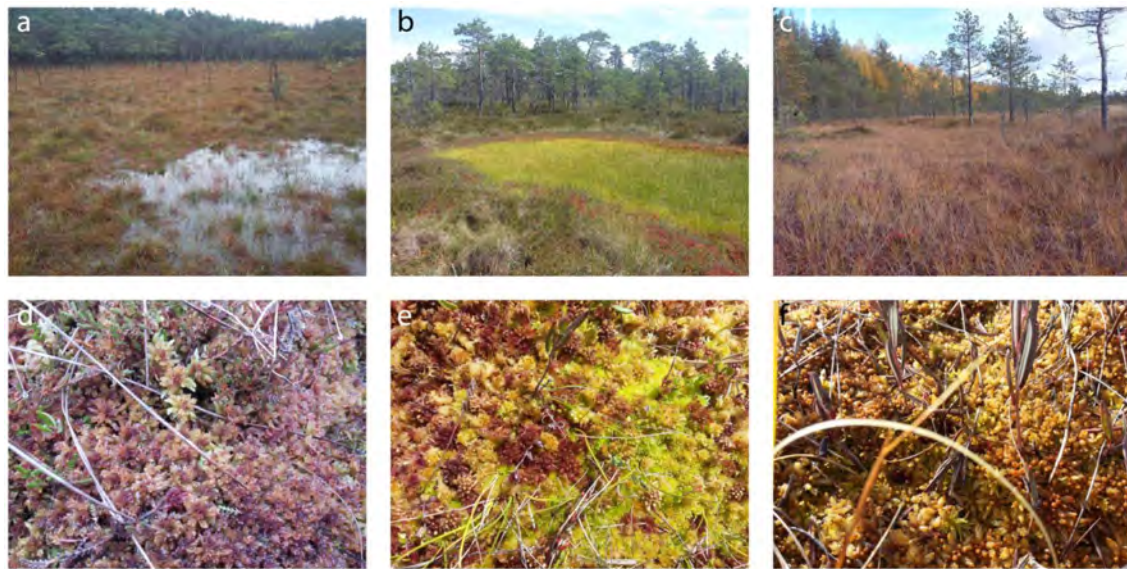


Figure I.11: Pictures of three peatlands located at different latitudes and climates, in Poland (a, d), Estonia (b, e) and Finland (c, f). The different peatlands exhibit different microhabitats, recognisable by the water table level, and the vegetation composition. The respective *Sphagnum* mats in the different peatlands (d-f) are composed by different *Sphagnum* species and are colonized by some vascular plants.

Thus, the community composition of phototrophic microbes in peatlands seems to follow spatial patterns at local or global scales, being driven by physico-chemical or biotic factors. However, the consequences for microbial photosynthesis are unknown. I expect the microbial contribution to peatland primary production to change. A reason is that a decoupling might exist between the structure and the function of peatland microbial communities (Andersen et al., 2013). The microbial processes might exhibit different intensities or mechanisms, modulating the ecosystem functioning in the different habitats. Another reason is that the production of the other primary producers is affected by environmental changes. In particular, different *Sphagnum* species have different productivities, varying by a factor of seven between the least and the most productive species (Gunnarsson, 2005). For instance, several studies have found a decreasing *Sphagnum* productivity with increasing latitude and decreasing temperatures (Gunnarsson, 2005; Moore, 1989; Wieder & Lang, 1983). Further, *Sphagnum* species found in hummocks are nearly two times less productive than the ones found in

hollows (Gunnarsson, 2005). An increase of vascular plant cover also increases the ecosystem production due to highest photosynthetic efficiency (Gavazov et al., 2018). These variations possibly affect the ratio between microbial and plant production, and may have consequences on the C dynamic.

3.2. Seasonal variations in peatland ecosystems

At northern latitudes, peatlands are subjected to seasonal variations affecting their functioning (e.g. Armstrong et al., 2015; Dinsmore et al., 2013; Sun et al., 2012). In particular, a seasonality in the C dynamic has been observed, and CO₂ fluxes towards the atmosphere can flip from negative to positive throughout the annual cycle (Bubier et al., 1998; Lafleur et al., 2001). Peatland C uptake increases after snowmelt, peaking in summer and declining toward the fall, while it is negative (C release) during snow cover (Lafleur et al., 2001). Such seasonality is linked with the dependence of both microbial (Fenner et al., 2005) and plant (M. Küttim et al., 2020) metabolic rates to meteorological conditions and especially temperature. For instance, some vascular plants or *Sphagnum* species can continue physiological processes and development under snow, but their metabolic rates are nevertheless reduced by the cold, limiting their C uptake (M. Küttim et al., 2020). Further, *Sphagnum* production can become negative under drought conditions (Jassey & Signarbieux, 2019). Similar to plants, the metabolic rates of phototrophic microbes might be dependent on seasonality. Further, microbes have short generation times, fast growths and turnovers (Schmidt et al., 2007; Schönborn, 1965), and their abundance and community structure can rapidly respond to environmental conditions (Schönborn, 1965). In peatlands, microbial communities vary throughout the annual cycle (e.g. Lamentowicz et al., 2013; Lara et al., 2011; Marcisz et al., 2014), and phototrophic microbes are no exception. Measures of chlorophyll *a* in peatland pore water show that the phototrophic microbial stocks peaks in late winter/spring (Lew et al., 2015). At the opposite, the abundance of anoxygenic phototrophic bacteria (aerobic anoxygenic phototrophs) peaks in summer, when irradiance and temperature are at their maximum (Lew et al., 2015). Further, the relative abundance of phototrophic microbes within the *Sphagnum* microbiome is maximum in spring and autumn (Reczuga et al., 2020). In addition to these abundance changes, other observations in peatland (though not a *Sphagnum*-dominated one) showed that the community structure of phototrophic microbes shifted during the growing season. Green algae and diatoms were more abundant in summer, Cyanobacteria peaked in late summer, while

Chrysophytes were more abundant in late spring (Rober et al., 2013). Abundance and structure changes of phototrophic microbial communities were further correlated with a variation of the phototrophic microbial production that peaked in late spring (Rober et al., 2014). These results show that microbial photosynthesis might not be stable in *Sphagnum*-dominated peatlands, but might change throughout the annual cycle according to environmental and meteorological conditions.

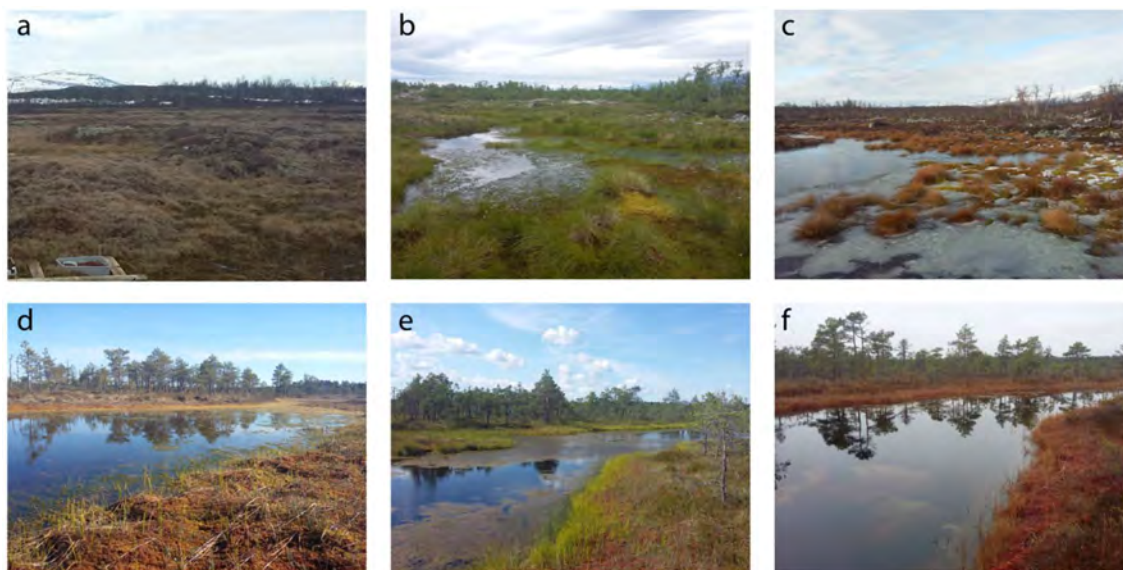


Figure I.12: Pictures of a Swedish (Abisko, a-c) and an Estonian (Männikjärve, d-f) peatland under three different seasons: spring (a, d), summer (b, e) and autumn (c, f).

3.3. The peatland sensitivity to climate change

Climate change includes increasing temperature along with shifts in precipitation patterns (Dai, 2013). Extreme precipitation events are expected to become more frequent, but interspersed with longer intervals without rains, leading to droughts. In northern latitudes, consequently to these changes, soil C dynamics are expected to change (Dai et al., 2018; Davidson & Janssens, 2006; Frank et al., 2015; Gerten et al., 2008), and so is it in peatlands (Barel et al., 2021; Blodau & Moore, 2003; Dorrepaal et al., 2009). In particular, the responses of northern peatland to climate change are a cause of important concern, as peatlands may turn from a C sink towards a C source. Such switch may have dramatic consequences on the global C cycle, and hence on climate. Rising temperature and elevated CO₂ are expected to increase the photosynthetic rates of peatland primary producers (Breeuwer et al., 2008; Dorrepaal et al., 2004; Gunnarsson, 2005; Jassey & Signarbieux, 2019; Ofiti et al., 2021; Weltzin et al.,

2001). For instance, the photosynthetic capacity of *Sphagnum fallax* can increase by 40% during wet and warm conditions. Further, climate warming can promote the growth and cover of vascular plants (Dieleman et al., 2015; Weltzin et al., 2003), that are more productive than *Sphagnum*. These changes suggest an intensification of the primary production in peatlands under climate change. However, despite a photosynthetic increase, community changes in the primary producers can affect the organic matter produced and destabilize the peatland C dynamic (Bu et al., 2011; Gavazov et al., 2018). For instance, vascular plants produce a more labile organic matter than *Sphagnum* mosses, stimulating decomposition (Robroek et al. 2016). Rising temperatures have thus the potential to enhance C release toward the atmosphere (Ofiti et al., 2021). Due to the antagonism in the two previous mechanisms, in which climate change stimulates both primary production and decomposition, some uncertainties remain in the direction and the intensity of the climate perturbation on the peatland C dynamic. Moreover, the effects of climate change are more complex than presented, being multifactorial and depending on the interaction between several factors, for instance soil moisture, habitats, seasons or species (e.g. Binet et al., 2017; Buttler et al., 2015; Jassey & Signarbieux, 2019). In these conditions, taking into account phototrophic microbes could bring a significant additional piece to better evaluate the global response of peatland primary production and C dynamic to climate change.

The strong effects of climate change on phototrophic microbes in several terrestrial ecosystems (e.g. Gray et al., 2020; Hui et al., 2018, 2021; Rindi, 2011) suggest the possibility of diverse outcomes in peatlands, with crucial consequences for the C dynamic. In northern peatlands, phototrophic microbes are early indicators of warming and their community structure is extremely sensitive to increasing temperature (Basińska et al., 2020). For instance, phototrophic protist biomass correlate positively with warming (Basińska et al., 2020), as does microbial chlorophyll *a* concentration in *Sphagnum*-dominated peatlands (Mieczan & Tarkowska-Kukuryk, 2021). Further, warming alters the community structure of bacteria, with an increase of the cyanobacterial relative abundance (Carrell et al., 2019). At the opposite, mixotrophic testate amoebae, and especially *Hyalosphenia papilio*, correlate negatively with rising temperature (Basińska et al., 2020; Jassey et al., 2015) with possible consequences that reduce ecosystem primary production (Jassey et al., 2015). Changing precipitation patterns can also affect phototrophic microbes, as wetter or dryer conditions alter the relative abundance of phototrophic microbes in the *Sphagnum* microbiome (Reczuga et al., 2020). Further, climate change has been showed to strongly alter the diversity and the abundance of predators in the

microbial food web. Drought or a temperature increase of 1.5°C can reduce the abundance of testate amoebae up to a 70% loss (Jassey et al., 2013; Lamentowicz et al., 2013; Reczuga et al., 2018a). The consequence is a decrease in the predator-prey mass ratio, with possible trophic cascades (Lamentowicz et al., 2013). In particular, the microbial loop is disturbed while lower trophic levels including phototrophic microbes are stimulated (Reczuga et al., 2018a). The consequences for the C cycle can be multiple. In a graminoid-dominated peatland, the loss of microbial top predators benefitted to herbivores. Carbon dioxide emissions were then increased due to the loss of microbial primary production (Wyatt et al., 2021).

Therefore, there is no doubts that climate change alters the community structure of phototrophic microbes in peatlands. Our knowledge remains nevertheless partial as for instance, a quantification of the response intensity is lacking, or as a modulation of the response by peatland habitats or seasonality might exist but remains unknown. In particular, the consequences of these community changes for the microbial primary production, and more globally for the peatland C dynamic are unexplored. In graminoid-dominated peatlands, warming is expected to increase phototrophic microbial abundance and to stimulate C decomposition through a higher release of labile exudates (Wyatt & Rober, 2020). This result suggests that a similar importance of phototrophic microbes in the C dynamic might exist in *Sphagnum*-dominated peatlands. It further shows the necessity to better know the role of phototrophic microbes in the ecosystem primary production and its possible evolution under climate change.

4. Objectives of the thesis

Despite the common recognition that phototrophic microbes are abundant and diverse in northern peatlands, their functional role as primary producers and their contribution to peatland C dynamic are still overlooked. The magnitude of the peat C accumulation result from a strong dependence between organic matter inputs and decomposition. Therefore, any shift in anabolic or catabolic activities likely influence the peatland C dynamic. In particular, the evolution of phototrophic microbial photosynthesis under climate change could destabilize the fragile balance between C uptake and C release and could alter the driving force of C sequestration in peatlands. To date, only few studies focussed on the role of phototrophic microbes in peatlands, and our knowledge about their diversity, abundance and photosynthetic activity remain partial. Previous studies mostly focussed on specific phototrophic taxa, and/or on specific peatland habitats. The spatial distribution of phototrophic microbes among small and large scales remain confuse.

The objectives of the thesis were therefore to (1) show the importance of phototrophic microbes as primary producers in the C uptake of northern peatlands, (2) explore the key role of interactions between *Sphagnum* and specific phototrophic microbes (mixotrophic testate amoebae) and the consequences for the food web structure, and (3) investigate the effect of climate change on microbial primary production.

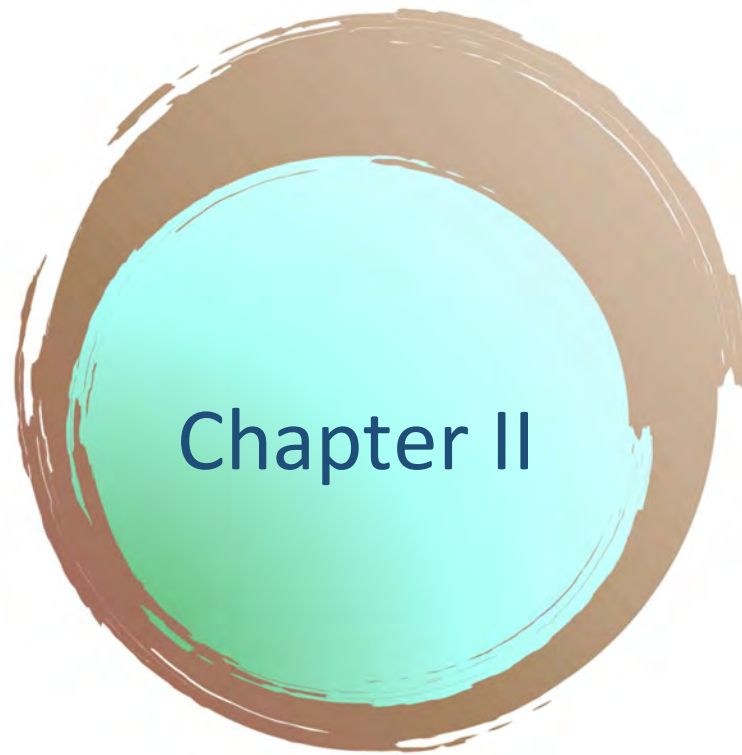
The work presented in this thesis aims (1) to explore the diversity of phototrophic microbial communities and their primary production encountered in multiple northern peatland habitats, (2) to identify their environmental drivers, (3) to explore if some structure-function relationships emerge, revealing the photosynthetic importance of particular taxa, (4) to estimate the contribution of microbial photosynthesis to peatland C uptake, and finally (5) to explore how phototrophic microbial communities and their production respond to climate change along seasonal variations. In order to meet these objectives, the approach of my thesis has been to conduct field work and a lab experiment to gather information about phototrophic microbial community structure, abundance and photosynthetic activities under different environmental, spatial, seasonal and climatic conditions.

Chapter II explores the phototrophic microbial communities and their primary production in the main microhabitats of a representative northern peatland.

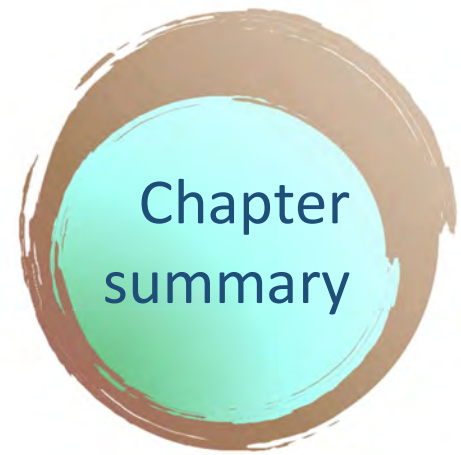
Chapter III explores the phototrophic microbial communities, their primary production and their contribution to peatland C uptake across a European latitudinal gradient.

Chapter IV shows the importance of the *Sphagnum* host species to determine the place of specific phototrophic microbes (mixotrophic testate amoebae) in *Sphagnum* microbial food webs.

Chapter V estimates climate change effects on phototrophic microbial communities and their photosynthesis throughout a growing season, using a reciprocal transplantation in natural conditions.



Peatland microhabitat heterogeneity
drives phototrophic microbe distribution
and photosynthetic activity



Chapter summary

Recent global estimates show that phototrophic microbes are widely distributed and abundant in all terrestrial ecosystems. Through their photosynthetic activities, they contribute to fix atmospheric C and they actively take part in ecosystem C dynamic. At the global scale, phototrophic microbial abundance and activity has been found to be driven by environmental factors including soil moisture or leaf area index of the above-ground plant community. Despite these general considerations, phototrophic microbes and their primary production remain underexplored in many terrestrial systems, including C-accreting systems such as northern peatlands. In particular, northern peatlands exhibit a mosaic of various microhabitats, characterised by different vegetation communities, microtopography or water table depth whose variation could alter phototrophic microbial communities, abundance and activities. Yet, the phototrophic microbial turnover between peatland microhabitats and the consequence for microbial photosynthesis are unknown.

In this chapter, I therefore aim to explore how phototrophic microbial communities vary between the different microhabitats of a northern peatland, and what environmental variables drive the observed changes. I further try to link these changes with variation in microbial photosynthesis. Using a natural gradient of microhabitats from pool to forest, I showed that the structure of phototrophic microbial communities deeply varied between microhabitats, shifting from a dominance of eukaryotes in pools to a dominance of prokaryotes in forests. I further identified environmental preferences of phototrophic microbial groups across the gradient. Along with structural changes, I

found that microbial photosynthesis strongly varied, from 0.05 to 1.0 $\mu\text{C}\cdot\text{h}^{-1}\cdot\text{cm}^{-3}$, and was unexpectedly the highest in the driest and shadiest microhabitats.

This study improves the current view on phototrophic microbes in peatlands, by giving a detailed picture of their diversity. This study further links these observations with the functionality of the communities. It gives the first estimate of microbial photosynthesis in different microhabitats of a northern peatland, and the results show that phototrophic microbial primary production is significant. It suggests that our current understanding of peatland C dynamics is probably lacking a significant piece, and it enjoins to consider the functional role of phototrophic microbes.

Peatland microhabitat heterogeneity drives phototrophic microbes distribution and photosynthetic activity.

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Abstract

Phototrophic microbes are widespread in soils but their contribution to soil carbon (C) uptake remains underexplored in most terrestrial systems, including C-accreting systems such as peatlands. Here, by means of metabarcoding and ecophysiological measurements, we examined how microbial photosynthesis and its biotic (e.g., phototrophic community structure, biomass) and abiotic drivers (e.g., *Sphagnum* moisture, light intensity) vary across peatland microhabitats. Using a natural gradient of microhabitat conditions from pool to forest, we show that the structure of phototrophic microbial communities shifted from a dominance of eukaryotes in pools to prokaryotes in forests. We identified five groups of co-occurring phototrophic operational taxonomic units (OTUs) with specific environmental preferences across the gradient. Along with such structural changes, we found that microbial C uptake was the highest in the driest and shadiest microhabitats. This study renews and improves current views on phototrophic microbes in peatlands, as the contribution of microbial photosynthesis to peatland C uptake has essentially been studied in wet microhabitats.

Introduction

The functioning of ecosystems across the Earth is inextricably linked with the existence of complex and diverse microbial communities (P. G. Falkowski et al., 2008). Microbes are omnipresent in soils, where they show a broad functional diversity and drive key ecosystem processes such as carbon (C) cycling (e.g. Bardgett and van der Putten, 2014; Fierer, 2017). A better understanding of soil microbial communities across the globe is therefore crucial for modelling and predicting ecosystem functioning and global biogeochemistry (Bardgett & van der Putten, 2014; Crowther et al., 2019; Fierer, 2017).

Until recently, most studies focused on the biogeographic patterns (e.g. Fierer and Jackson, 2006; Martiny *et al.*, 2006; Chu *et al.*, 2020) and the functional role of heterotrophic microorganisms in soil biogeochemical cycles (e.g. Bates *et al.*, 2013; Tedersoo *et al.*, 2014; Karimi *et al.*, 2018), overlooking other life forms. Heterotrophic microbes indeed drive important ecosystem processes such as the recycling of essential elements (Gougoulias et al., 2014; Wagg et al., 2014). Aside from heterotrophs, phototrophic microbes are also omnipresent and widely distributed in soils (Cano-Díaz et al., 2020; Oliverio et al., 2020), and therefore potentially contribute to biogeochemical cycles too (Elbert et al., 2012a). They provide organic matter to soils through the fixation of atmospheric C by photosynthesis. Hence, they can balance the catabolic fluxes of C and actively take part in the global C cycle (Elbert et al. 2012). However, despite their potential global importance, soil phototrophic microbes remain essentially studied in systems with few or no plants, where they dominate the C fixation (e.g. drylands, glacial systems; Anesio *et al.*, 2009; Maier *et al.*, 2018; Chen *et al.*, 2020). They are thus largely overlooked in vegetated ecosystems, including the ones that play a key role in the global C cycle such as peatlands (Bardgett et al., 2008; D. S. Schimel et al., 1994; Yu et al., 2011).

Phototrophic microbes are very abundant in northern peatlands (Hamard et al., 2021a) where the dominant plants, *Sphagnum* mosses, provide a suitable habitat for microbial communities (Bragina et al., 2012; Gilbert & Mitchell, 2006a), and moist conditions foster phototrophic growth (Starks et al., 1981). Phototrophic microbes live either freely in pore water or in *Sphagnum* dead cells (Gilbert et al., 1998a) and show a tremendous diversity of taxa and life styles (Gilbert and Mitchell, 2006a; Lara *et al.*, 2011; Hamard *et al.*, 2021). Not all phototrophic microbes in peatlands are strict autotrophs. They rather form a continuum between autotrophy and heterotrophy, with the presence of diverse taxa including strict photoautotrophs (e.g. protists such as Chlorophyta), mixotrophs (i.e. organisms combining photoautotrophy and heterotrophy such as some Ciliophora, Lobosa, many

Alphaproteobacteria or Cyanobacteria), or photoheterotrophs species (e.g. *Chloroflexia*) (Jassey *et al.*, 2015; Nowicka and Kruk, 2016; Hamard *et al.*, 2021). Only a handful studies suggest that phototrophic microbes fix significant amounts of atmospheric C in northern peatlands (Goldsborough and Robinson, 1996; Gilbert *et al.*, 1998b; Wyatt *et al.*, 2012; Jassey *et al.*, 2015; Hamard *et al.*, 2021). The most recent studies estimated the contribution of phototrophic microbes to approximately 10% of total peatland C uptake (Hamard *et al.*, 2021), highlighting the crucial importance of these organisms to the peatland C cycle. However, these estimations remain partial as they do not embrace the diversity of peatland microhabitats, which strongly limits our understanding of the importance of phototrophic microbes into peatland C dynamics.

Northern peatlands exhibit a mosaic of various microhabitats, characterised by different vegetation communities (Kvillner & Sonesson, 1980). Microhabitat changes are underpinned by different environmental factors shaping plant assemblages, such as microtopography, distance to bog-pools, water table depth or nutrient availability (Rydin *et al.*, 2013). For instance, peatlands microhabitats range from wet to dry as the distance to bog-pools and to water table increases, with consequences on *Sphagnum* and vascular plant assemblages. Denser *Sphagnum* species are found far from the water table, while vascular plants shift from graminoids to shrubs and eventually to tree species as distance from the water table increases (Gunnarsson, 2005; Kvillner & Sonesson, 1980). These changes in the vegetation cover generate additional environmental gradients, for instance light gradients as the light intensity reaching the ground surface decreases as the vascular plant layer increases.

We also know that peatland microbial communities are sensitive to plant diversity and community composition (Jassey *et al.*, 2014; Robroek *et al.*, 2015b). This suggests a turnover of microbial phototrophic species across microhabitats. As microbial photosynthetic rates in peatlands strongly depend on the phototrophic community structure (Hamard *et al.*, 2021), these structural changes may alter phototrophic C fixation rates among peatland microhabitats. Therefore, studying phototrophic communities and their C uptake along different peatland microhabitats would bring relevant information on the role of phototrophic microbes in peatland C dynamics.

In this study, we explored the community structure and the photosynthetic activity of phototrophic microbes along a gradient of microhabitats in a boreal peatland, the Männikjärve complex (Estonia). This gradient began from bog-pools, and included the following six microhabitats

that came in succession as the distance to bog-pools increased: pools, *Sphagnum*-pools (*Sphagnum* growing in the shallow edge of the pools), lawns, hummocks, wooded-hummocks and forested-ditches. Specifically, we studied the relationships between the structure, the abundance and the C fixation rate of phototrophic microbial communities along three transects covering the six microhabitats (6 microhabitats x 3 transects = 18 plots in total; Supplementary Fig. SII.1). In each plot, we monitored the phototrophic microbial community composition using 23S rDNA gene sequencing (Sherwood & Presting, 2007), their absolute abundance and photosynthetic properties (photosynthetic efficiency, photosynthetic pigments content and C fixation rates). We hypothesized (i) that microbial photosynthetic activity varies between microhabitats, and (ii) that this variation is the consequence of species turnover along with micro-environmental conditions of the microhabitats. In particular, we expected to find higher photosynthetic rates in microhabitats close to the water table, where water and light availability are not limited and allow favourable conditions for phototrophic growth.

Results

Description of the microhabitats

The depth to the water table increased from pools (open water) to wooded-hummocks (> 50cm), and was only 4 cm in the forested-ditches (Table 1). While all microhabitats (except pools) were dominated by *Sphagnum* mosses, the nature of the vascular plant layer shifted from a dominance of graminoids in lawns, to shrubs and trees in wooded-hummocks and forested-ditches. These variations of the vascular plant layer induced a light gradient at the surface of microhabitats, with only 50% of photosynthetically active radiations reaching the ground in forested-ditches, versus 90% in lawns and 100% in pools ($F_{(4,11)} = 7.02$, $P = 0.013$). Further, *Sphagnum* species differed in each microhabitat except in hummocks and wooded-hummocks where *S. fuscum* dominated. Physical characteristics of the *Sphagnum* mat varied along with *Sphagnum* species, with, in particular, a higher *Sphagnum* water content in the less dense *Sphagnum* species present in *Sphagnum*-pools and forested-ditches ($F_{(4,11)} = 10.62$, $P = 0.004$).

Table 1: Environmental variables measured in the six different microhabitats.

Microhabitat	Dominant <i>Sphagnum</i> species	Vascular plants	Water table depth (cm)	Shadow (Reduction of the incident PAR at the ground surface in %)	<i>Sphagnum</i> water content (g H ₂ O.g ⁻¹ DW)	Density of the <i>Sphagnum</i> mat (mg DW.cm ⁻³)
Pool (Po)	n.a.	n.a.	Open water	0 ± 0	n.a.	n.a.
<i>Sphagnum</i> -pool (Sp)	<i>S. cuspidatum</i>	n.a.	-2.1 ± 1.3	0 ± 0	43.3 ± 14.7	1.4 ± 0.6
Lawn (La)	<i>S. medium</i> , <i>S. balticum</i>	<i>Eriophorum vaginatum</i> , <i>Scheuchzeria palustris</i> , <i>Drosera rotundifolia</i> , <i>Andromeda polifolia</i> , <i>Vaccinium oxycoccos</i>	10.2 ± 2.6	11 ± 10	19.3 ± 3.1	9.2 ± 3.0
Hummock (Hu)	<i>S. fuscum</i>	<i>Andromeda polifolia</i> , <i>Vaccinium oxycoccos</i> , <i>Empetrum nigrum</i>	> 50.0	17 ± 13	10.6 ± 1.4	20.7 ± 2.3
Wooded-hummock (Wh)	<i>S. fuscum</i>	<i>Pinus sylvestris</i> , <i>Calluna vulgaris</i> , <i>Empetrum nigrum</i> , <i>Ledum palustre</i> , <i>Betula nana</i>	> 50.0	43 ± 27	11.5 ± 1.6	17.8 ± 0.4
Forested-ditch (Fd)	<i>S. riparium</i>	<i>Picea abies</i> , <i>Betula pendula</i> , <i>Scheuchzeria palustris</i>	3.9 ± 0.2	53 ± 4	37.4 ± 9.8	2.4 ± 0.8

n.a. = not applicable

Community structure and environmental preferences of phototrophic microbes

Phototroph-specific 23S metabarcoding analyses revealed the presence of 129 phototrophic operational taxonomic units (OTUs), gathering a total of 1 116 phototrophic microbial sequences in the 18 plots. Among the 129 OTUs, 68 were associated to phototrophic micro-eukaryotes, 60 to phototrophic prokaryotes, and one unassigned. We identified nine phyla of phototrophic microbes, out of which seven were eukaryotic and two were prokaryotic (Supplementary Fig. SII.2). On average, phototrophic microbial communities were dominated by one eukaryotic phylum, Chlorophyta (relative abundance of 34% on average), and two prokaryotic phyla, Cyanobacteria (33%) and Proteobacteria

(15%). Trebouxiophyceae, Cyanobacteria and Alphaproteobacteria were the main representative class of these respective phyla on average (Supplementary Fig. SII.2; Supplementary Table SII.1).

We found important discrepancies in the composition and the structure of phototrophic microbial communities along the microhabitats. First, the OTU richness (Chao1 index) of the phototrophic community was altered along the microhabitats ($F_{(5, 12)} = 3.81$, $P = 0.034$), with a richness significantly lower in the forested-ditches (5 OTUs on average) compared to the other microhabitats (28 OTUs on average) (Fig. II.1A). Second, the OTU diversity (Shannon index) showed a similar pattern with a lower diversity found in the forested-ditches compared to other microhabitats ($F_{(5, 12)} = 6.92$, $P = 0.005$; Fig. II.1A). Third, in each microhabitat, 45% of OTUs on average were specific of the site (Supplementary Fig. SII.3). This proportion was the highest in the pools where 80% of the OTUs were microhabitat specific ($F_{(5, 12)} = 5.43$, $P = 0.011$). On one hand, wooded-hummocks, hummocks and lawns, and on the other hand, pools and *Sphagnum*-pools were the microhabitats that shared the highest number of OTUs in common (Supplementary Fig. SII.3).

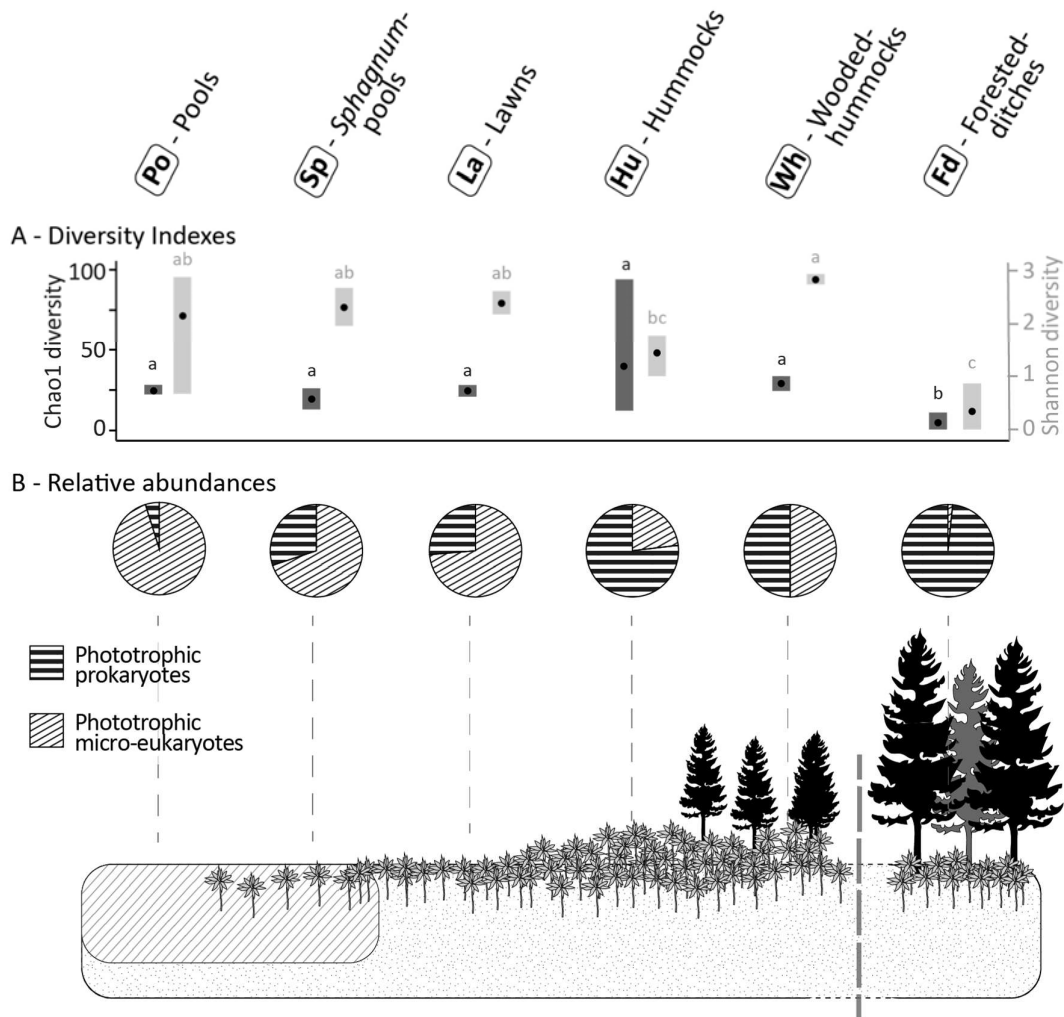


Figure II.1: Biodiversity of the phototrophic communities found in the different microhabitats. OTU richness (Chao1 diversity; dark grey) and diversity (Shannon index; light grey) are presented in the A panel. The proportion of phototrophic prokaryotes and phototrophic micro-eukaryotes in the microbial phototrophic community is presented in the B panel.

A permutational multivariate analysis of variance revealed that the community structure of phototrophic microbes strongly depended on the microhabitats ($R^2 = 0.63$, $P < 0.001$). At the domain level, we found a shift in the phototrophic community structure between the different microhabitats ($F_{(5,12)} = 27.72$, $P < 0.001$; Fig. II. 1B). Whilst micro-eukaryotes strongly dominated the phototrophic community in pools (95.2%), the relative abundance of phototrophic prokaryotes gradually increased along the microhabitat gradient, and prokaryotes strongly dominated in forested-ditches (98.4%). In parallel with these changes, the number of micro-eukaryotic OTUs strongly decreased, from 32 OTUs in pools to three OTUs in forested-ditches. Furthermore, we identified five clusters of highly co-

occurring phototrophic OTUs (Fig. II.2A). They evidenced a clear transition from the pools to the forested-ditches ($R^2 = 0.53$, $P < 0.001$; Fig. II.2B). Cluster 1 and 2 were specific of pools and *Sphagnum*-pools, being almost absent in the other microhabitats. Cluster 1 dominated the pools (65% of the phototrophic relative abundance), while cluster 2 dominated the *Sphagnum*-pools microhabitats (73%). Cluster 3 showed a low abundant on both extremes of the transects (3% in pools and forested-ditches), but increased toward the middle of the transect to dominate in lawns (87%). Cluster 5 gradually increased from the pools (0%) to the forested-ditches (97% while Cluster 4 was present from *Sphagnum*-pools to wooded-hummocks and dominated in hummocks (85%).

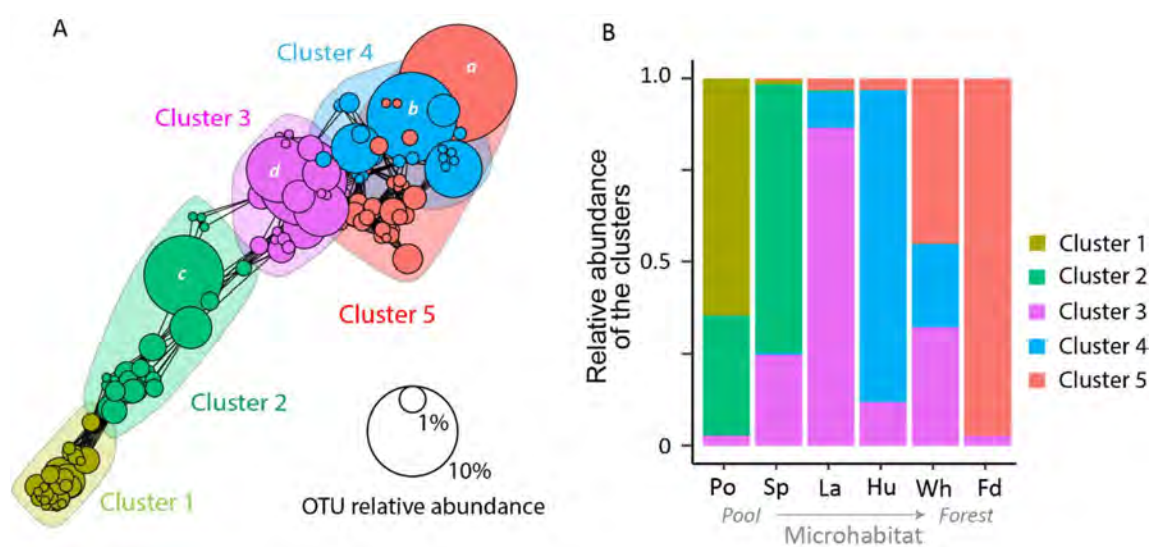


Figure II.2: Clusters of co-occurring OTUs. In the network (A) one dot represent one OTU, and its diameter is proportional to its relative abundance averaged in the six microhabitats. The four dominant OTUs are *a*: *Nostoc sp* (15% of total sequences); *b*: *Cylindrospermum stagnale* (10%); *c*: *Chlorella variabilis* (9%) and *d*: *Mesotaenium caldariorum* (7%). The bar plot (B) shows the relative abundance of the different clusters within the phototrophic microbial communities of the six microhabitats.

Each cluster grouped OTUs belonging to various taxa, meaning that co-occurring OTUs formed phylogenetically complex communities (Supplementary Fig. SII.4; Supplementary Table SII.2). Unifrac distance showed that the cluster 1 had the highest phylogenetic distance from the other clusters (Unifrac distance of 0.81 with the other clusters on average), while the clusters 4 and 5 were the most similar (distance of 0.52 between them; Supplementary Table SII.3). In terms of relative abundance, Chlorophyta and Proteobacteria were well-represented in the five clusters, contributing on average to

nearly 66% of the cluster sequences. Chlorophyta especially dominated in the cluster 3 (78%), while Proteobacteria dominated in the cluster 1 and 5 (35% and 56%, respectively). Cyanobacteria, Streptophyta and Ochrophyta constituted respectively a large part of the cluster 1, 2 and 4 (28%, 28% and 42%, respectively; Supplementary Table SII.2). In line with this uneven distribution of phyla, only few OTUs dominated the different clusters (Fig. II.2A). Two OTUs belonging to *Nostocaceae* (Cyanobacteria) dominated the clusters 4 and 5 (28% and 22% respectively), while an OTU belonging to *Mesotaenium* (Streptophyta) accounted for 21% of the cluster 2. One OTU belonging to *Chlorella* dominated the cluster 3 with 30% of the sequences.

Environmental parameters affected the relative abundance of the clusters 3, 4 and 5 (Fig. II.3). The cluster 3 was negatively related to *Sphagnum* water content ($F_{(1,16)} = 4.55$, $P = 0.050$), while the cluster 5 was positively related to shadow ($F_{(1,16)} = 43.78$, $P < 0.001$). The cluster 4 was negatively related to *Sphagnum* water content ($F_{(1,16)} = 8.03$, $P = 0.014$) and positively related to water table depth ($F_{(1,16)} = 15.46$, $P = 0.001$).

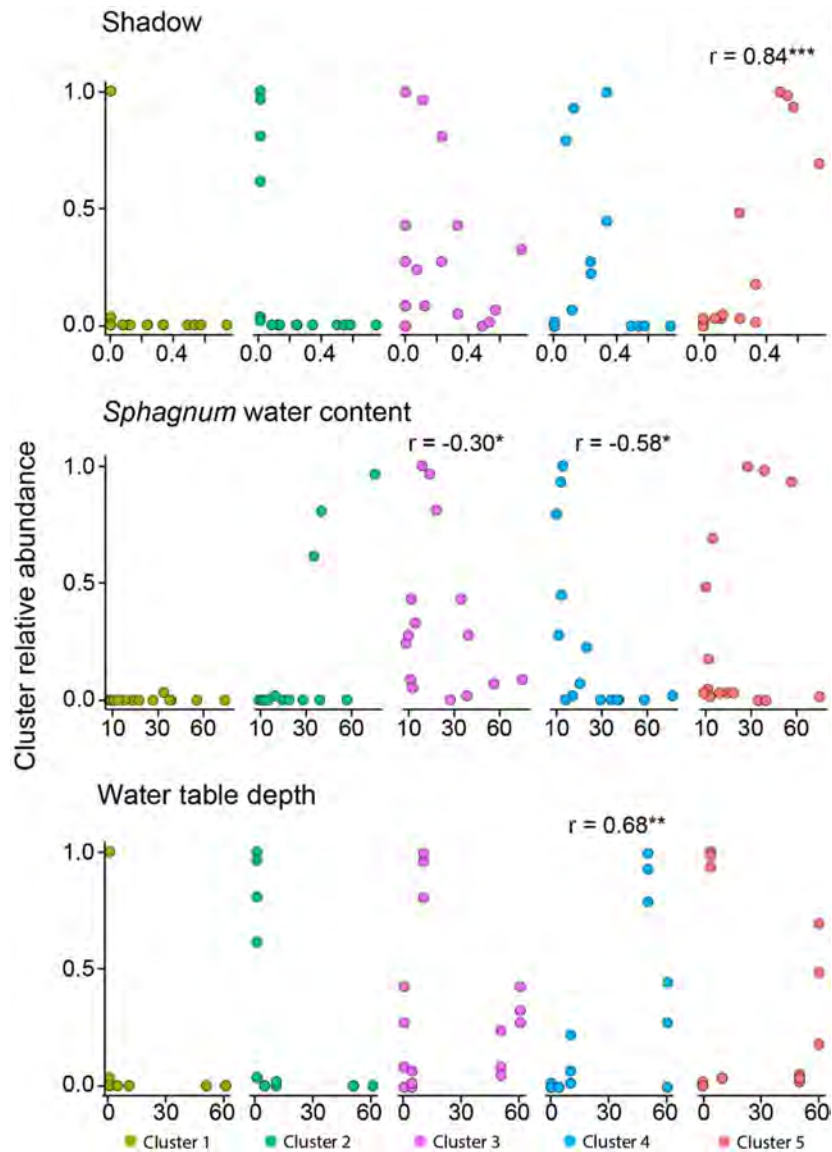


Figure II.3: Environmental parameters affecting the repartition of the different clusters and their relative abundance in the phototrophic community. The correlation coefficient (r) is indicated for significant correlations ($P < 0.05$) between environmental parameters and relative abundance of the clusters. * $0.05 > P > 0.01$; ** $0.01 > P > 0.001$; *** $P < 0.001$.

Phototrophic metabolic rates and C fixation

We quantified the chlorophyll *a* (chl_a) content and the maximum electron transport rate (ETR) per unit of phototrophic biomass (μgC) to estimate the metabolic and photosynthetic rates of phototrophic microbes. The chl_a content per biomass of phototrophic microbes significantly differed between the microhabitats ($F_{(5,12)} = 4.00$, $P = 0.034$; Fig. II.4A), and was the lowest in pools and lawns (8.8 ± 6.1 and

7.7 ± 2.9 ng chla per µgC, respectively), while it was nearly five and four times higher in hummocks and wooded-hummocks (44.1 ± 30.6 and 28.8 ± 10.4 ng chla per µgC, respectively). The maximum ETR (Em) was reached for low light intensities, with an average PAR of 85 ± 24 µmol.m⁻².s⁻¹ (Supplementary Fig. SII.5). The maximum ETR followed the same pattern than the chla content, being the lowest in pools and lawns (67.3 ± 35.5 and 1316 ± 376 fmol e⁻.s⁻¹.µgC⁻¹, respectively) and the highest in hummocks and wooded-hummocks (6290 ± 3194 and 7060 ± 2666 fmol e⁻.s⁻¹.µgC⁻¹, respectively) ($F_{(5,12)} = 24.93$, $P < 0.001$; Fig. II.4B).

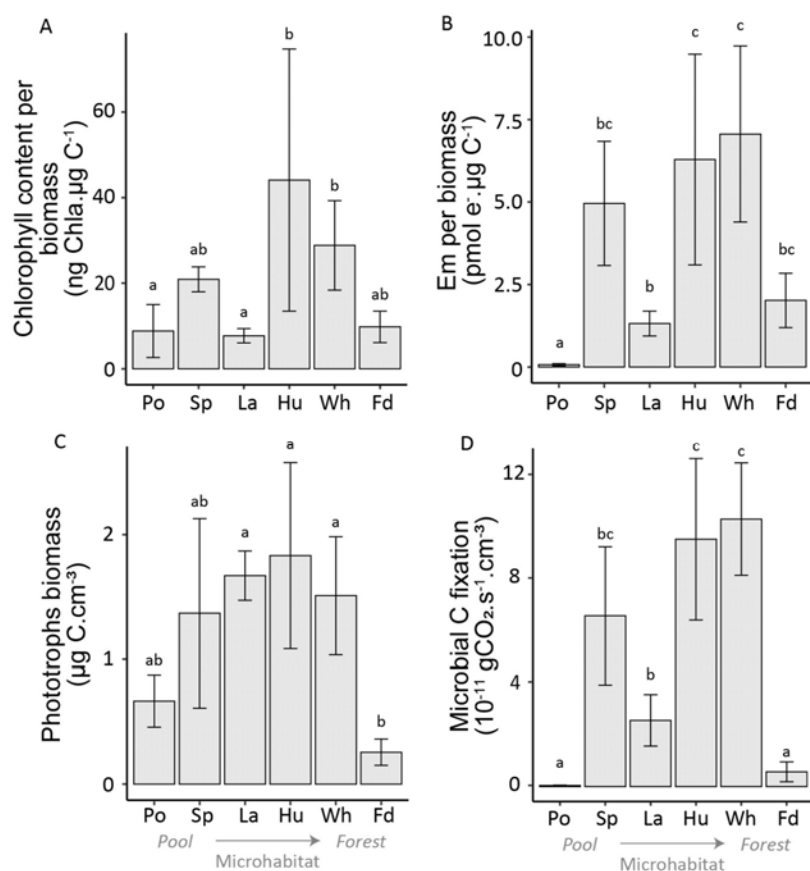


Figure II.4: Allometric features of phototrophic microbes in the six microhabitats. A: Chlorophyll *a* content per unit of phototrophic biomass phototrophic microbes. B: Maximum electron transport rate per unit of phototrophic biomass. C: Total biomass of phototrophic microbes expressed as µg C per cm³ of *Sphagnum* (or µg C per cm³ of water in pools). Error bars present standard error. Significant differences ($P < 0.05$) are indicated by different letters above bars.

We then quantified the community-weighted mean biomass per cell ($\mu\text{gC}\cdot\text{cell}^{-1}$) and the total biomass of phototrophic microbes per cubic centimetre of *Sphagnum* ($\mu\text{gC}\cdot\text{cm}^{-3}$), allowing an estimation of microbial photosynthetic and C fixation rates at the microhabitat level. We observed variations in the phototrophic biomass between microhabitats. The phototrophic biomass per phototrophic cell was on average 2.5 times lower in emerged *Sphagnum* than in pools ($F_{(5,12)} = 9.59$, $P = 0.002$; Supplementary Fig. SII.6), while the total biomass was the highest in lawns, hummocks and wooded-hummocks ($1.67 \pm 0.47 \mu\text{gC}\cdot\text{cm}^{-3}$ on average) and the lowest in forested-ditches ($0.26 \pm 0.11 \mu\text{gC}\cdot\text{cm}^{-3}$) ($F_{(5,12)} = 3.31$, $P = 0.041$; Fig. II.4C). Concerning C fixation rates, phototrophic microbes fixed $174 \pm 41 \text{ ngCO}_2\cdot\text{h}^{-1}\cdot\text{cm}^{-3}$ on average along the microhabitat gradient. However large discrepancies could be observed between microhabitats ($F_{(5,12)} = 29.66$, $P < 0.001$; Fig. II.4D). Microbial C fixation was the highest in hummocks and wooded-hummocks ($350 \pm 93 \text{ ngCO}_2\cdot\text{h}^{-1}\cdot\text{cm}^{-3}$ on average), intermediate in *Sphagnum*-pools and lawns ($161 \pm 64 \text{ ngCO}_2\cdot\text{h}^{-1}\cdot\text{cm}^{-3}$), and the lowest in pools and forested-ditches ($11 \pm 7 \text{ ngCO}_2\cdot\text{h}^{-1}\cdot\text{cm}^{-3}$).

Drivers of microbial photosynthesis

We built a path analysis (structural equation model, SEM) that explained 85% of the total variation of microbial C fixation at the microhabitat level (Fig. II.5). First, the SEM showed that microbial C fixation was directly mediated by the total biomass (path = 0.62) and the photosynthetic rates of phototrophs per unit of biomass (path = 0.75). Second, the SEM highlighted the importance of micro-environmental conditions in determining microbial C fixation through cascading effects: environmental parameters affected phototrophic community structure that in turn affected both total biomass and photosynthetic rates of phototrophic microbes. More precisely, we found that shadow was a good predictor of the relative abundance of the cluster 5 (path = 0.91), while *Sphagnum* density was a good predictor of the cluster 4 (path = 0.79). Clusters 4 and 5 altered the diversity of the phototrophic microbial community (path = -1.06 and path = -0.92, respectively), which in turn influenced the photosynthetic rates of phototrophic microbes (path = 0.95) and their total biomass (path = 0.56). In particular, additional linear models confirmed that the total biomass of phototrophs was positively correlated with their diversity (Shannon index; $F_{(1,16)} = 5.18$, $P = 0.037$, $r = 0.44$). Additional linear models further showed correlations between the relative abundance of specific OTUs and phototrophic biomass and photosynthetic rates. For instance, we found a positive correlation between

a cyanobacteria from the *Nostoc* genus, dominant in the cluster 4, and the photosynthetic rates of phototrophs ($F_{(1,16)} = 6.94$, $P = 0.018$, $r = 0.51$). We also found a negative correlation between the dominant OTU of the cluster 5, another cyanobacteria from the *Nostoc* genus, and the total biomass of phototrophic microbes ($F_{(1,16)} = 9.21$, $P = 0.008$, $r = -0.57$).

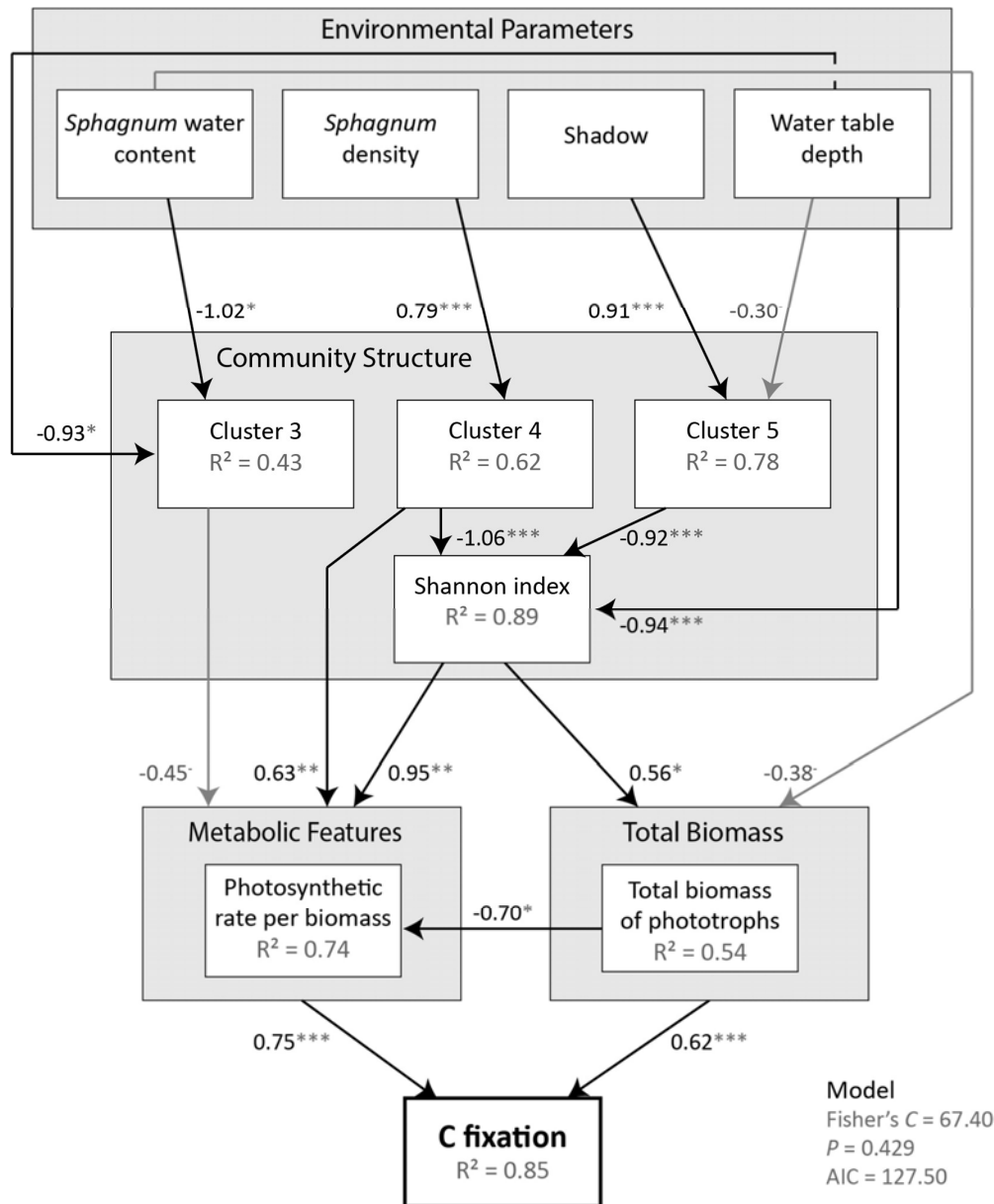


Figure II.5: Structural equation modelling of the correlations between environmental parameters, structure of phototrophic microbial communities (relative abundance of the clusters and Shannon index), their total biomass per cm^3 and metabolic features, and microbial C fixation per cm^3 . Numbers in the boxes indicate the percentage of variance explained by the model (adjusted R-squared), while numbers along the arrows indicate the weight of the path relationship (* $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$). Grey arrows indicate non-significant relationships ($0.05 < P < 0.10$).

Discussion

Recent studies have suggested that phototrophic microbes play an important role in the C cycle of northern peatlands, fixing significant amounts of atmospheric C through photosynthesis (Wyatt *et al.*, 2012; Hamard *et al.*, 2021). However, the role of microhabitat diversity in supporting C fixation by photosynthetic microbes remained unexplored. Here, by means of metabarcoding and eco-physiological analyses, we show that the community structure of phototrophic microbes change drastically among peatland microhabitats, with consequences on microbial C fixation rates. In particular and contrary to our hypothesis, we reveal that the most productive areas were neither the moistest nor the open microhabitats, but instead the relatively dry and closed microhabitats found on hummocks and wooded-hummocks.

Phototrophic microbial diversity and community structure

The use of the 23S marker for metabarcoding analysis, which allows for a simultaneous study of both eukaryotic and prokaryotic phototrophic microbes, showed that the structure of phototrophic microbial communities was highly variable among peatland microhabitats. While several studies revealed a high spatial heterogeneity of microbial communities in different peatlands microhabitats (Chroňáková *et al.*, 2019; Heger *et al.*, 2018b; L. Küttim *et al.*, 2017; Oloo *et al.*, 2016), we showed here that such heterogeneity also exists for phototrophic microbes. In total we identified 129 phototrophic OTUs distributed in nine phyla. This richness is lower than the one found in peatland lawns along a 3000 km latitudinal gradient (351 OTUs and 11 phyla with 16S/18S metabarcoding; Hamard *et al.*, 2021) or than the one found in a peatland along a gradient of drainage (794 OTUs with 18S metabarcoding; Heger *et al.*, 2018). The 23S metabarcoding analyses should perform better than the 18S or 16S analyses to reveal the presence of phototrophic OTUs (Marcelino & Verbruggen, 2016). We found, using additional metabarcoding analyses, that 16S/18S gave comparable perceptions of the phototrophic community structure in our samples than 23S (Supplementary Fig. SII.7). Therefore, the low number of phototrophic OTUs in our study may rather come from a low sequencing depth. Rarefaction curves revealed nevertheless a near saturation at the microhabitat level (Supplementary Fig. SII.8), which indicates that a majority of the diversity of the six microhabitats was captured. Although our 23S metabarcoding analyses did not give an exact picture of the phototrophic

community, it remains an interesting proxy to study phototrophic community changes along peatland microhabitats.

Our results showed that phototrophic microbial communities experienced strong structural variations along the few dozen meters forming the microhabitat gradients. In particular, a key finding of this study was the drastic shift in the phototrophic prokaryote to eukaryote ratio, which strongly increased from the pools toward the forested-ditches. Such variations emphasized the importance of micro-environmental conditions in the structure of phototrophic microbial communities, and pointed out that phototrophic prokaryotes and eukaryotes responded in antagonistic ways to changes in environmental conditions. More particularly, we identified five clusters of co-occurring OTUs, forming phylogenetically complex communities and grouping both eukaryotic and prokaryotic OTUs. Environmental conditions, mainly water and light availability, influenced the proportions of the clusters in the phototrophic community, and led to the prokaryotic to eukaryotic shift. This result is in line with another study, where a higher sensitivity of prokaryotes (Cyanobacteria) to high solar and UV radiations led to a partitioning between phototrophic prokaryotes and eukaryotes in a lake (Winder, 2009).

Besides water and light availability, other environmental factors that we did not take into account likely intervened in the structural variations of phototrophic communities along the microhabitat gradient. For instance, differences in the nutrient status in the different microhabitats could drive species turnovers as calcium content affects phototrophic eukaryotes (Heger et al., 2018b) and/or nitrogen supply increases the abundance of Cyanobacteria compared to microalgae in peatlands (Gilbert et al., 1998b). As the vegetation changes across the gradient, it is also likely that pH changes between pools and forested-ditches, which could feedback on phototrophic microbial communities (Heger et al., 2018b). Furthermore, the abundance of predators among microhabitats could also be an important factor to take into account. Indeed, many algalivorous protozoa and metazoan are sensitive to water table depth (Lamentowicz and Mitchell, 2005; Jassey *et al.*, 2011). Predator shifts along microhabitats could induce different top-down controls on phototrophic communities and favour some phototrophic taxa, as shown in marine systems where high predation rates induce a selection toward smaller phototrophic cells and favour prokaryotic abundance (Tamigneaux et al., 1995). Finally, the plant community composition may also influence phototrophic communities (Heger *et al.*, 2018; Hamard *et al.*, 2021). In temperate forests, needle litter favour

Chlorophyta while leaf debris favour Cyanobacteria (Maltsev et al., 2017; Maltsev & Maltseva, 2018). In our study we observed similar patterns with more Chlorophyta in the pine-covered wooded-hummocks, and more Cyanobacteria in the forested-ditches, where birch and deciduous trees were also present. However, this pattern could also be related to water regime and nutrient status, as vegetation changes are underpinned by shifts in nutrients, water and light availability as well (Song et al., 2019).

Another key result of this study is that phototrophic communities in pools were more dissimilar compared to the phototrophic communities from *Sphagnum* mosses. Several taxa such as Rhodophyta or Cryptophyta and a high proportion of OTUs were specific to the pools, while different phototrophic taxa were found in *Sphagnum* habitats. We acknowledge that we sampled only the surface water of the pools, which might lead to an underestimation of the phototrophic richness. However, bog-pools are particular systems with very dark water that limit phototrophic growth deep in the water column (Lew et al., 2016; Umanskaya et al., 2020). The difference between pools and *Sphagnum* phototrophic communities nevertheless reveals that a sampling of free or pore water is not sufficient to capture the full composition of the phototrophic community in *Sphagnum*, most probably because many microbes live in close association with mosses (Bragina et al., 2012; Gilbert et al., 1998a). Our results further suggest that *Sphagnum* mosses are important in structuring phototrophic microbial communities, even if the *Sphagnum* species differ. Such close association could derive from similar physical properties provided by *Sphagnum* mosses (e.g. hyaline dead cells), but also from specific chemical interactions between *Sphagnum* mosses and microbes. Indeed, recent findings evidenced the strong linkages between *Sphagnum* chemicals and phototrophic microbes in peatlands (Sytiuk et al., 2021a).

Despite alterations in the phototrophic community structure along the microhabitats, OTU richness and diversity remained similar in most of the microhabitats except in the forested-ditches (lower richness and diversity). Especially, we found a strong decrease in the number of micro-eukaryotic OTUs in the forested-ditches (three OTUs while there were 32 in the pools), which suggests that only few phototrophic micro-eukaryotic species were able to live under the environmental conditions present in the forested-ditches. On the contrary, the number of prokaryotic OTUs stayed the same. This could be link with the fact that Cyanobacteria can establish symbiosis with other plants (Black & Osborne, 2004) or have a high plasticity in their photosynthetic machinery (Bengtsson et al., 2018), which could help them to overcome the light limitation of forested-ditches microhabitats. As

microbial richness and diversity drive soil functions (e.g., Nannipieri *et al.*, 2003; Coleman and Whitman, 2005; Delgado-Baquerizo *et al.*, 2017), this result suggested that phototrophic functions were probably not affected along the microhabitat gradient at the exception of forested-ditches, due to functional redundancy (Louca *et al.*, 2018a). However, the measurements of microbial photosynthetic rates among microhabitats rebutted such hypothesis.

Spatial changes in microbial C fixation rates

We observed higher C fixation rates in hummocks and wooded-hummocks. By comparison, C fixation rates were much higher than in the other microhabitats, being for instance nearly four time higher than in lawns and 17 times higher than in forested-ditches. While previous studies showed the importance of phototrophic microbes in *Sphagnum* lawns, where they contributed to 10% of C uptake (Wyatt *et al.*, 2012; Hamard *et al.*, 2021), we show here that phototrophic microbes had even a higher primary production in hummocks and wooded-hummocks. This striking result is important because it shows that phototrophic communities are more productive in microhabitat distant from the water table and under dense plant cover darkening the incident light. In fact, we found that phototrophic microbes were well adapted to these environments, reaching their maximal C fixation rates for low light intensities (under $115 \mu\text{mol.m}^{-2}.\text{s}^{-1}$).

Our structural equation model (SEM) revealed the drivers of microbial C fixation rates. In particular, our SEM showed that the community structure drove microbial C fixation through a dual effect. First, the community structure affected the total biomass of phototrophs, which can be seen as the photosynthetic workforce. Second, the community structure affected the averaged metabolic rates of phototrophs, which can be seen as the photosynthetic potential. The combination of both photosynthetic workforce and potential determined the microbial C fixation rates.

Overall, the total biomass of phototrophic microbes positively correlated with phototrophic diversity, denoting resource limited environments (Bastida *et al.*, 2021). The total biomass of phototrophic microbes was further intimately correlated with specific OTUs. Only few studies explored the role of specific phototrophic species in driving phototrophic biomass, yet it has been showed that colonial species could increase the total phototrophic biomass in oceanic environments (Finkel *et al.*, 2010). In our study, we found a negative correlation between one *Nostoc* cyanobacteria and the total phototrophic biomass. This was somehow unexpected because Cyanobacteria species from the *Nostoc*

genus often form colonies in peatlands (e.g., Elster *et al.*, 2012), and are able to fix nitrogen, a nutrient known to promote algal production (Piorreck *et al.*, 1984). However, some cyanobacteria, and more particularly, *Nostoc* species can also produce toxic and allelopathic compounds (Nowruzi *et al.*, 2012), thus potentially limiting the development of other phototrophs and competitors, as shown in freshwater ecosystems (e.g., Carmichael, 1997; Leflaive and Ten-Hage, 2007).

The metabolic rates of phototrophic microbes depended on phototrophic community structure. While metabolic rates negatively correlated with the relative abundance of cluster 3 and positively correlated with cluster 4, we did not find significant correlations with the relative abundance of specific phototrophic taxa. This shows that metabolic rates are not driven by a little number of taxa or OTUs but rather by an association of multiple OTUs. In particular, as fluorescence measurements of photosynthetic efficiency often underestimate cyanobacterial photosynthetic rates (Schuurmans *et al.*, 2015), we expected to find a negative correlation between metabolic rates and the proportion of cyanobacteria in the phototrophic community. We however did not find such bias in our study (Supplementary Fig. SII.9). Instead, we found higher photosynthetic rates in hummocks and wooded-hummocks, where phototrophic cells were the smallest; a results in line with a general observation showing that metabolic rates per biomass unit are negatively correlated with body size (Finkel *et al.*, 2010).

Consequences for peatland functioning

These differences in the amount of microbial C fixation between microhabitats might profoundly affect their C dynamics. Phototrophic microbes release a great part (40%) of the C they fix as labile exudates and hence promote dissolved organic C and heterotrophic respiration in peatlands (Wyatt & Turetsky, 2015b). It is therefore highly probable that the balance between algal and plant C input determine the chemical composition of organic matter and eventually its fate in the ecosystem, as it is the case in several soil systems (Kögel-Knabner, 2002). In hummocks and wooded-hummocks, phototrophic microbes are more productive, but at the opposite, *Sphagnum* species living in these microhabitats are less productive than the one living in lawns (Gunnarsson, 2005; M. Küttim *et al.*, 2020). This indicates that phototrophic microbes contribute more to C uptake in hummocks and wooded-hummocks than in other microhabitats, and subsequently affect the C dynamics of these microhabitats. Further research would be needed to explore this hypothesis and to quantify the net

effects of microbial C fixation on peatland C fluxes. Indeed, the fate of phototrophic-fixed C is still virtually unknown, and species turnover among microhabitats may influence this dynamic. Further, the role of phototrophic microbes in peatland is certainly not limited to the contribution to C fixation. Phototrophic microbes could affect peatland functioning in many other ways, for instance by fixing nitrogen (Granhall & Selander, 1973), or by structuring global microbial communities, either as food for predators (Seppey et al. 2017 SBB), through allelochemical interactions (Sytiuk et al. 2021), or through competition as recently suggested (Hsu & Moeller, 2021).

Conclusion

Microhabitats are important drivers of the structure of heterotrophic microbial communities in peatlands with consequences on the peatland C dynamics (Barreto & Lindo, 2018; Robroek et al., 2015b). Microhabitats are also primordial in the structure of phototrophic communities, as structural shifts are associated with important alterations of microbial primary activity. Microbial C fixation indeed experience huge variations along short microhabitats gradients, with an increase of up to 17 times over few decametres. As the structure of peatland phototrophic communities changes throughout the year (Reczuga et al., 2020) it is probable that the microbial C fixation could change in the different microhabitats according to the sampling season. Despite this limitation, our study shows that peatlands are complex ecosystems where phototrophic microbes might play a significant role. Our findings further highlight that the current understanding of peatland C dynamics is lacking a significant piece. A better understanding of the role of phototrophic microbes in peatlands, and to the whole diversity of peatlands microhabitats is urgently needed to improve our predictions of the peatland C balance under future global changes.

Methods

Study site and sampling

The Männikjärve ombrotrophic bog is situated in central Estonia (58°52'30 N, 26°15'04 E, 78 m a.s.l.) and is representative of northern (or boreal) peatland types (Masing, 1984). It has a well-developed microhabitat complex, structured along gradients extending from pools to wooded-hummocks. The margins of the Männikjärve bog are colonized by a wooded bog and a forest (Lode et al., 2017; Masing, 1982). In early October 2019, we selected three different transects in the bog that were related with three different pools (Supplementary Fig. SII.1). Getting some distance from the pools, we set plot locations that were representative of five different microhabitats: pools (Po), *Sphagnum*-pools (Sp, corresponding to *Sphagnum* growing in the shallow edge of the pools), lawns (La), hummocks (Hu) and wooded-hummocks (Wh). On top of this, we set three other plot locations in the ditches of the margin forest (forested-ditches, Fd; Supplementary Fig. SII.1). The plots had an area of 20 cm per 20 cm. Except for the pools (water), we made an inventory of the vegetation of the different microhabitats. They were all dominated by *Sphagnum* species, that formed a continuous *Sphagnum* carpet. In each plot, we measured the light intensity at the ground surface. Measurements were done in comparable conditions and at the same time. We also collected *Sphagnum* in PVC-tubes (diameter 8.5 cm; height 6 cm), and weighted it fresh and dry in order to determine the *Sphagnum* mat density and the *Sphagnum* water content (pools excepted). Further, we sampled surface water in the pools and apical part of *Sphagnum* mosses (0-3 cm from the capitulum) in other plots for analysis of microbial diversity, abundance and biomass as well as photosynthetic rate.

DNA extraction and metabarcoding

We sampled three capitula of *Sphagnum* with sterile equipment from each plot, cut them into small pieces and placed them into sterile tubes containing 3 ml of Lifeguard (Qiagen). For pools, we filtered 5 ml of pool surface water on 0.25 µm filters using sterile equipment, and we placed the filters into 3 ml of Lifeguard. For each sample, DNA was extracted using the DNeasy PowerSoil Pro Kit (Qiagen) and following the manufacturer's instructions. The DNA was eluted in 70 µl of final solution and its concentration in each extract was quantified using a Nanodrop ND-1000 spectrophotometer. Extracts were stored at -80°C before proceeding to DNA amplification.

To investigate photosynthetic microorganisms, we used the 23S rDNA metabarcoding marker, allowing the replication of a DNA fragment of 365 base pair (Presting, 2006). The pair of primers was tagged with Illumina adapter sequences. PCRs were conducted in a total volume of 50 μ l containing 13 μ l of Mastermix AmpliTaq Gold (Thermofisher), 1 μ l of each primer (0.4 μ M final concentration), 35 ng of DNA (up to 10 μ l) and completed to 50 μ l with DNA-free water. The primers' sequences and the PCR programs used are presented in Supplementary Table SII.4. The sequencing was performed by the GeT-PlaGe platform (Genotoul, Toulouse, France) with Illumina MiSeq technology and using the V3 chemistry (2x250 bp).

Paired-end fastq sequences were analysed using the FROGS pipeline (Find Rapidly Operational Taxonomic Units Galaxy Solution) on the Galaxy platform (Escudié et al., 2018). Paired-end reads were merged using VSEARCH (10% of mismatch; (Rognes et al., 2016)). Sequences were filtered based on their length and primer mismatches were removed. Sequences were then dereplicated and clustered into OTUs using the SWARM clustering method with an aggregation distance of three (Mahé et al., 2014). Chimera were identified and removed using VSEARCH. Filters were then applied to remove singletons. OTUs were assigned at different taxonomic levels using Blast. We used the Silva 138 database (Quast et al., 2013) for the 23S assignment. After these steps, the 18 samples contained 418 618 curated reads in total, belonging to 589 phototrophic OTUs associated to plants and phototrophic microbes.

Further analyses were conducted with the Phyloseq R package (McMurdie & Holmes, 2013). In particular, we removed plant-associated sequences and kept only microbial phototrophic OTUs. For the 18 samples, we obtained 26 981 microbial sequences belonging to 262 phototrophic microbial OTUs. To alleviate sequencing artefact, we then performed a rarefaction for each sample, and obtained 1 116 microbial sequences (62 per sample) belonging to 129 phototrophic microbial OTUs (Supp Fig. S8). Finally, we checked the profiles of the rarefaction curves. At the sample level, not every sample reached the saturation, but when considering the six microhabitats, rarefaction curves revealed a near saturation (Supplementary Fig. SII.8). This indicated that the majority of the diversity of the six microhabitats was captured.

Microbial abundance

We sampled three shoots of *Sphagnum* (0-3 cm) in each plot and 5 ml of surface water in pools, and fixed them in 10 ml of glutaraldehyde (2% final concentration). Microorganisms were extracted by adapting the method of Jassey *et al.* (2011). We vigorously shook the samples for 2 min on a vortex, then we passed them through a 100 μm mesh. The retained moss was pressed with a spatula to extract the maximum of filtrates. The remaining fraction was dried at 80°C for 48 h, weighted and converted into cubic centimetre using the *Sphagnum* density calculated previously. Phototrophic microbes were enumerated by flow cytometry with a Guava® easyCyte™ 11HT cytometer. Aliquots of 300 μl were placed in a 96-well microplate and run unstained in the flow cytometer at a flow of 0.59 $\mu\text{l}\cdot\text{s}^{-1}$. A total of 5000 events were recorded in each sample. Forward and side light scatter (size indication) as well as green fluorescence (presence or absence of chlorophyll) were used to discriminate photosynthetic microorganisms from non-photosynthetic microorganisms. Abundance data were expressed as the number of individuals per cubic centimetre and were then converted in biomass ($\mu\text{g C}$) per cubic centimetre using the community-weighted mean biomass. To measure the community-weighted mean biomass of phototrophic microbes, 3 ml of each sample were settled for 2 h in a plankton chamber and analysed at x 400 magnification by inverted microscopy. Along several transects of the plankton chamber, we counted and measured the geometrical shapes of every phototrophic microbe encountered. Geometrical shapes were then converted to biovolume and C biomass using conversion factors from the literature (Borsheim & Bratbak, 1987; Gilbert *et al.*, 1998a; Weisse *et al.*, 1990). We counted a minimum of five transects or 500 phototrophic microbes per sample to estimate the community-weighted mean biomass.

Microbial photosynthesis efficiency, chlorophyll *a* and electron transport rate

For microbial photosynthesis measurements, five shoots of *Sphagnum* (0-3 cm) were sampled in each plot and immersed in 20 mL demineralized water. Microbial communities were extracted and filtered on a GF/F Whatman® filter, while the remaining *Sphagnum* material was dried at 80°C for 48 h, weighted and converted into cubic centimetre (following Hamard *et al.*, 2021). In pools, we filtered 10 ml of pool surface water on GF/F Whatman® filters. Filters containing the microbial communities were dark adapted for 30 min after what they were exposed to increasing light in order to measure the light curve of the quantum yield of photosystem II (Φ_{PSII}). Measurement were conducted with a

Phyto-PAM (Walz, Effeltrich, Germany). The chlorophyll *a* content of phototrophic microbes was assessed following Hamard *et al.*, 2021. The filters used for microbial photosynthetic efficiency and containing microbial communities were frozen at -80°C and freeze-dried in the dark. Pigments were extracted from the freeze-dried filters, then quantified on an HPLC (Barlow *et al.*, 1997). We assessed the concentration of several pigments including chlorophyll *a*, pheophytin *a* and pheophorbide *a*. As pheophytin *a* and pheophorbide *a* are alteration products of chlorophyll *a* (Jeffrey *et al.*, 2005), we summed the abundance of these three pigments to have an estimate of overall chlorophyll *a* in the samples (hereafter named chlorophyll *a*). Chlorophyll *a* (Chla) was expressed in ng per cubic centimetre. It was then divided by the total biomass of phototrophs to have an estimate of the chlorophyll *a* content per unit of biomass (expressed in ng.µg C⁻¹).

We quantified the microbial photosynthetic activity in each plot by calculating the photosynthetic electron transport rate per biomass (ETR) as described in Wilken *et al.* (2013), and following Falkowski and Raven (2013):

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

where ETR was calculated at increasing light intensity (*I*) from 0 to 400 µmol.m⁻².s⁻¹ to provide a light curve. ETR at light intensity *I* (ETR^(*I*)) depends on the importance of the microbial photosynthetic machinery (Chla per biomass, $\frac{\text{Chla}}{\text{biomass}}$) and on its photosynthetic efficiency at light intensity *I* (quantum yield of photosystem II, $\Phi_{\text{PSII}}^{(I)}$). Here, *a** was the spectrally averaged chlorophyll-specific absorption cross section, for which we took a value of 26.86 m².g Chla⁻¹ as estimated in (Wilken *et al.*, 2013). The ETR was expressed in mol e⁻.µg C⁻¹.s⁻¹.

For each plot, we fitted the light curves of ETR and we calculated the photosynthetic-irradiance parameters using the fitPGH function from the Phytotools R package (Silsbe & Malkin, 2015). We extracted the maximal ETR (Em) from each light curve, as well as the light intensity at which Em was reached (Pm) and the light intensity at which ETR decreased to Em/2 as a measure of photoinhibition.

Microbial C fixation rate and contribution to bryosphere C uptake

Phototrophic microbial C fixation rates (*C*_{fixed}) were calculated in each plot based on the maximum ETR (Em):

$$(2) \text{ C}_{\text{fixed}} = 0.25 \times \text{Em} \times \text{biomass}$$

where we assumed a maximum fixation of 0.25 mol CO₂ per mol of electron (Wilken et al., 2013). We took into account the total biomass of phototrophic microbes per cubic centimetre (biomass) and therefore expressed the microbial C fixation rates in mol CO₂.s⁻¹.cm⁻³. We then converted the microbial C fixation rates in g CO₂.s⁻¹.cm⁻³.

Numerical analyses

Metabarcoding data were used to explore the relative abundance and the structure of phototrophic microbial communities. Alpha-diversity measures (OTU richness and Shannon's entropy) were used to estimate diversity in each plot and for each metabarcoding marker. We used analysis of variance (ANOVA) to test the variations of diversity indexes along microhabitats. We further used a permutational multivariate analysis of variance (PERMANOVA) to test for structural differences between the phototrophic communities of the different microhabitats.

To explore if some associations of phototrophic microbes were specific of some microhabitats, we built co-occurrence networks based on the 23S analyses and following (Borcard et al., 2018). First, we built a presence-absence matrix of the OTUs in the different plots. Then we computed a matrix composed of the a component of the Jaccard's S_7 coefficient, which is a measure of co-occurrence among species (Borcard et al., 2018). We assessed the probability of each "a component" by means of 99999 permutations and obtained a "a" distance matrix. We then calculated an adjacency matrix from the "a" distance matrix in which we only kept significant co-occurrences. To know if co-occurrences were significant, we computed a matrix of the Spearman's rho rank correlation and assessed their P-values using the rcorr function from the Hmisc R package (Harrell & Dupont, 2008). Co-occurrences of the adjacency matrix were conserved if they were associated to a P-value lower than 0.05. Then we built the co-occurrence network. We looked for structures (or clusters) in the network, that is to say we looked for OTUs associations that were densely connected, using the cluster_optimal function from the igraph R package (Csardi, 2008). Finally, we looked at the repartition of the different clusters in the different microhabitats. We calculated the Unifrac dissimilarity between the communities of the different clusters.

We tested variations of phototrophic microbial abundance, chlorophyll content, electron transport rate and C fixation rates between sites using analysis of variance (ANOVA).

We used structural equation modelling (SEM; Grace et al. 2014) to study the complex interactions determining the phototrophic C fixation. Following current knowledge on phototrophic eco-physiology (Huete-Ortega et al., 2012; Kalchev et al., 1996; Padfield et al., 2018), we developed an *a priori* model of hypothesized relationships (Supplementary Fig. SII.10) within a path diagram allowing a causal interpretation of microbial C fixation rates in relation to microbial community structure (relative abundance of the five clusters), to total phototrophic biomass, to metabolic parameters (photosynthetic activity per unit of biomass) and to environmental parameters (Supplementary Table SII.5). In this diagram, each path is a component of the model, and represent a linear model between the explanatory and the explained variable. All components of the model were united using the `psem` function from the `piecewiseSEM` R package (Lefcheck, 2016). The goodness-of-fit of our *a priori* SEM model was evaluated using Akaike Information Criterion (AIC) and Fisher's statistic. Based on the outputs of the *a priori* model and by step-wise exclusion/selection of variables, we found the model minimizing the AIC. The main drivers of microbial C fixation were determined from this final model. All statistical analyses were performed using R version 3.6.2 (R Core Team, 2019).

Acknowledgments

The authors have no conflict of interest to declare. This work has been supported by the MIXOPEAT project funded by the French National Research Agency (Grant No. ANR-17-CE01-0007 to VJ). MK was supported by the research fund of Tallinn University (project AlgaePeat) and by the Life project Peat Restore. We gladly acknowledge the support from Liisa Küttim for her help on sampling, and from Chloé Argouet for her help on metabarcoding. We also acknowledge the *Genome & Transcriptome* platform of Genopole Toulouse (Genotoul) where environmental DNA sequencing was performed, and the Bioinformatics platform of Genotoul from which we used computing clusters to perform DNA bioinformatic analyses. We thank the *Plateforme Analyses Physico-Chimiques* from the Laboratoire Ecologie Fonctionnelle et Environnement (Toulouse) and especially Didier Lambrigtot for the help and the provision of an HPLC (pigments quantification).

Supplementary materials

Supplementary Tables

1 **Supplementary Table SII.1:** Relative abundance of the different classes of phototrophic microbes in the different samples. Relative abundances are
 2 expressed relatively to the phototrophic microbial community, as a proportion of phototrophic microbial reads (%).
 3

Sample	Alphaproteobacteria	Bacillariophyceae	Chlorophyceae	Chrysophyceae	Cryptophyceae	Cyanobacteria	Eustigmatophyceae	Floriidophyceae
Pools 1	1.6	0.0	6.5	1.6	22.6	0.0	16.1	0.0
Pools 2	3.2	1.6	3.2	0.0	9.7	1.6	1.6	14.5
Pools 3	6.5	0.0	1.6	0.0	0.0	0.0	0.0	0.0
Sphagnum-pools 1	17.7	1.6	1.6	0.0	0.0	24.2	0.0	0.0
Sphagnum-pools 2	6.5	16.1	21.0	0.0	0.0	29.0	0.0	0.0
Sphagnum-pools 3	9.7	0.0	14.5	0.0	0.0	3.2	0.0	0.0
Lawns 1	19.4	0.0	6.5	0.0	0.0	0.0	0.0	0.0
Lawns 2	24.2	0.0	4.8	0.0	0.0	3.2	0.0	0.0
Lawns 3	32.3	0.0	3.2	0.0	0.0	0.0	0.0	0.0
Hummocks 1	8.1	0.0	0.0	0.0	0.0	85.5	0.0	0.0
Hummocks 2	6.5	0.0	3.2	0.0	0.0	75.8	0.0	0.0
Hummocks 3	1.6	0.0	4.8	0.0	0.0	53.2	0.0	0.0
Wooded hummocks 1	27.4	0.0	3.2	0.0	0.0	25.8	6.5	0.0
Wooded-hummocks 2	30.6	0.0	3.2	0.0	0.0	8.1	0.0	0.0
Wooded-hummocks 3	58.1	0.0	1.6	0.0	0.0	0.0	9.7	0.0
Forested-ditches 1	0.0	0.0	0.0	0.0	0.0	100.0	0.0	0.0
Forested-ditches 2	3.2	0.0	0.0	0.0	0.0	96.8	0.0	0.0
Forested-ditches 3	14.5	0.0	0.0	0.0	0.0	80.6	0.0	0.0

Sample	Gammaproteobacteria	Gracilibacteria	Mamiellophyceae	Raphidophyceae	Synurophyceae	Trebouxioiophyceae	Ulvophyceae	Unclassified	Zygnemophyceae
Pools 1	0.0	0.0	25.8	0.0	24.2	0.0	0.0	1.6	0.0
Pools 2	0.0	0.0	22.6	3.2	37.1	1.6	0.0	0.0	0.0
Pools 3	0.0	0.0	0.0	0.0	0.0	6.5	0.0	0.0	85.5
Sphagnum-pools 1	0.0	0.0	0.0	0.0	0.0	40.3	0.0	0.0	14.5
Sphagnum-pools 2	0.0	0.0	0.0	0.0	0.0	9.7	0.0	0.0	17.7
Sphagnum-pools 3	0.0	0.0	0.0	0.0	0.0	32.3	0.0	0.0	40.3
Lawns 1	0.0	0.0	0.0	0.0	0.0	74.2	0.0	0.0	0.0
Lawns 2	0.0	0.0	0.0	0.0	0.0	66.1	0.0	0.0	0.0
Lawns 3	0.0	0.0	0.0	0.0	0.0	64.5	0.0	0.0	0.0
Hummocks 1	0.0	0.0	0.0	0.0	0.0	6.5	0.0	0.0	0.0
Hummocks 2	0.0	0.0	0.0	0.0	0.0	12.9	0.0	0.0	0.0
Hummocks 3	0.0	0.0	0.0	0.0	0.0	40.3	0.0	0.0	0.0
Wooded hummocks 1	0.0	0.0	0.0	0.0	0.0	37.1	0.0	0.0	0.0
Wooded-hummocks 2	0.0	0.0	0.0	0.0	0.0	58.1	0.0	0.0	0.0
Wooded-hummocks 3	0.0	0.0	0.0	0.0	0.0	30.6	0.0	0.0	0.0
Forested-ditches 1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Forested-ditches 2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Forested-ditches 3	0.0	0.0	0.0	0.0	0.0	4.8	0.0	0.0	0.0

4

5

Supplementary Table SII.2: Composition of the five clusters of co-occurring OTUs. The table shows the number of OTUs per phyla in each cluster (number in black) and the relative abundance of the different phyla within each cluster (percentage in grey).

	Cluster1	Cluster2	Cluster3	Cluster4	Cluster5
Bacillariophyta	0 0%	2 10%	0 0%	0 0%	0 0%
Chlorophyta	5 19%	3 22%	12 78%	9 42%	7 19%
Cryptophyta	7 12%	0 0%	0 0%	0 0%	0 0%
Ochrophyta	14 28%	0 0%	0 0%	0 0%	2 2%
Oomycota	0 0%	0 0%	0 0%	1 1%	0 0%
Rhodophyta	1 5%	0 0%	0 0%	0 0%	0 0%
Streptophyta	0 0%	5 28%	0 0%	0 0%	0 0%
Cyanobacteria	0 0%	6 19%	0 0%	3 42%	1 22%
Proteobacteria	2 35%	11 21%	11 22%	7 15%	19 56%
Unclassified	1 1%	0 0%	0 0%	0 0%	0 0%

Supplementary Table SII.3: Unifrac distance between the five clusters of co-occurring OTUs identified in the study.

	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5
Cluster 1					
Cluster 2	0.82				
Cluster 3	0.82	0.70			
Cluster 4	0.80	0.60	0.56		
Cluster 5	0.79	0.68	0.55	0.52	

Supplementary Table SII.4: Primers and PCR programs used in the study.

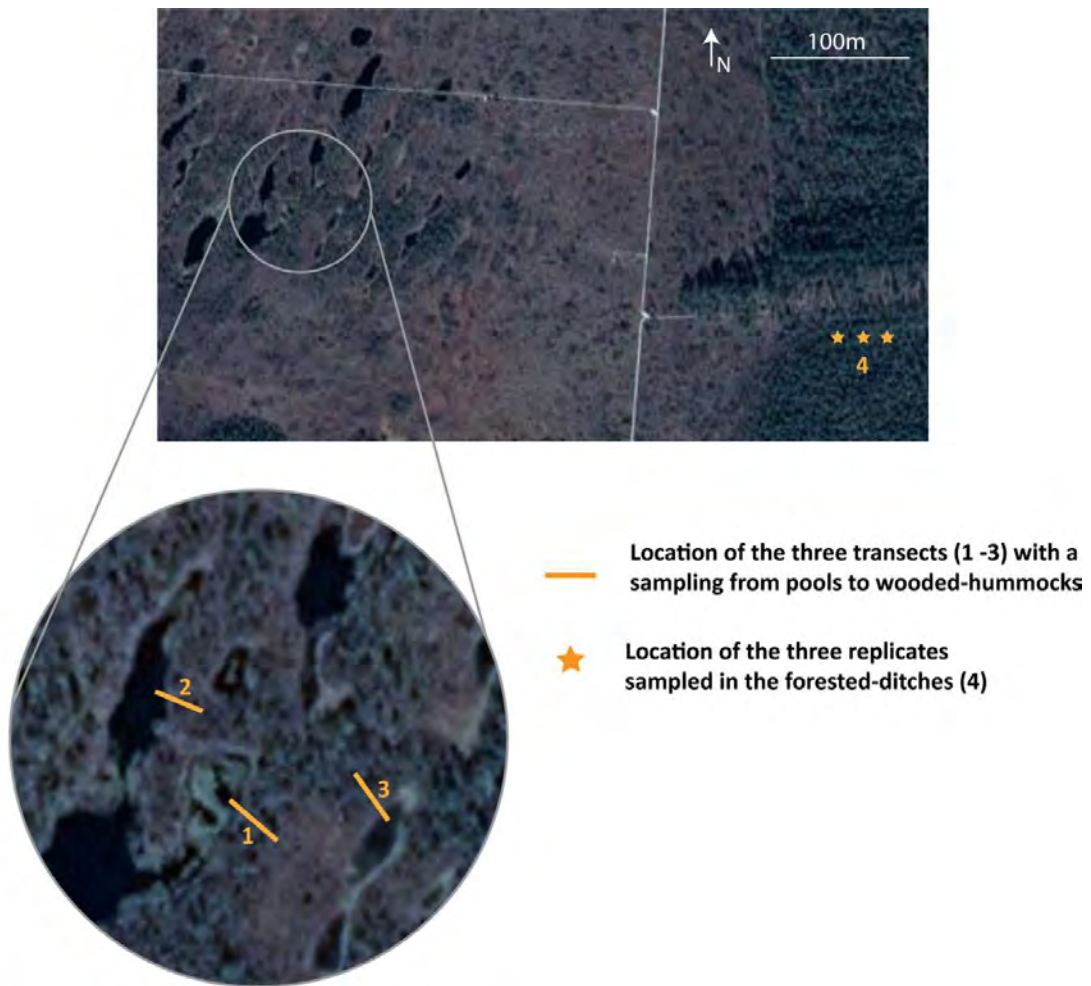
Analyses	23S
Primers	P23SrV_f1 P23SrV_r1
Sequence of the primers (5' – 3')	GGACAGAAAGACCCTATGAA TCAGCCTGTTATCCCTAGAG
Program of the PCRs	Activation : 10 min – 95°C 30 cycles: 60 s – 94°C 40 s – 65°C 30S – 72°C Final elongation : 10 min – 72°C

Supplementary Table SII.5: Components of hypotheses represented by the structural equation model.

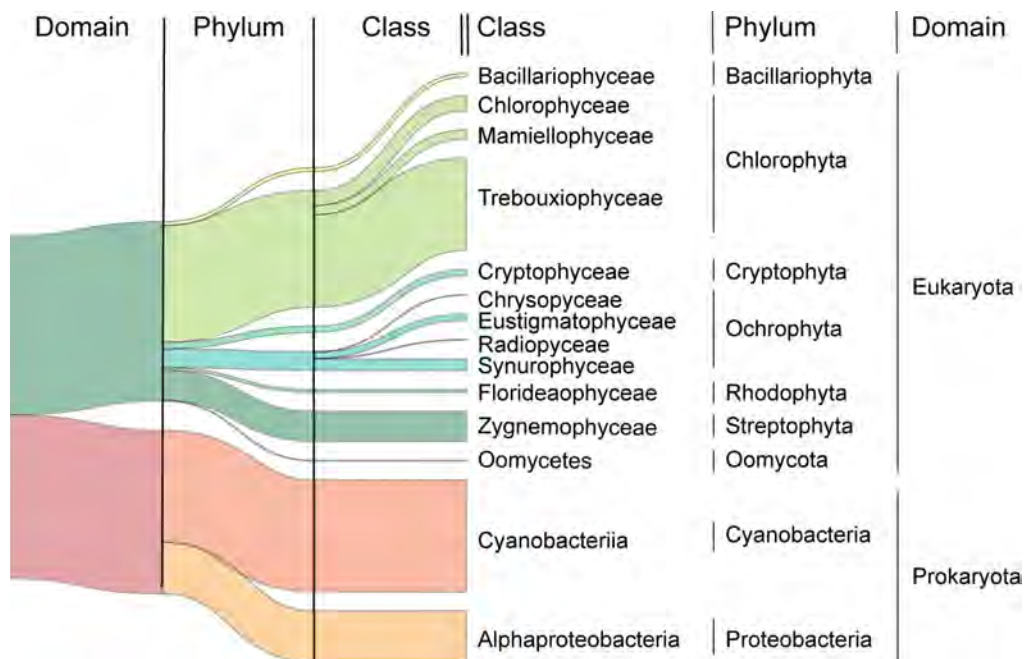
Path	Causal hypothesis
E1	Environmental parameters alter the community structure of phototrophic microbes (Heger et al., 2018b).
E2	<i>Sphagnum</i> parameters (water content) alter the capacity of sheltering phototrophic microbes.
E3	Light intensity alter the chlorophyll content of phototrophic microbes (Ferreira et al., 2016).
C	Richness and diversity of the phototrophic microbial community depend on its cluster composition.
S1	Changes in the community structure of phototrophic microbes affect their metabolic rates
S2	The total biomass of phototrophic microbes depends on the structure of their community.
P	An increase of the photosynthetic rate per biovolume promotes the total amount of C fixed by the phototrophic microbial community.
B	An increase of the total biomass of phototrophs promotes the total amount of C fixed by the phototrophic microbial community.

Supplementary Figures

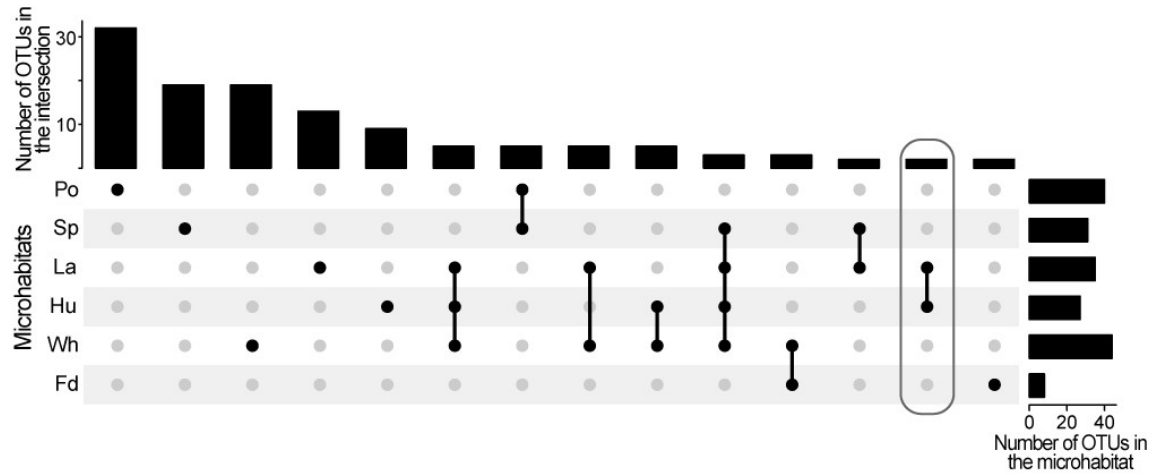
Supplementary Figure SII.1: Location of the three transects (pools to wooded-hummocks) and the three extra sampling (forested-ditches) in the Männikjärve bog (58.8750N, 26.2510E).



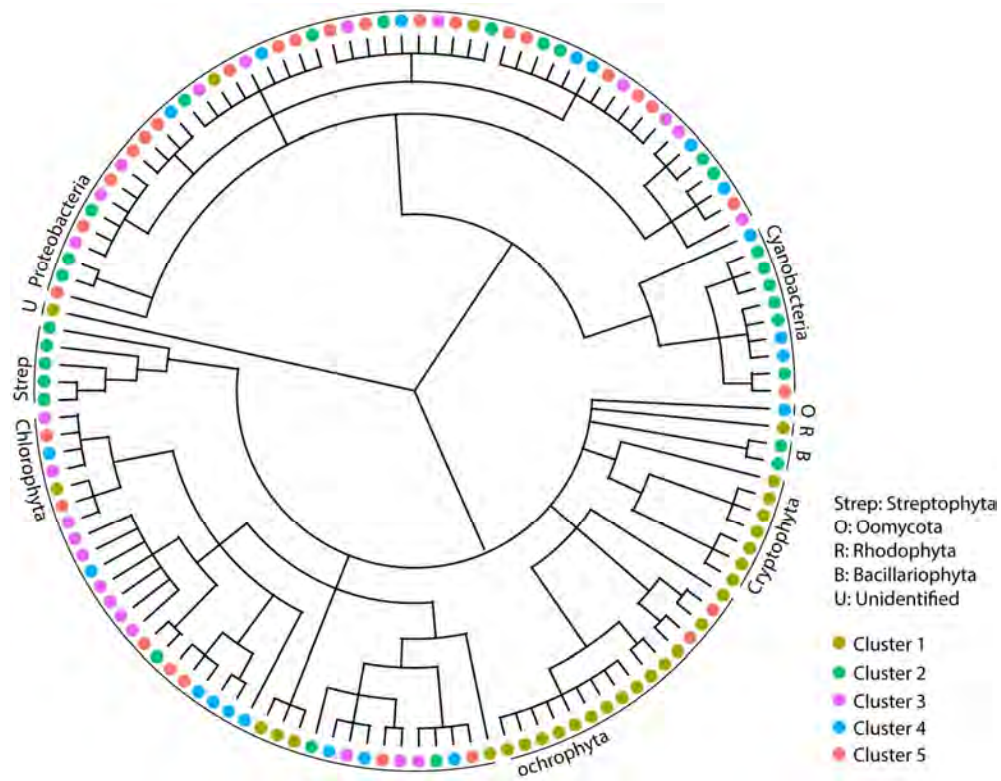
Supplementary Figure SII.2: Sankley graphs showing the relative abundance of the different taxa identified with 23S metabarcoding and averaged for all microhabitats. The width of the branches is proportional to the relative abundance of the taxa.



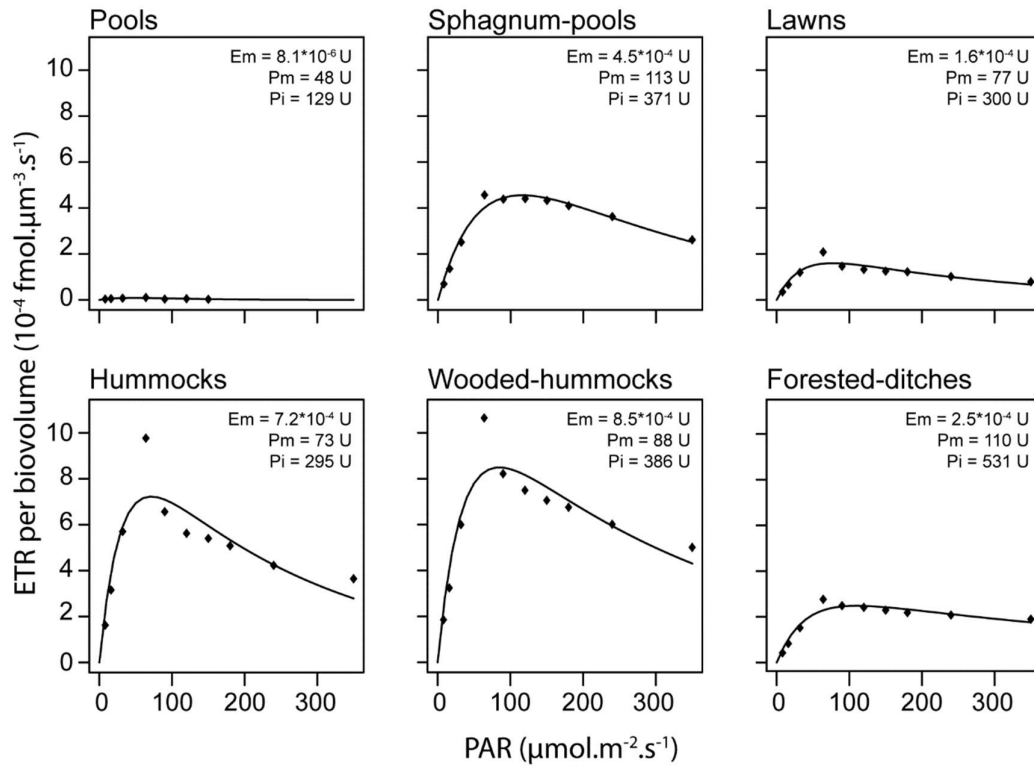
Supplementary Figure SII.3: Number of OTUs shared between the different combinations of microhabitats intersection. In this figure, the rows of the bottom matrix represent the different microhabitats, while the columns of the matrix represent the intersections between the microhabitats. For each intersection, the microhabitats concerned are represented by black circles in the corresponding row, and are linked by vertical black lines. The number of OTUs shared in the intersection is shown as a bar chart placed on top of the matrix. For instance, the circled column shows the intersection between lawns and hummocks, and two OTUs are exclusively present in these two microhabitats. Intersections with only one OTU are not shown. A second bar chart showing the number of OTUs in each microhabitat is shown to the right of the matrix.



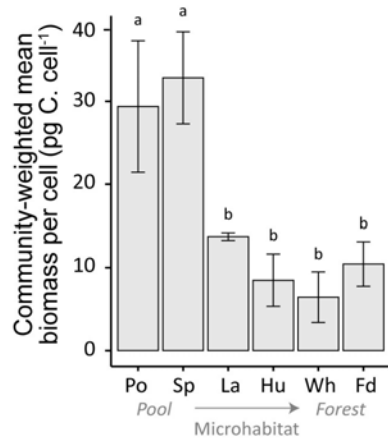
Supplementary Figure SII.4: Taxonomic tree of the 129 OTUs identified in the study and their affiliation in the different phyla. Coloured dots show the membership to the five clusters of co-occurring OTUs.



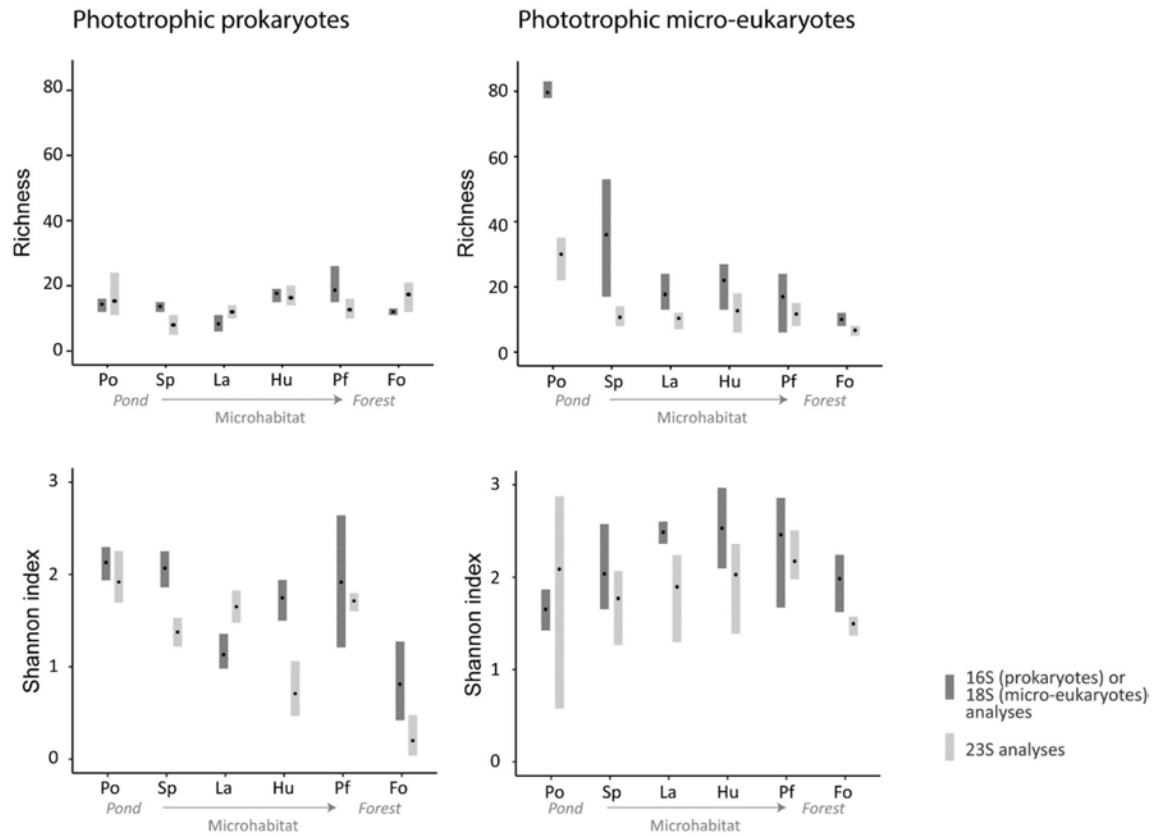
Supplementary Figure SII.5: Light response curves of microbial electron transport rate (ETR) in the six microhabitats. E_m = maximal ETR ($\text{fmol} \cdot \mu\text{m}^{-3} \cdot \text{s}^{-1}$); P_m = PAR at which ETR equals E_m ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$); P_i = PAR at which ETR equals $E_m/2$ ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$).



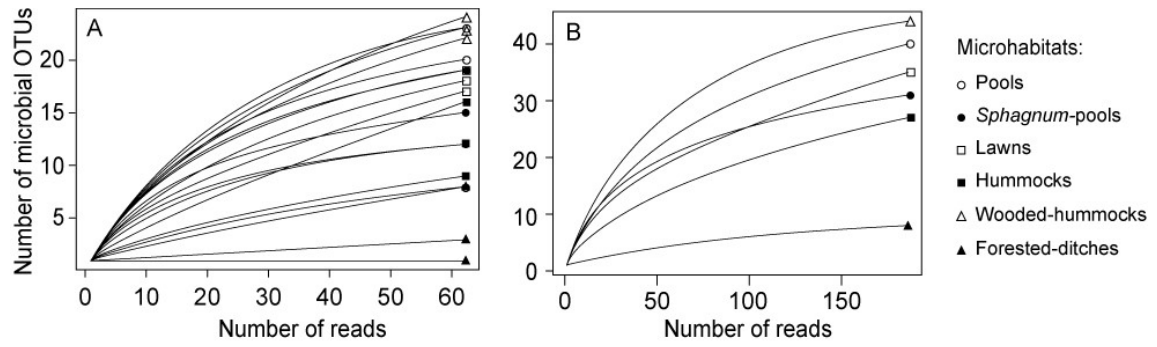
Supplementary Figure SII.6: Bar plot showing the community weighted mean biomass per cell in each microhabitat. Error bars present standard error. Significant differences ($P < 0.05$) are indicated by different letters above bars.



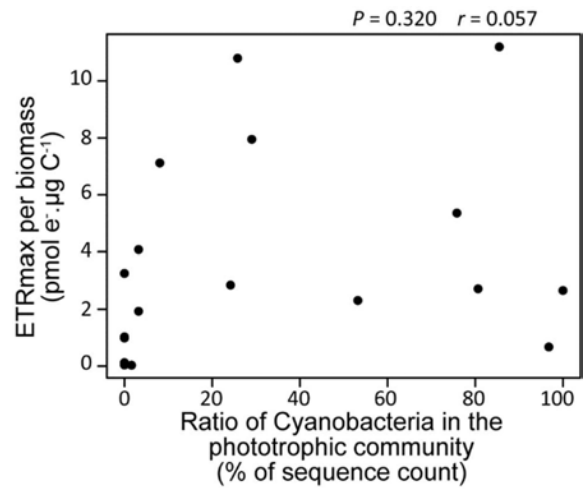
Supplementary Figure SII.7: Alpha diversity indexes in the six microhabitats, showing OTU richness (top) and Shannon index (bottom) in the communities of phototrophic prokaryotes (left) and micro-eukaryotes (right). The indexes are calculated based on 23S (light grey) or 16S and 18S (dark grey) analyses.



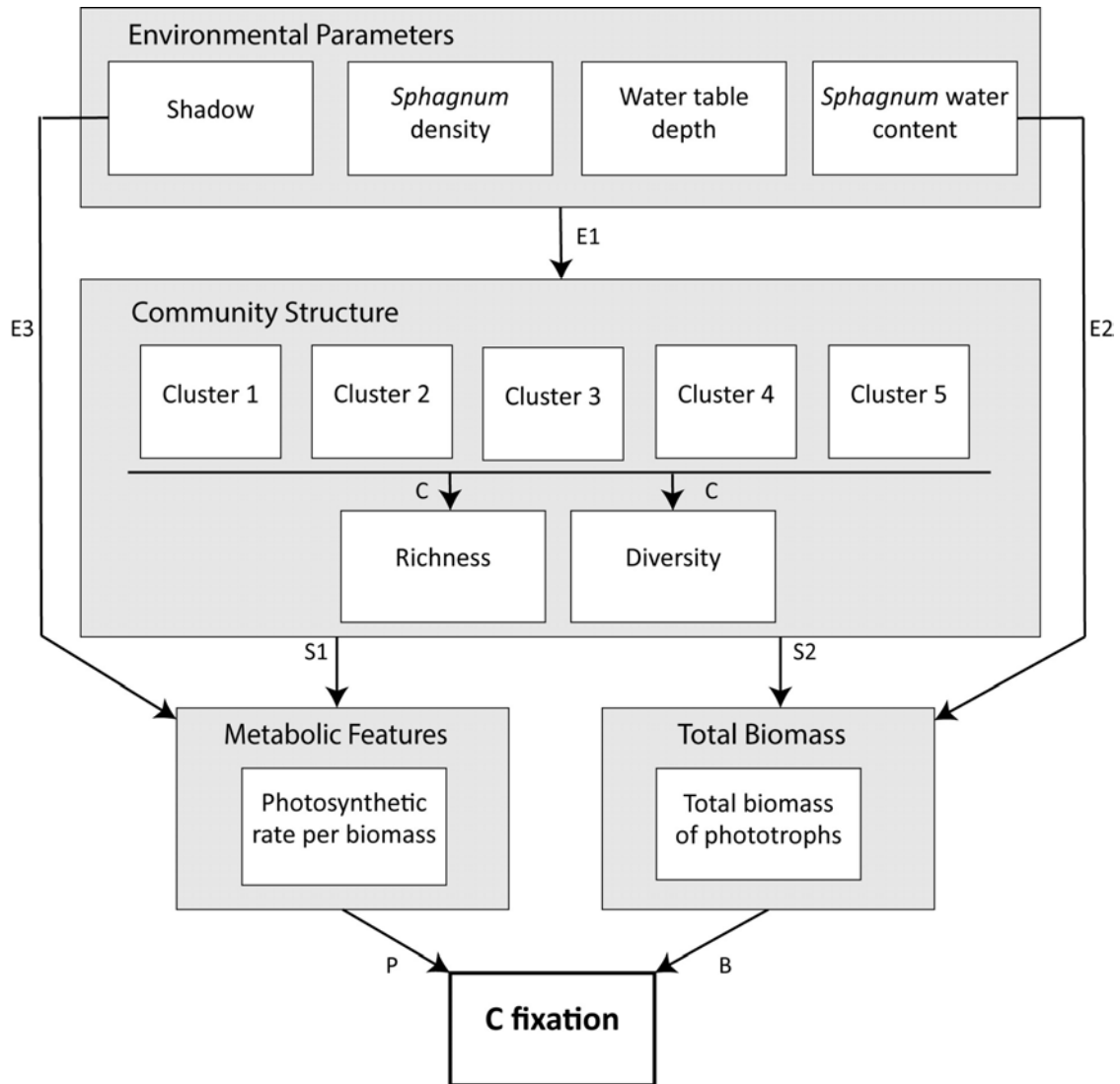
Supplementary Figure SII.8: Rarefaction curves of phototrophic microbial sequences after normalisation of the number of sequences, in each sample (A) and in the six microhabitats (B).

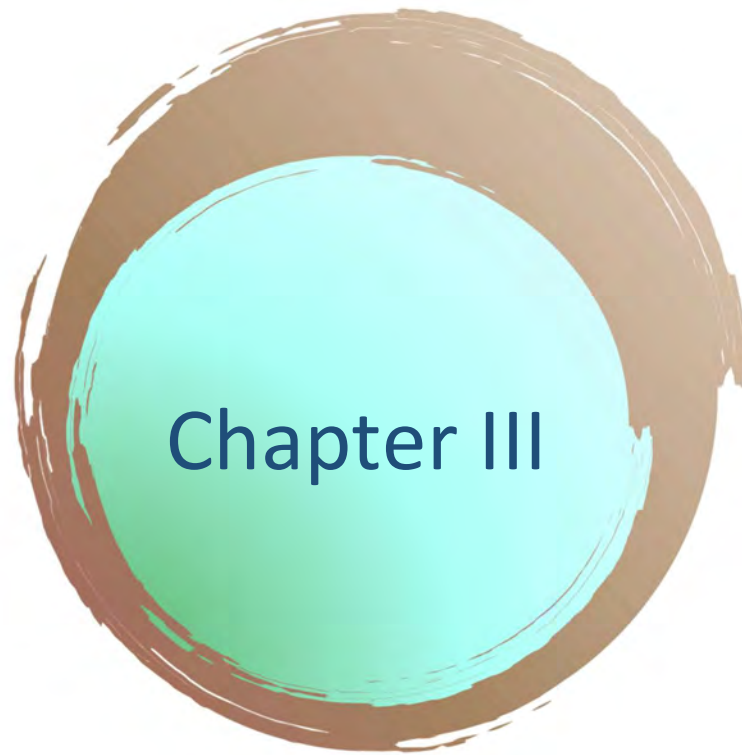


Supplementary Figure SII.9: Photosynthetic rates of the phototrophic microbial communities as a function of the proportion of cyanobacteria in the phototrophic communities.

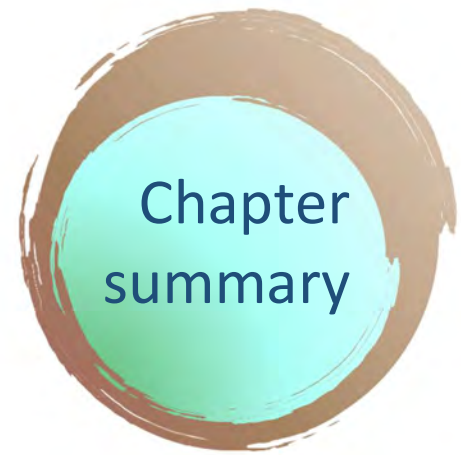


Supplementary Figure SII.10: A priori conceptual structural equation model (SEM) depicting pathways by which micro-environmental conditions may affect phototrophic community structure and cascade to microbial C fixation. Letters correspond to hypothetical pathways (Supplementary Information Table S4).





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



Recent global estimates show that phototrophic microbial abundance and activity is partly driven by climate in terrestrial ecosystems, with an important role of annual precipitations and mean temperature (Jassey et al., 2022). Northern peatlands spread over a large part of the northern hemisphere, from mid to high latitudes (above 40°N), and are submitted to several climates from oceanic to polar. I therefore wondered if the peatland phototrophic microbial communities would shift along with climatic conditions, and what would be the consequences for microbial photosynthesis. In the previous chapter, I found that community structure strongly varied under the effects of moisture content and light availability. I wanted to know if other environmental variables such as precipitation or temperature would be added in the determination of community structure. Further, I hypothesized that phototrophic microbes would significantly contribute to peatland C uptake at all latitudes.

To answer these questions, I studied phototrophic microbial communities in five peatlands distributed along a latitudinal gradient in Europe. I found a high diversity of phototrophic microbes, whose community structure was mainly shaped by water availability and plant composition. Despite environmental shifts in community structure, I showed that microbial C-fixation rates remained similar along the latitudinal gradient. My results further revealed that phototrophic microbes accounted for approximately 9% of peatland C uptake. These findings reveal the significant contribution of phototrophic microbes to peatland uptake. A rough estimate shows that phototrophic microbes could fix 75 MT CO₂ per year in northern peatlands, which highlights the importance of phototrophic microbes for the peatland C cycle.

Contribution of microbial photosynthesis to peatland carbon uptake along a latitudinal gradient.

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Abstract

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

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

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

4. *Synthesis.* Our findings show that phototrophic microbes are extremely diverse and abundant in peatlands. While species turnover with environmental conditions, microbial photosynthesis similarly contributed to peatland C uptake at all latitudes. We estimate that phototrophic microbes take up around 75 MT CO₂ per year in northern peatlands. This amount roughly equals the magnitude of projected peatland C loss due to climate warming and highlight the importance of phototrophic microbes for the peatland C cycle.

Introduction

Microbes only represent one-sixth of the living biomass on Earth (93 PgC for fungi, protists, bacteria and archaea; Bar-On et al., 2018) but they drive some of the most important carbon (C) fluxes at the global scale (Caron et al., 2017; Fierer, 2017; B. K. Singh et al., 2010). For instance, oceanic phytoplankton contributes to one third of the global photosynthetic CO₂ fixation with 50 PgC fixed each year, while the remaining amount is consensually attributed to terrestrial plants (Ciais et al., 2013). The input of organic matter to oceanic and terrestrial food webs is therefore attributed to the photosynthetic activity of either oceanic phytoplankton or terrestrial plants, respectively (Krumins et al., 2013; Liang et al., 2017; Worden et al., 2015). This consensus, however, ignores terrestrial photosynthetic microorganisms also known as micro-algae (hereafter, phototrophic microbes), which are natural components of the soil flora (Bates et al., 2013; Cano-Díaz et al., 2019; Oliverio et al., 2020), and can reach several millions of individuals per gram of soil (Zancan et al., 2006).

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

Peatlands play an important role in the global C cycle as they are major C sinks and store a large pool of soil C (500 – 1000 PgC; Bridgham et al., 2006; Nichols & Peteet, 2019; Yu, 2012). Peat mosses (i.e., *Sphagnum* spp.) serve a variety of key functions in peatlands, notably primary production and C sequestration (Turetsky, 2003; van Breemen, 1995). *Sphagnum* mosses also provide a habitat for a large diversity of microbes living either inside or at the surface of *Sphagnum* leaves (Gilbert et al., 1998a). This association between *Sphagnum* mosses and microbes forms the bryosphere (Lindo & Gonzalez, 2010). *Sphagnum*-associated phototrophic microbes include bacteria (e.g., Cyanobacteria,

Alphaproteobacteria), protists (e.g., Chlorophyta) and other mixotrophic micro-eukaryotes (e.g., many Ochrophyta or endosymbiotic Lobosa) (Gilbert et al., 1998; Gilbert & Mitchell, 2006; Jassey et al., 2015; Lara et al., 2011; Tian et al., 2019) and can be highly abundant. For instance, the biomass of phototrophic microbes in surface peat (0.5 mg C.l^{-1} ; Gilbert & Mitchell, 2006) can exceed the phytoplankton biomass of some of the most productive oceanic locations (c.a. 0.08 mg C.l^{-1} ; Behrenfeld, 2014). Yet, despite such high abundance, only a handful studies focused on algal production in peatlands, mostly in water-logged rich fens (Gilbert et al., 1998a; Goldsborough & Robinson, 1996; Wyatt et al., 2012). Phototrophic microbial production remains largely overlooked in all other peatland types including *Sphagnum*-dominated bogs and poor fens, which constitute the largest part of peatlands at a global scale (Hugelius et al., 2020). *Sphagnum*-dominated peatlands occupy extensive areas of land at different latitudes and across a wide variety of climates (Halsey et al., 2000; Robroek et al., 2017b). Hence, improving our understanding of the spatial and environmental patterns of phototrophic microbial contribution to bryosphere C uptake across environmental gradients is likely to improve our understanding of biogeochemical cycles in peatlands.

Here, we explore the diversity of phototrophic microbes and their primary production in different peatlands under varying climates and peatland conditions, using a latitudinal transect covering a broad range of environmental conditions. Specifically, we tested the relationships between phototrophic microbial community composition, structure, and photosynthetic rate in five European *Sphagnum*-dominated peatlands distributed from southern France to northern Sweden. We hypothesized (i) that phototrophic microbes make a significant contribution to the bryosphere C uptake, and that (ii) this contribution depends on environmental conditions such as climate (temperature, precipitation) and/or edaphic factors. More specifically, we expected (iii) that environmental conditions strongly influence the taxonomic composition of phototrophic microbial communities, affecting community structure with cascading effects on phototrophic abundance and C fixation rates. We analysed phototrophic microbial community composition by means of environmental 16S and 18S rDNA gene sequencing for prokaryotes and eukaryotes, respectively. We further evaluated phototrophic microbial abundance through flow cytometry and microscopy, and we assessed phototrophic microbial C fixation rates by measuring their photosynthetic efficiency and photosynthetic pigments content.

Methods

Sites description and sampling

We collected samples in five European peatlands distributed along a latitudinal gradient ranging from 42 °N (south of France) to 68°N (north of Sweden) in July 2018. From south to north (3000 km as the crow flies), the five peatlands were Counozouls (Lapazeuil) in France (42°41'16 N, 2°14'18 E, 1350 m a.s.l.), Kusowo (Kusowkie Bagno) in Poland (53°48'48 N, 16°35'12 E, 250 m a.s.l.), Männikjärve in 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.) and Abisko (Stordalen) in Sweden (68°20'54 N, 19°04'09 E, 350 m a.s.l.) (Fig. III.1A). These sites were characterised by flat topographies on a local scale and were associated with different peatland types. Counozouls is a minerotrophic fen, Kusowo and Männikjärve are ombrotrophic bogs, Siikaneva is a boreal oligotrophic fen, and Abisko a palsa mire. The vegetation at all five sites contained a sparse vascular plant layer, and was dominated by bryophytes from the *Sphagnum* genus: *S. warnstorffii* in Counozouls, *S. magellanicum* and *S. fallax* in Kusowo, *S. rubellum*, *S. magellanicum* and *S. fuscum* in Männikjärve, *S. papillosum* in Siikaneva and *S. balticum* in Abisko. At each site, we selected five homogeneous plots (50 x 50 cm). In each plot we sampled the apical part of *Sphagnum* mosses (0-3 cm from the capitulum) for analysis of microbial diversity, abundance and biomass as well as photosynthetic rates. We further quantified bryosphere C fixation rates from the same location (see below).

Vegetation, climatic and edaphic parameters

The vegetation cover (Supplementary Table SIII.1) was assessed in each site and in each plot by taking four pictures of each plot as explained in Sytiuk et al. (2020). The quality and quantity of *Sphagnum* water-extractable organic matter (Supplementary Table SIII.2) was assessed in each site according to Jasey et al. (2018). Several physico-chemical properties were analysed including pH, dissolved organic carbon and total nitrogen (measured by combustion on a Shimadzu TOC-L), ion concentration (measured on Dionex lcs-5000+ and Dionex DX-120) and dissolved organic matter quality (measured by spectrometry and fluorescence following Hansen et al. (2016). All values were corrected by a blank consisting of demineralized water. *Sphagnum* shoots were weighted fresh just after sampling. Then they were oven-dried (60°C for 48 hours) and weighted after extraction to calculate *Sphagnum* water content and to express the variables per g of *Sphagnum* dry weight (g DW). *Sphagnum* water content

was expressed in g of water per g of *Sphagnum* DW. Finally, long-term bioclimatic variables such as mean annual temperature, annual precipitation and temperature seasonality were retrieved from WorldClim 2.0 (Supplementary Table SIII.3).

Diversity and community structure of peatland phototrophic microbes

Microbial DNA extraction

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

Microbial DNA sequencing

To investigate prokaryote communities, we amplified a part of the 16S rDNA gene, using the primers PCR1_515F and PCR1_928R (Y. Wang & Qian, 2009). Eukaryote communities were investigated by amplifying a part of the 18S rDNA gene with the primers TAREuk454FWD1 and TAREukREV3 (Tanabe et al., 2016). Both prokaryotic and eukaryotic pairs of primers were tagged with Illumina adapter sequences. PCRs were conducted in a total volume of 50 µl containing 13 µl of Mastermix AmpliTaq Gold (ThermoFisher), 1µl of each primer from the chosen pair (0.4 µM final concentration), 35 ng of DNA (up to 10 µl) and supplemented to 50 µl with DNA-free water. The primers' sequences and the PCR programs used are presented in Supplementary Table SIII.4. All PCR products were checked on an agarose gel and samples were then frozen at -80°C until sequencing was performed by the GeT-PlaGe platform (Genotoul, Toulouse, France) with Illumina MiSeq technology and using the V3 chemistry (2x250 bp).

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

(10% of mismatch; Rognes et al., 2016). Sequences were filtered based on their length and primer mismatches were removed, leading to a total of 770 602 prokaryotic sequences and 813 098 eukaryotic sequences for all samples. Sequences were then de-replicated and clustered into operational taxonomic units (OTUs) using the Swarm clustering method with an aggregation distance of 3 (Mahé et al., 2014). Chimeras were identified and removed using Vsearch. Filters were then applied to remove singletons. In total 677 947 sequences clustered in 2 063 OTUs were kept for prokaryotes, and 718 684 sequences clustered in 2 050 OTUs were kept for eukaryotes. OTUs were assigned at different taxonomic levels using Blast. We used the Silva 138 database (Quast et al., 2013) for prokaryotic assignment and the PR² v4.12.0 database (Guillou et al., 2013) for eukaryotic assignment.

Identification of phototrophic OTUs

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

Absolute abundance of phototrophic microbes

To determine the absolute abundance of phototrophs in every site, we sampled five shoots of *Sphagnum* (0-3 cm) in each plot, fixed them in 20 ml of glutaraldehyde (2% final concentration), and

extracted microorganisms from *Sphagnum* tissues following the method of Jassey et al. (2011). Then, we quantified the absolute abundance of phototrophic microbes from microbial extracts by means of either flow cytometry or microscope analyses according to microbial body size.

Phototrophic microbes with a body length smaller than 40 μm were enumerated using flow cytometry. To do so, we filtrated 300 μl aliquots of microbial extract with 40 μm Nitex® filters, and placed them in a 96-well microplate. Then, aliquots were run unstained in a Guava® easyCyte™ 11HT 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 and side light scatter (size indication) as well as green fluorescence (presence or absence of chlorophyll) were used to discriminate photosynthetic microorganisms from non-photosynthetic microorganisms (bacteria) (Olson et al., 1989).

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

Flow cytometry and inverted microscope abundance data were expressed as the number of individuals per gram of *Sphagnum* dry weight (DW). We further converted abundance data to C biomass (μg C per gram of *Sphagnum* DW) by measuring the biovolume of each species using geometrical shapes under microscope (Gilbert et al., 1998a; Mitchell et al., 2003). Biovolumes were then converted to C biomass using conversion factors from the literature (Borsheim & Bratbak, 1987; Gilbert et al., 1998a; Weisse et al., 1990).

Microbial photosynthetic rates

Chlorophyll *a* (Chl *a*) concentrations and the quantum yield of photosystem II (Φ_{PSII}) were measured in each plot. Chl *a* concentrations provide an estimate of the amount of photosynthetic machinery, while Φ_{PSII} gives the fraction of the absorbed quanta that are used for photosynthetic electron transport and

thus provides a measure of photosynthetic efficiency (Wilken et al., 2013). For these analyses, five shoots of *Sphagnum* (0-3 cm) were sampled in each plot and immersed in 20 mL demineralized water. Samples were kept at 4°C in the dark and microorganisms were extracted immediately upon return to the laboratory. Samples were shaken at 150 rpm for 1.5 h and then squeezed to extract microorganisms. The remaining solution was filtered at 100 µm with Nitex® filters to remove any *Sphagnum* residue, while the remaining *Sphagnum* material was dried at 80°C for 48 h and weighted. Each microbial extract was filtered on a GF/F Whatman® filter (0.7 µm) to recover the microbial community.

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

$$(3) \text{ ETR} = 0.5 \times I \times \frac{\text{Chla}}{\text{cell}} \times \Phi_{PSII} \times a^*$$

where ETR is the photosynthetic rate, expressed per cell as a measure of the community-weighted mean photosynthetic rate. It was calculated at a light intensity (I) of 32 µmol.m⁻².s⁻¹. The calculation of ETR relies on the importance of the microbial photosynthetic machinery (cellular Chla content, $\frac{\text{Chla}}{\text{cell}}$) and on its photosynthetic efficiency (effective quantum yield of photosystem II, Φ_{PSII} , measured at a PAR of 32 µmol.m⁻².s⁻¹). Here, a^* was the spectrally averaged chlorophyll-specific absorption cross section, for which we took a value of 26.86 m².g Chla⁻¹ as estimated in (Wilken et al., 2013). The ETR was expressed in mol e⁻.cell⁻¹.s⁻¹.

To obtain Chl *a* concentrations, the filters used for microbial photosynthetic efficiency and containing microbial communities were frozen at -80°C and freeze-dried in the dark. Adapting the methodology from Capdeville et al. (2019), we soaked lyophilized filters in 1.5 ml of methanol buffered with 2 %v of ammonium acetate (1 mol.l⁻¹). Samples were sonicated for 2 min in an ice bath, then cooled at -20°C in the dark for 15 min and centrifuged for 5 min at 10 000 rpm. The supernatant was recovered (solution 1) while 1 ml of buffered methanol was added to the pellet (solution 2). The process was repeated for solution 2 and its supernatant was merged with solution 1. Then, 1.5 ml of

this composite solution was filtered at 0.2 μm with a syringe filter and frozen at -80°C before analysis on an HPLC (Barlow et al., 1997). We assessed the concentration of several pigments including Chl *a*, pheophytin *a* and pheophorbide *a*. As pheophytin *a* and pheophorbide *a* are alteration products of Chl *a* (Jeffrey et al., 2005), we summed the abundance of these three pigments to have an estimate of overall Chl *a* in the samples (hereafter named Chl *a*). Chl *a* was expressed in mg per g of *Sphagnum* DW and divided by phototroph abundance to have an estimate of cellular Chl *a* content (expressed in $\text{mg}\cdot\text{cell}^{-1}$).

Microbial C fixation rate and contribution to bryosphere C fixation rate

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

$$(4) C_{\text{fixed}} = 0.25 \times \text{ETR} \times \text{cell} \times \text{Area}_{\text{DW}}$$

where we assumed a maximum fixation of 0.25 mol CO_2 per mol of electron (Wilken et al., 2013), and took into account phototrophic microbial abundance (*cell*) and specific surface of *Sphagnum* (Area_{DW}) measured in each plot as the area per gram of *Sphagnum* DW (0-3 cm). Carbon fixation rates were expressed in mg of CO_2 fixed per hour and per m^2 of *Sphagnum*.

We measured the bryosphere photosynthetic capacity (A_{MAX} , maximum net CO_2 assimilation rate) in each plot from three *Sphagnum* shoots as described in Jassey & Signarbieux (2019). The A_{MAX} was measured with an open-path infrared gas analyser (IRGA) system connected to a 2.5 cm^2 PLC-5 chamber (TARGAS-1; PP-Systems) under optimum conditions for light (i.e., $600 \mu\text{mol}$ of photons $\text{m}^{-2} \cdot \text{s}^{-1}$, which was previously determined in the field). Bryosphere C fixation was expressed in $\text{mg CO}_2 \text{ h}^{-1} \cdot \text{m}^{-2}$, allowing comparisons with microbial C fixation rates. To estimate bryosphere C fixation per Chl *a*, we also estimated the Chl *a* content of *Sphagnum* in each plot. We extracted Chl *a* from two lyophilized *Sphagnum* shoots and followed the same extraction method as for phototrophic microbes.

Numerical analyses

Meta-barcoding data were used to explore the diversity and taxonomy of phototrophic microbes, and their community composition. Biostatistics were conducted separately on prokaryotic and eukaryotic microbial communities. Alpha-diversity, non-metric multidimensional scaling (NMDS), and beta-diversity metrics based on Bray-Curtis dissimilarity were used to estimate diversity and species turnover between sites. Environmental drivers of phototrophic microbial species turnover were tested

using generalized dissimilarity modelling (GDM). The environmental matrix included a selection of variables such as plant community composition (Supplementary Table SIII.1), *Sphagnum* physico-chemical parameters (Supplementary Table SIII.2), and climatic variables (Supplementary Table SIII.3). We selected the most representative and least collinear environmental variables using the package ClustOfVar (12) with an ascendant hierarchical clustering of all available environmental variables. To maximise the stability of partition, nine clusters of variables were retained. In each cluster, the most representative variables were kept for GDM (Supplementary Fig. SIII.2). Variable significance in GDM was determined using matrix permutations and comparing models with each variable permuted and un-permuted. At each step, the least important variables were dropped until all non-significant predictors were removed. The GDM was then fit using only significant environmental predictors, and model significance was checked.

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

The variability of phototrophic C fixation can be determined by numerous interconnected eco-physiological mechanisms that operate simultaneously at different individual to community scales (Padfield et al., 2018; Yvon-Durocher et al., 2015). One approach to studying such complex interactions is Structural Equation Modelling (SEM; Grace et al. 2014). Following current knowledge on phototrophic eco-physiology (Huete-Ortega et al., 2012; Kalchev et al., 1996; Padfield et al., 2018), we developed an *a priori* model of hypothesized relationships (Supplementary Fig. SIII.3) within a path diagram allowing a causal interpretation of microbial C fixation rates in relation to microbial community structure (bacteria and protists), to allometric features (abundance, community-weighted mean body size) and metabolic parameters (Chl α , photosynthetic rate) (Supplementary Table SIII.5). In this diagram, each path is a component of the model, and represent a linear model between the explanatory and the explained variable. All components of the model were united using the psem function from the piecewiseSEM R package (Lefcheck, 2016). The goodness-of-fit of our *a priori* SEM model was evaluated using Fisher's statistic and Akaike Information Criterion (AIC). Based on the

outputs of the *a priori* model and by step-wise exclusion and selection of variables, we found the model with the lowest AIC value. The main drivers of microbial C fixation were determined from this final model. We used the first axes of phototrophic prokaryotic and eukaryotic NMDS as indicators of microbial community structure, and electron transport rate (ETR) as indicator of photosynthetic activity. To test to what extent environmental variables affected microbial C fixation and the phototrophic mechanisms underpinning it, we ran our SEM model a second time with microbial variables corrected for the co-varying environmental variables (residual data). To correct microbial variables for environmental conditions, we used the residuals of linear models computed between every microbial variable and the environmental variables identified in the GDM (i.e., precipitation, *Sphagnum* water content, plant community composition and dissolved organic carbon).

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

Results

Diversity and community composition of phototrophic microbes

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

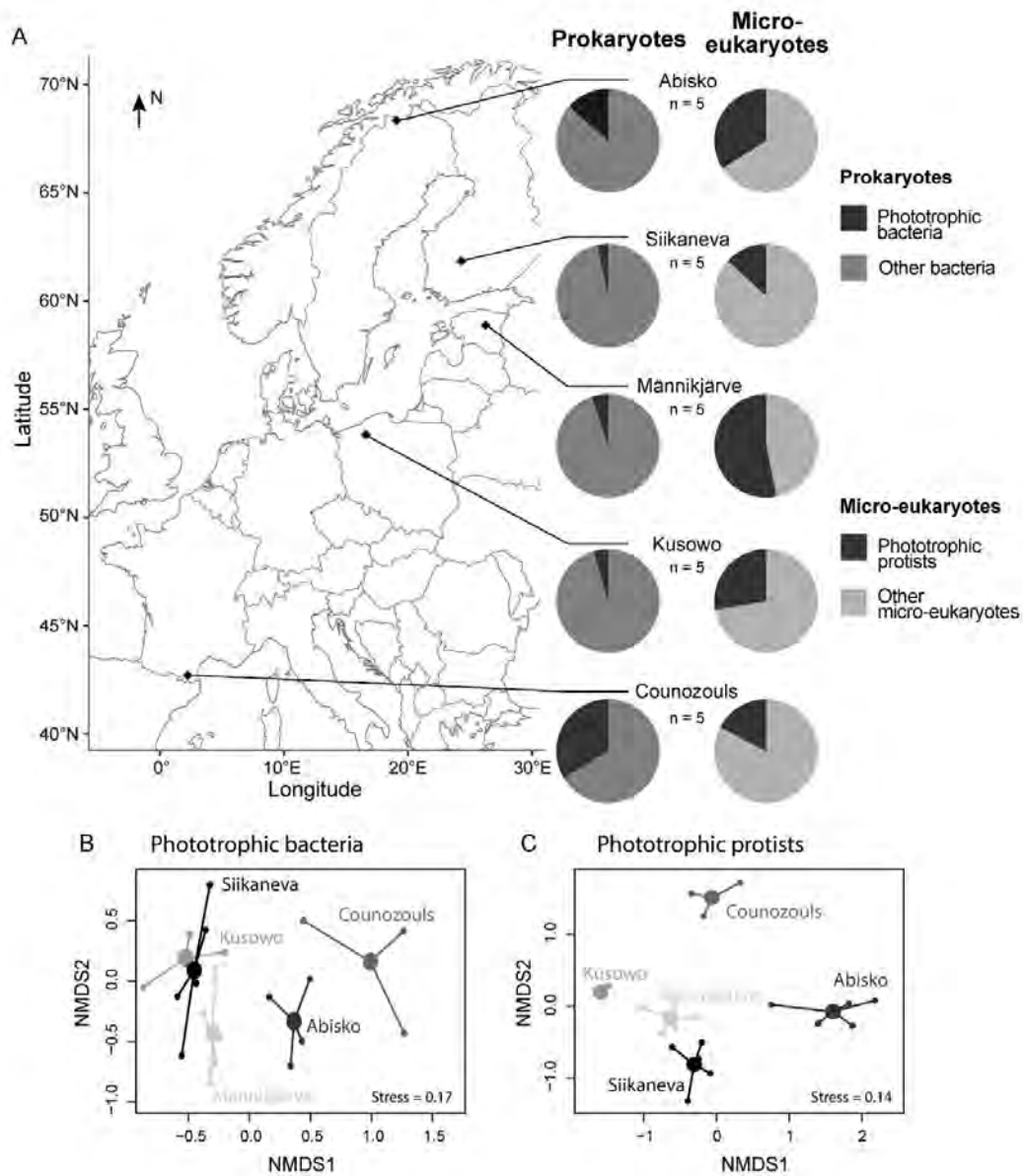


Figure III.1: Geographic locations of the five European peatlands and structure of microbial prokaryotic and eukaryotic communities **(A)**. NMDS of the communities of phototrophic bacteria **(B)** and phototrophic protists based on phototrophic OTUs **(C)**.

Overall, we observed 74 OTUs of phototrophic bacteria and 277 OTUs of phototrophic protists. For phototrophic bacteria, COUNOZOULS had by far the highest OTU richness with on average 30 species per sample ($F_{(4, 12)} = 28.0, P < 0.001$; Fig. III.2B), whilst Siikaneva had the lowest richness (10 species per sample on average). Despite significant variation in OTU richness, we found that phototrophic bacteria diversity (Shannon's entropy) was stable across sites ($F_{(4, 12)} = 0.9, P = 0.48$, Fig. III.2B). For phototrophic

protists, we found the highest OTU richness in Männikjärve (52 species) ($F_{(4,12)} = 3.2, P = 0.05$; Fig. III.2B) and the lowest in Abisko (31 species). Phototrophic protist diversity followed the latitudinal gradient with a slight but significant decrease from Counozouls to Abisko ($F_{(4,12)} = 4.6, P = 0.02$; Fig. III.2B).

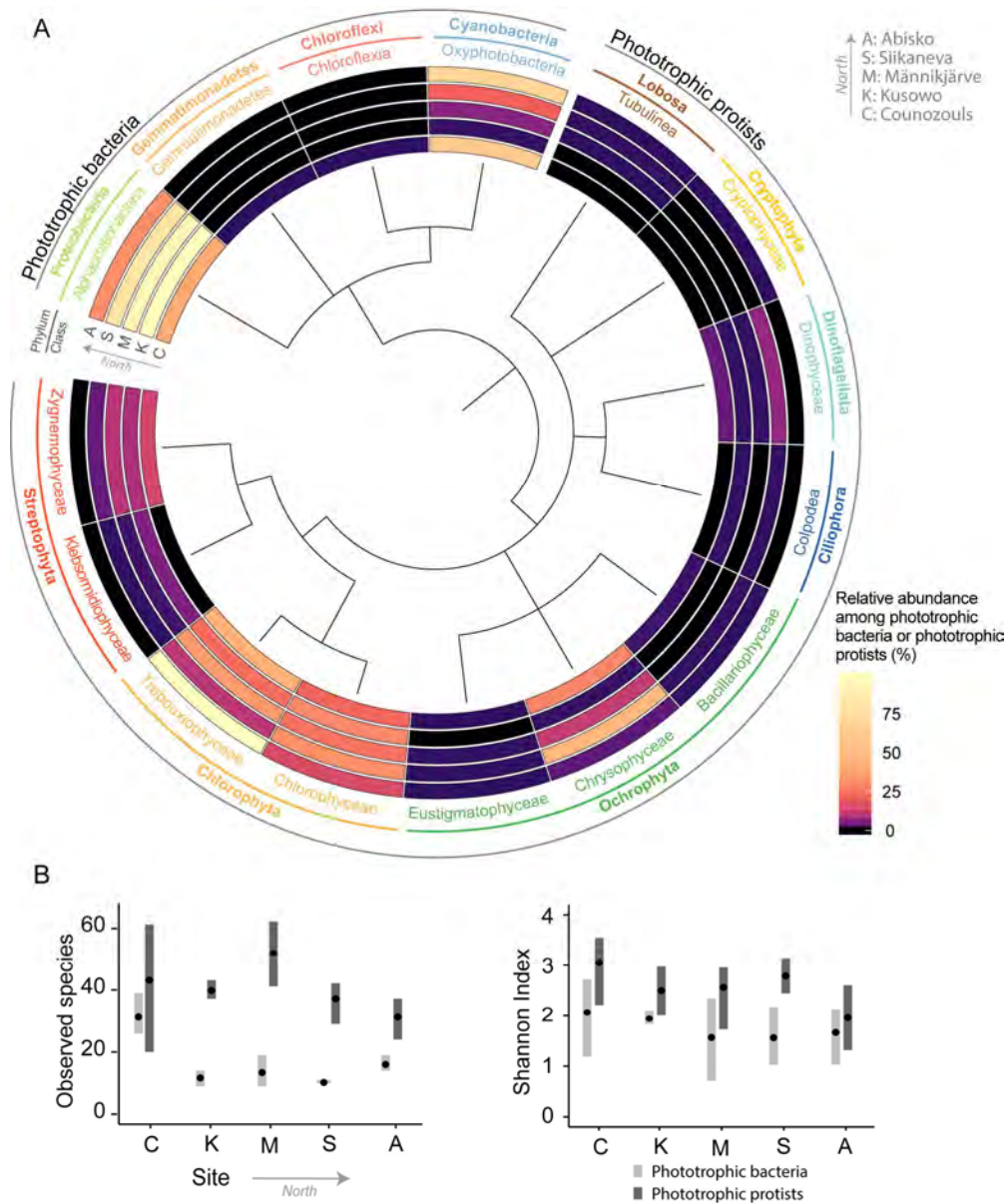


Figure III.2: Phylogenetic tree, relative abundance (A), and diversity (B) of the phototrophic OTUs identified in the five peatland sites along the latitudinal gradient. Phototrophic OTUs include endosymbiotic mixotrophs (e.g., *Hyalosphenia papilio*, *Lobosa*). Relative abundance of phototrophic OTUs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

We identified four phyla of phototrophic bacteria, distributed in four classes and eight orders (Supplementary Fig. SIII.5). Proteobacteria and Cyanobacteria dominated phototrophic bacteria across sites. Proteobacteria ($F_{(4,12)} = 113.24$, $P < 0.001$) were relatively more abundant in Kusowo, Männikjärve and Siikaneva (>80 %), while Cyanobacteria ($F_{(4,12)} = 10.4$, $P < 0.001$) relatively dominated in Counozouls (60.8 %) and Abisko (68.5 %) (Fig. III.2A). Gemmatimonadetes and Chloroflexi were only present in Counozouls (Fig. III.2A). Proteobacteria were primarily represented by the orders Acetobacterales and Rhizobiales, whereas Cyanobacteria were mostly represented by Nostocales (Supplementary Fig. SIII.5). We further identified seven phyla of phototrophic protists, distributed in 13 classes and 21 orders (Supplementary Fig. SIII.5). Chlorophyta (75.1 % of the average phototrophic protist relative abundance), Ochrophyta (15.3 %) and Streptophyta (7.4 %) were the three most relatively abundant phyla (Fig. III.2A, Supplementary Fig. SIII.5). At the class level, Chlorophyta were mainly represented by Trebouxiophyceae and Chlorophyceae; Ochrophyta by Chrysophyceae; and Streptophyta by Zygnemophyceae and Klebsormidiophyceae. The relative abundance of the different classes varied significantly along the latitudinal gradient (Fig. III.2A, Supplementary Fig. SIII.5).

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

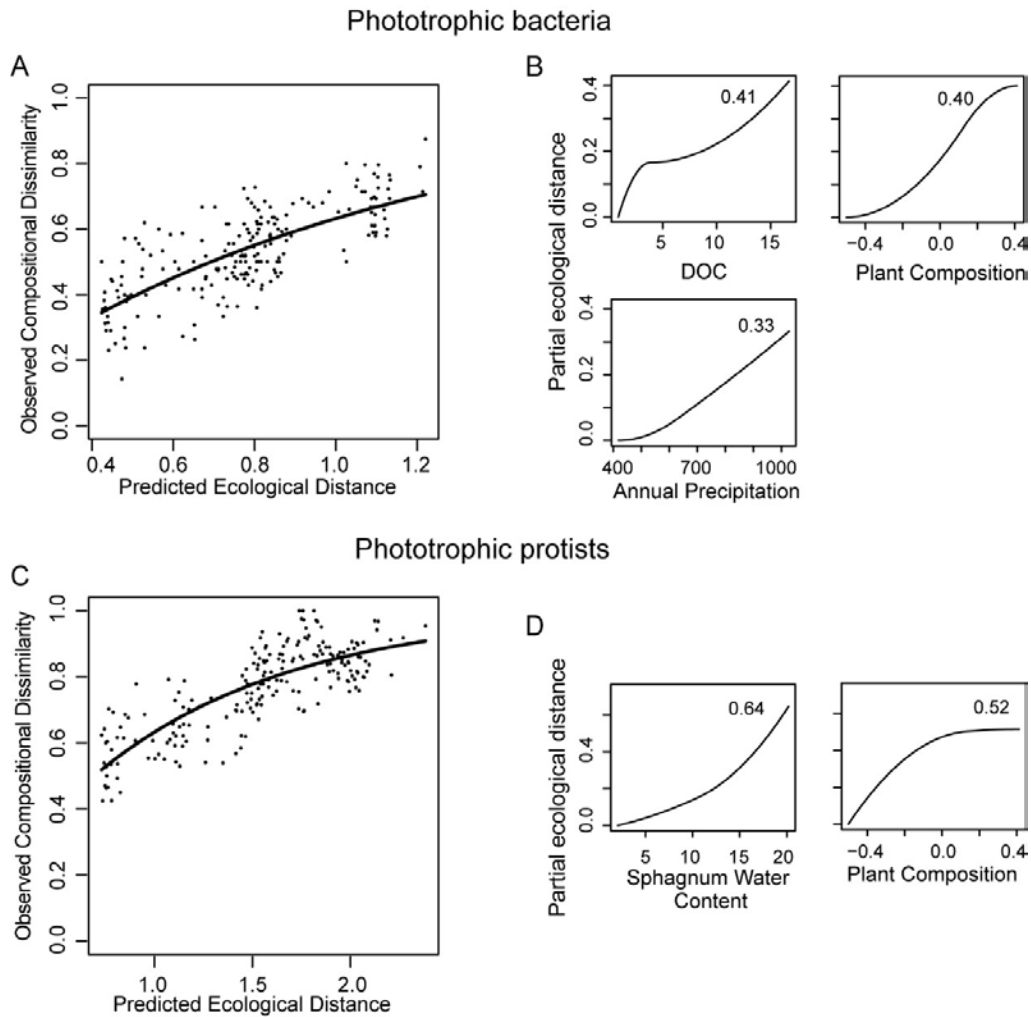


Figure III.3: Generalised dissimilarity modelling and taxonomic turnover along environmental gradients. Relationship between compositional dissimilarity between site pairs (species turnover or beta-diversity) and their predicted environmental dissimilarity, for phototrophic bacteria communities **(A)**,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

Absolute abundance, biomass and size structure of phototrophs

The absolute abundance of phototrophic microbes strongly decreased along the latitudinal gradient with a drop from $194.0 \times 10^6 \text{ ind.g}^{-1} \text{ DW}$ in COUNZOULS to $45.3 \times 10^6 \text{ ind.g}^{-1} \text{ DW}$ in ABISKO ($F_{(4,16)} = 25.1$, $P < 0.001$; Fig. III.4A). This pattern was mostly driven by phototrophic microbes with a body size $< 40 \mu\text{m}$ that constituted the majority of microbial phototrophs (98.5 %, Supplementary Fig. SIII.7). Large phototrophic microbes and large mixotrophs (body size $> 40 \mu\text{m}$) were less abundant and showed opposite patterns with an increase of their absolute abundance toward high latitudes ($F_{(4,16)} = 11.8$, $P < 0.001$ and $F_{(4,16)} = 20.3$, $P < 0.001$ respectively, Supplementary Fig. SIII.7, Fig. III.4B). Consequently, the community-weighted mean body size per cell increased toward high latitudes ($F_{(4,16)} = 20.3$, $P < 0.001$), with phototrophic microbes being on average 28 times larger in Abisko than in COUNZOULS (Fig. III.4C). On the whole, the total biomass of the phototrophic community tended to increase toward high latitudes, from $1049 \mu\text{gC.g}^{-1} \text{ DW}$ in COUNZOULS to $1634 \mu\text{gC.g}^{-1} \text{ DW}$ in ABISKO ($F_{(4,16)} = 46.3$, $P < 0.001$; Fig. III.4D). Within the phototrophic community, Cyanobacteria had a higher absolute abundance in COUNZOULS and in ABISKO ($1.04 \times 10^6 \pm 0.01 \text{ ind.g}^{-1} \text{ DW}$) than in the other sites ($0.20 \times 10^6 \pm 0.04 \text{ ind.g}^{-1} \text{ DW}$) ($F_{(4,16)} = 20.3$, $P < 0.001$; Supplementary Fig. SIII.8). However, considering biomasses, the ratio Cyanobacteria to phototrophic microbes was higher in COUNZOULS and KUSOWO (0.61 ± 0.17) compared to the other sites (0.13 ± 0.03) ($F_{(4,16)} = 16.9$, $P < 0.001$; Supplementary Fig. SIII.8).

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

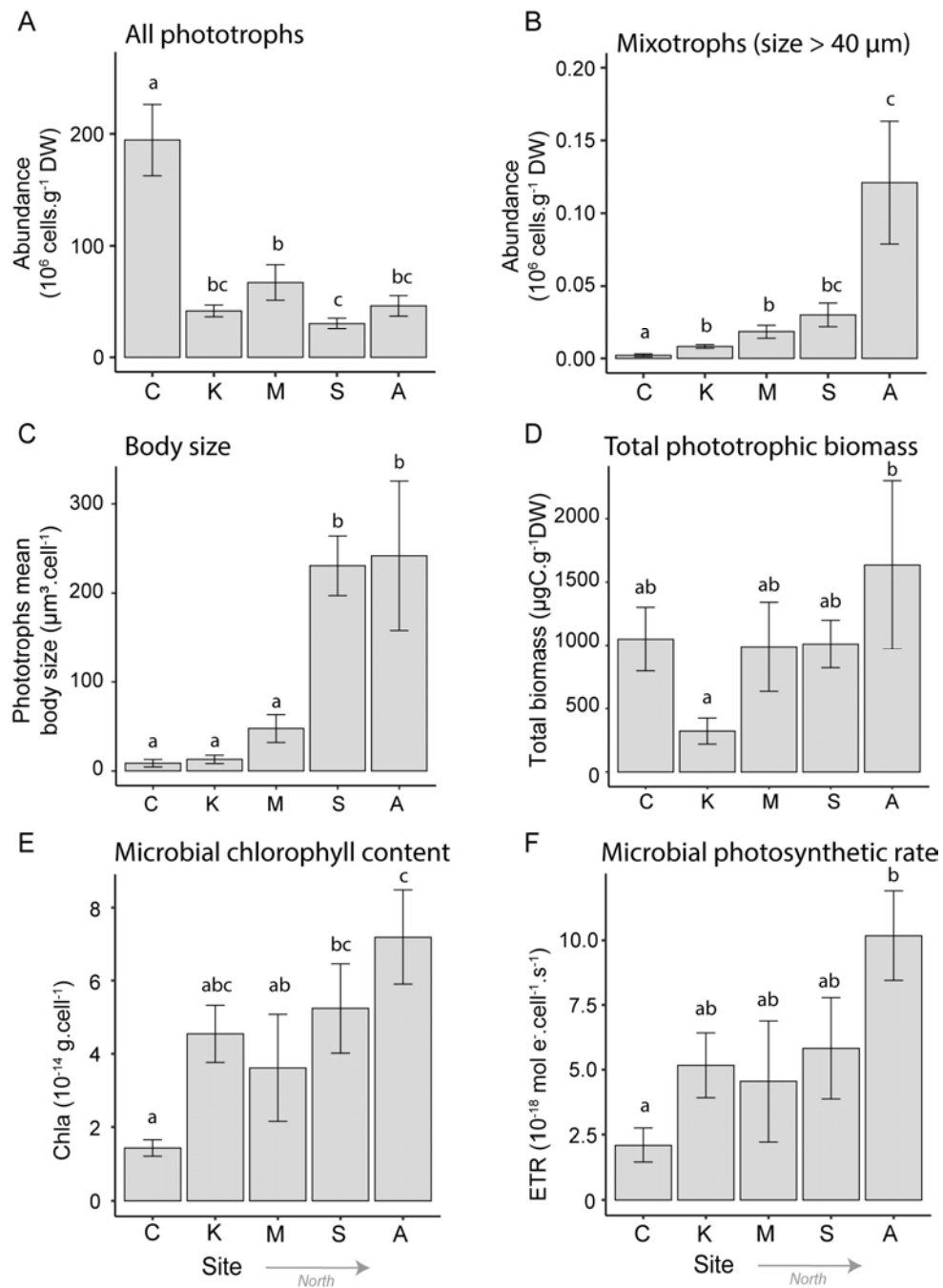


Figure III.4: Abundance of all phototrophs **(A)** and large mixotrophs (body size > 40 μ m) **(B)** in the five peatlands. Community-weighted mean body size of phototrophic microbes **(C)** and total phototrophic biomass **(D)** in the five peatlands. Chlorophyll *a* cellular content of phototrophs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

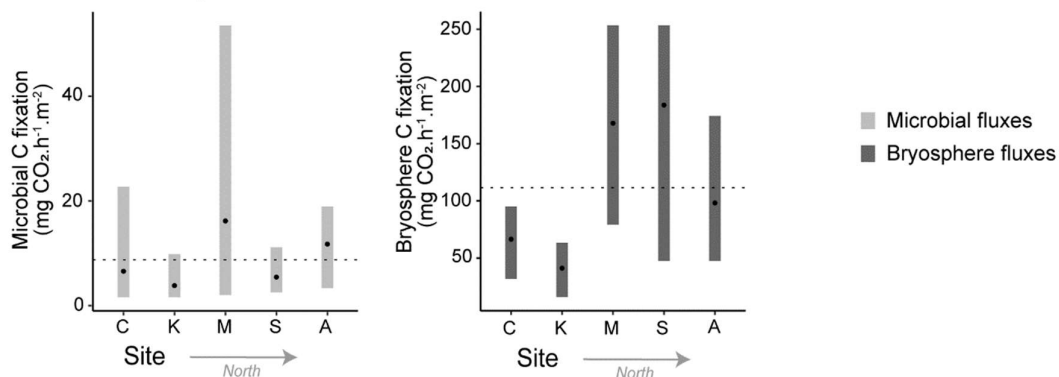
Photosynthetic rates and C fixation of phototrophic microbial communities

The chlorophyll content of phototrophic microbes increased along the gradient (+400 % between COUNOZOULS and ABISKO; $F_{(4,16)} = 5.78$, $P = 0.005$; Fig. III.4E). Similar patterns were found for photosynthetic rates (+380 %; $F_{(4,16)} = 3.7$, $P = 0.02$; Fig. III.4F). On average, phototrophic microbes fixed 8.8 (3.8 – 16.2) mg CO₂.h⁻¹.m⁻² over the gradient. Phototrophic microbial C fixation varied between sites, from 16.2 mg CO₂.h⁻¹.m⁻² in MÄNNIKJÄRVE to 3.8 mg CO₂.h⁻¹.m⁻² in KUSOWO, but differences among sites were not significant ($F_{(4,12)} = 1.10$, $P = 0.39$; Fig. III.5A).

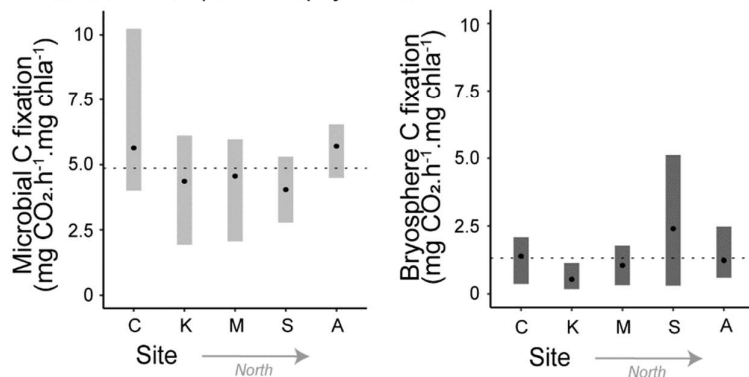
Our SEM model showed that microbial C fixation was directly mediated by the direct influence of phototrophic abundance (path = 0.42) and metabolism (photosynthetic rate, path = 0.70) (Fig. III.6). Indirectly, microbial C fixation was mediated by the community structure of phototrophic bacteria and protists, which influenced phototrophic allometry. In particular, community structure influenced the microbial abundance (path = 1.09 and path = -0.43 for bacteria and protist community structure, respectively) and the community-weighted mean body size (path = -0.46 and path = 0.70 for bacteria and protist community structure, respectively), which had cascading effects on phototrophs metabolism (chlorophyll content per individual, and finally photosynthetic rate). A comparison with the SEM model corrected from environmental variables did not reveal strong alterations of the pathways (Supplementary Fig. SIII.9). This indicated that the phototrophic mechanisms identified in our SEM model were independent from environmental changes.

In comparison with microbial C fixation, bryosphere C fixation showed a different latitudinal pattern with higher C uptake in the three northern sites compared to the two southern sites ($F_{(4,12)} = 6.70$, $P = 0.002$; Fig. III.5A). The bryosphere fixed on average 111.5 mg CO₂.h⁻¹.m⁻². The microbial C fixation normalised by Chl *a* showed that phototrophic microbes fixed nearly four times more C than the bryosphere for a given amount of Chl *a* ($F_{(1,48)} = 79.15$, $P < 0.001$; Fig. III.5B). We further estimated that phototrophic microbes contributed by 9.4% (1.1% - 37.5%) to the bryosphere C fixation across all sites (Fig. III.5C). This contribution ranged on average from 4.1% in Siikaneva to 12.4% in Abisko (Fig. III.5C), but differences among sites were not significant ($F_{(4,12)} = 1.44$, $P = 0.27$).

A Carbon fluxes per surface unit



B Carbon fluxes per chlorophyll content



C Microbial contribution to bryosphere fluxes

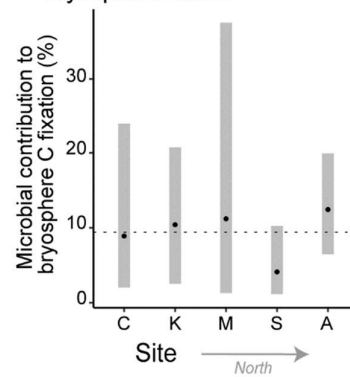


Figure III.5: Microbial (light grey) and bryosphere (dark grey) C fixation rates, expressed per surface unit **(A)** or normalised by the chlorophyll *a* content **(B)**; and contribution of microorganisms to bryosphere C fixation **(C)** in the five peatlands. Bars range between minimum and maximum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

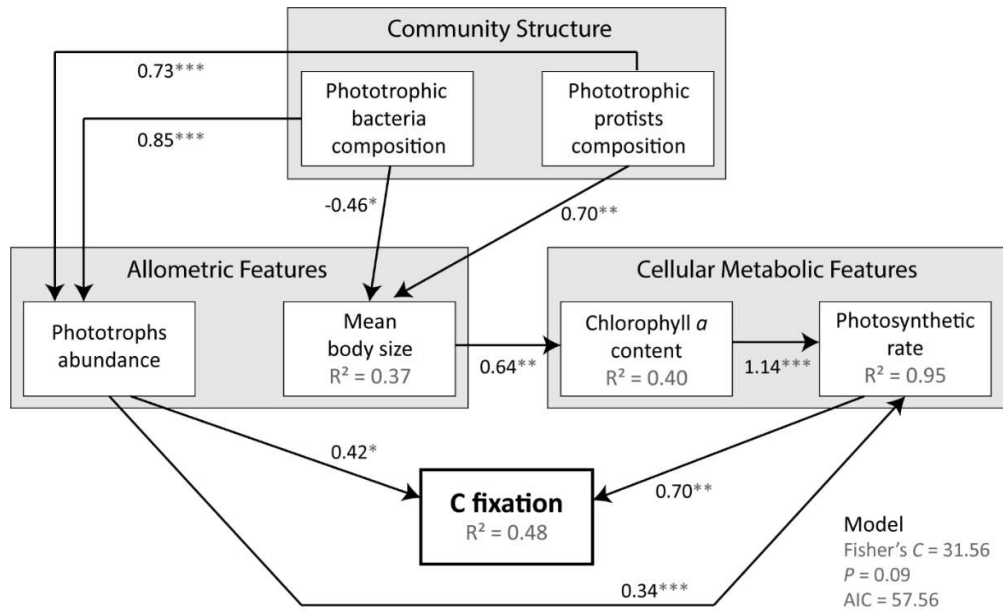


Figure III.6: Structural equation model (SEM) of the correlations between the structure of phototrophic microbial communities, their allometric and metabolic features and microbial C fixation. Numbers in the boxes indicate the percentage of variance explained by the model (adjusted R-squared), while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

Discussion

Microbial communities play an important role in maintaining multiple ecosystem functions that are important for C cycling. Whilst methanogens, fungi and other bacteria are known for their key role in C mineralization and respiration (e.g., (Galand et al., 2005; Myers et al., 2012; Thormann, 2006)), we show that, across a wide range of climatic conditions, phototrophic microbial communities are important for peatland C dynamics through their contribution to C uptake. Our study revealed that phototrophic microbes were phylogenetically diverse and highly abundant in peatlands throughout the latitudinal gradient. The structure and abundance of phototrophic microbial communities varied along the latitudinal gradient, driven by shifts in biotic and abiotic environmental factors (e.g., climate, plant composition). Despite microbial species turnover, our findings demonstrated a constant microbial CO₂ fixation along the gradient. Our results therefore provide the first *in situ* evidence for the role of phototrophic microbes in peatland C uptake at a continental scale.

Phototrophy is a dominant microbial process in surface peat

On average, we found 7.5×10^7 microbial phototrophic cells per gram of dry moss in the top 3 cm of the *Sphagnum* carpet. This number is in line with previous studies, where phototrophic microbial abundance typically ranged between 10^6 and 10^8 cells per gram of dry moss (Basińska et al., 2020; Jassey et al., 2015). We found that phototrophic microbes represented an approximate biomass of 1.0 mg C per gram of dry moss. This is, by comparison, higher than the heterotrophic bacterial biomass (approximately 0.5 mg C per g DW), or the biomass of heterotrophic protists (approximately 0.15 mg C per g DW) found in peatlands at the same depth (Jassey et al., 2011, 2015; Mitchell et al., 2003). Phototrophic microbes constitute therefore the most important component of microbial C biomass in the apical part of the *Sphagnum* carpet, which suggests that phototrophy is a dominant microbial process in the upper peatland layer.

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

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

Peatland phototrophic communities are diverse and environment-specific

We identified 351 phototrophic microbial OTUs over the gradient, belonging to diverse prokaryotic and eukaryotic taxonomic clades. While phototrophic communities were relatively dominated by Chlorophyta (micro-eukaryote) and Alphaproteobacteria (prokaryotes), we nevertheless identified

seven phyla of phototrophic micro-eukaryote, and four out of the seven existing phyla of phototrophic prokaryotes (Zeng et al., 2014). In link with this high taxonomic diversity, we identified a wide range of photosynthetic pathways. Within micro-eukaryotes, we found strict phototrophic organisms (e.g., phototrophic Ochrophyta, Chlorophyta) and mixotrophic organisms (e.g., endosymbiotic Ciliophora, Lobosa). Within prokaryotes, the OTUs identified formed a continuum between photoautotrophy and photoheterotrophy (Kulichevskaya et al., 2014; Yurkov et al., 1993), with uncertainty about the levels of autotrophy. For instance, Cyanobacteria can acquire organic C and downregulate their photosynthesis when in symbiosis with other plants (Black & Osborne, 2004), while some phototrophic Proteobacteria can grow both photoautotrophically and photoheterotrophically (K.-H. Tang et al., 2011). Even though the occurrence of Cyanobacteria and phototrophic Proteobacteria is generally accepted in peatlands, they remain poorly explored and this calls for a deeper consideration of their role in peatland C cycling.

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

The microbial C fixation depends on the community structure of phototrophic microbes

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

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

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

Implications of microbial C fixation for peatland C dynamics

Phototrophic microbes fixed on average 8.8 (3.8 – 16.2) mg CO₂ h⁻¹ m⁻² across sites, which represented on average 9% (4% - 12%) of the total bryosphere C fixation. This contribution might seem relatively high considering the low C biomass of phototrophs in *Sphagnum* (1 mg C.g⁻¹ DW). Yet, the photosynthetic rate per chlorophyll content of phototrophs is four to ten times higher than for *Sphagnum*. It explains why phototrophic microbes contribute significantly to the bryosphere C fixation despite their small size and biomass. It further indicates that the small fraction of C found in

phototrophic biomass does not reflect the amount of C they fix. This result is in line with a previous study suggesting that Cyanobacteria and green algae can display a 50-fold higher efficiency in CO₂ fixation compared to plants due to their faster growth rate (Rossi et al., 2015).

Regarding the proportion of C fixed by phototrophic microbes, we argue it is very likely that phototrophic microbes play an important– and until now overlooked– role in peatland C cycling. Assuming that our data are representative for northern peatlands, we roughly estimated that phototrophic microbes would fix a global amount of *ca.* 75 MT CO₂ per year in northern peatlands (Supplementary Methods, Supplementary Table SIII.7). By comparison, this amount is about the same magnitude as C loss from northern peatlands in response to climate warming (Dorrepaal et al., 2009). We note that our estimates of microbial contribution to annual peatland C uptake are based on several assumptions that might lead to uncertainty. For example, seasonal climatic variation in microbial phototrophic activity could influence the values that we present here. In particular, water availability and *Sphagnum* water content vary over the year, and thus shape the community structure and C fixation rates of phototrophic microbes accordingly. Yet, phototrophic microbial communities respond fast to water availability changes in peatlands (less than two weeks, Reczuga et al., 2018). We thus believe that our estimations are representative of the summer conditions at the time we sampled. Moreover, phototrophic microbial abundance have been shown to peak in spring and autumn (Reczuga et al., 2020), when their abundance can double (Rober et al., 2014). This suggests that the annual C fixation by microbial phototrophs might therefore be higher than expected. We also acknowledge that our fluorescence-based measurements of microbial photosynthesis could introduce some bias in our estimates. In particular, the high proportion of Cyanobacteria in some sites could lead to an underestimation of photosynthetic rates, as chlorophyll fluorescence measurements are often underestimated in Cyanobacteria due to their prokaryotic nature (Ogawa et al., 2017; Schuurmans et al., 2015). We however did not observe this effect in our samples (Supplementary Fig. SIII.10). Similarly, measurements of chlorophyll fluorescence do not take into account the photosynthesis performed by the bacteriochlorophyll of phototrophic prokaryotes. However, microbial C fixation rates estimated using fluorescence were of the same magnitude as C fixation rates quantified using a gas analyser (Supplementary Fig. SIII.11). Finally, we caution that the estimate of peatland surface used for upscaling (Leifeld & Menichetti, 2018b) is not restricted to *Sphagnum*-dominated peatlands and includes rich fens. However, *Sphagnum*-dominated peatlands (ombrotrophic bogs and poor fens)

represent a high proportion of total peatlands, accounting for instance for more than 65% in North America (Hugelius et al., 2020). Further, phototrophic microbial C fixation in rich fens has been found of either similar or higher magnitude than our estimates (Wyatt et al., 2012). Despite these limitations, our findings clearly underline the importance of phototrophic microbes for peatland C cycle through the large amount of C they fix.

Conclusions and perspectives

The current consensus on C pathways in terrestrial ecosystems is that plants are the only or at least the main route for soil C uptake (Krumins et al., 2013; Liang et al., 2017). Our study questions this assumption and shows that phototrophic microbial photosynthesis could represent about 10% of peatland primary production, demonstrating that phototrophic microbes cannot be ignored in peatland C dynamics. Their role remains nevertheless obscure in terms of C sequestration, as the fate of microbial-fixed C in peatlands is currently unknown. The only study to date suggests that microbial fixed C would not promote peatland C accumulation. This study shows that phototrophic microbes in a fen ecosystem release 20 to 40% of the C they fix as exudates (Wyatt & Turetsky, 2015), contributing to DOC concentrations and promoting heterotrophic respiration (Wyatt et al., 2014; Wyatt & Turetsky, 2015a). The fate of the remaining C fixed (60 to 80%) is however unknown. If less labile than exudates, this C could contribute to peat formation. We show here that our current understanding of peatland C dynamics is missing a large piece of the jigsaw puzzle, highlighting the urgent need to further explore phototrophic microbes. Including microbial C uptake in biogeochemical peatland C models would certainly improve predictions of the peatland C balance under future global changes. Particular attention should be given to seasonal variation across phototrophic microbial communities, and to the fate of the C they fix. The incorporation of these aspects in future ecological models to refine our understanding of peatland C biogeochemical cycles is a worthy challenge.

Acknowledgments

This work was supported by the MIXOPEAT project (Grant No. ANR-17-CE01-0007 to VEJJ) funded by the French National Research Agency. EL was funded by an “Atracción de Talento Investigador” (2017-130 T1/AMB-5210) grant from the Consejería de Educación, Juventud y Deporte Comunidad de Madrid (Spain). PK acknowledges funding from the Swedish Research Council Formas. Tallinn University Research Fund and the project “Life Peat Restore” supported MK. We gladly acknowledge the support from the *Genome & Transcriptome* platform of Genopole Toulouse (Genotoul) where environmental DNA sequencing was performed, and from the Bioinformatics platform of Genotoul from which we used computing clusters to perform DNA bioinformatic analyses. We thank the *Plateforme Analyses Physico-Chimiques* from the Laboratoire Ecologie Fonctionnelle et Environnement (Toulouse) for their analyses (water extractable organic matter) and for the provision of an HPLC (pigments quantification). We also thank Bruno Leroux from the *Fédération Aude Claire* and the *Syndicat Forestier de Counozouls* for giving the access to the site of Counozouls.

Author contribution

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

Supplementary materials

Supplementary methods

Extrapolation of microbial C fixation in peatlands – scaling approach

We upscaled microbial C fixation to the northern hemisphere to roughly estimate the potential contribution of annual microbial C fixation in northern peatlands. Considering that COUNOZOULS and KUSOWO were temperate peatlands, MÄNNIKJÄRVE and SIIKANNEVA were boreal peatlands and ABISKO a sub-arctic peatland, we multiplied the ground surface area of each type of peatland from LEIFELD and MENICHETTI (2018) by the corresponding mean microbial C fixation. We then multiplied this value by the duration of the growing season. We constrained microbial photosynthetic activity to 8 h per day and 205 days per year in temperate peatlands, to 10 h per day and 175 days per year in boreal peatlands, and to 12 h per day and 120 days per year in sub-arctic peatlands. These constraints on photosynthetic activities (growing season) were retrieved from PAR measurements recorded in each site for one year at the ground surface (= *Sphagnum* surface; Supplementary Fig. SIII.12). We considered that the growing season was active from the first to the last day of the year when daily maximum PAR exceeded $600 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Our weather station in Kusowo was damaged by wild animals and data were only collected for part of the year. We therefore used the growing season length of 200 days, an intermediate between COUNOZOULS and MÄNNIKJÄRVE. Annual microbial and bryosphere C fixation were expressed in mega tons of CO₂ per year (MT CO₂·year⁻¹).

Supplementary Tables

Supplementary Table SIII.1: Plant species (and litter) relative abundance expressed in % cover of the total plot area. C = Counozouls, K = Kusowo, M = Männikjärve, S = Siikaneva, A = Abisko.

	Moss									Litter
Site	<i>Polytrichum strictum</i>	<i>Sphagnum balticum</i>	<i>Sphagnum rubellum</i>	<i>Sphagnum magellanicum</i>	<i>Sphagnum fallax</i>	<i>Sphagnum fuscum</i>	<i>Sphagnum palustre</i>	<i>Sphagnum papillosum</i>	<i>Sphagnum warnstorffii</i>	Litter
C	0.36±0.24	0±0	0±0	0±0	0±0	0±0	2.14±1.26	0±0	30±4.68	15.3±3.14
K	0±0	0±0	0±0	37.6±14.2	25.65±15.82	0±0	0±0	0±0	0±0	15.54±7
M	0±0	0±0	34.76±10.19	22.26±4.88	0±0	20.71±8.71	0±0	0±0	0±0	5±0.96
S	0±0	0±0	0±0	0±0	0±0	0±0	0±0	73.15±3.15	0±0	12.92±1.13
A	0±0	61.96±3.21	0±0	0±0	0±0	0±0	0±0	0±0	0±0	19.11±1.43

	Dwarf-shrubs			Herbaceous (non-woody) vascular plants								
Site	<i>Andromeda polifolia</i>	<i>Empetrum nigrum</i>	<i>Vaccinium oxycoccus</i>	<i>Carex sp. 1</i>	<i>Carex sp.2</i>	<i>Drosera rotundifolia</i>	<i>Eriophorum vaginatum</i>	<i>Molinia</i>	<i>Oxycoccus palustris</i>	<i>Potentilla anglica</i>	<i>Rubus chamaemorus</i>	<i>Ranunculus sp.</i>
C	0±0	0±0	0±0	0±0	6.37±2.02	0.3±0.19	0±0	24.17±5.19	0±0	3.51±1.22	0±0	15.83±8.46
K	0.12±0.07	0±0	1.55±0.88	0±0	0±0	0.12±0.07	17.56±1.77	0±0	0.12±0.07	0±0	0±0	0±0
M	5.65±1.16	0±0	3.81±1.19	0±0	0±0	1.79±0.46	3.57±1.19	0±0	0±0	0±0	0±0	0±0
S	3.27±1.05	0.3±0.13	1.85±0.8	0±0	0±0	0.71±0.45	6.96±1.29	0±0	0±0	0±0	0±0	0±0
A	1.85±0.61	0.42±0.42	0±0	15.89±3.57	0±0	0±0	0±0	0±0	0±0	0±0	0.18±0.19	0±0

Supplementary Table SIII.2: Quantity and quality of *Sphagnum* water extractable organic matter. C = Counozouls, K = Kusowo, M = Männikjärve, S = Siikaneva, A = Abisko. DOC = Dissolved organic matter, TN = Total nitrogen, PRS = Soluble reactive phosphorus.

Site	<i>Sphagnum</i> Water content	pH	DOC	TN	PRS	Fluor	Chlore	Brome	Nitrate	Sulfate	Sodium
	g.g-1 DW		mg.g-1 DW	E-1 mg.g-1 DW	E-2 mg.g-1 DW	E-1 mg.g-1 DW	mg.g-1 DW	E-4 mg.g-1 DW	E-3 mg.g-1 DW	E-2 mg.g-1 DW	E-1 mg.g-1 DW
C	11.4 ± 1.3	4.9 ± 0.4	3.4 ± 1.0	0.9 ± 0.2	2.4 ± 0.4	0.5 ± 0.2	0.4 ± 0.2	0.0 ± 0.0	9.3 ± 2.0	0.6 ± 0.1	2.7 ± 0.4
K	4.1 ± 2.5	3.6 ± 0.2	11.8 ± 3.9	1.6 ± 0.5	0.7 ± 0.2	1.2 ± 0.8	1.4 ± 0.3	9.4 ± 3.3	9.3 ± 2.1	1.8 ± 2.4	5.0 ± 1.3
M	9.8 ± 3.4	4.1 ± 0.2	5.4 ± 2.3	0.7 ± 0.3	0.6 ± 0.3	0.3 ± 0.2	0.3 ± 0.1	2.0 ± 2.3	9.3 ± 2.2	0.4 ± 0.2	3.1 ± 1.0
S	10.6 ± 1.6	3.9 ± 0.1	1.5 ± 0.5	0.2 ± 0.1	0.5 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	1.2 ± 2.7	9.3 ± 2.3	0.2 ± 0.1	2.2 ± 0.7
A	14.0 ± 4.0	3.8 ± 0.1	4.0 ± 1.1	0.9 ± 0.5	2.3 ± 2.1	0.9 ± 1.1	0.1 ± 0.1	0.7 ± 0.2	9.3 ± 2.4	0.2 ± 0.1	3.3 ± 1.3

Site	Ammonium	Potassium	Magnesium	Calcium
	E-3 mg.g-1 DW	E-1 mg.g-1 DW	E-2 mg.g-1 DW	E-1 mg.g-1 DW
C	3.2 ± 3.0	2.3 ± 1.9	4.5 ± 1.5	1.6 ± 0.9
K	0.0 ± 0.0	7.4 ± 5.0	8.6 ± 4.9	0.8 ± 0.3
M	0.0 ± 0.0	1.1 ± 0.4	0.8 ± 0.5	0.3 ± 0.2
S	0.0 ± 0.0	0.3 ± 0.3	0.1 ± 0.1	0.0 ± 0.0
A	0.0 ± 0.0	0.1 ± 1.6	4.1 ± 6.2	4.1 ± 6.8

Supplementary Table SIII.3: Climatic variables retrieved from worldClim 2.0 for the different sites. C = Counozouls, K = Kusowo, M = Männikjärve, S = Siikaneva, A = Abisko.

Site	MAT	MDR	Iso	TS	MTWM	MTCM	TAR	MTWQ	MTDQ	MTWaQ	MTCQ	AP	PWM	PDM	PS	PWQ	PDQ	PWaQ	PCQ	WTD
	(°C)	(°C)	(°C)	(°C)	(°C)	(°C)	(°C)	(°C)	(°C)	(°C)	(°C)	(mm)	(mm)	(mm)	(mm)	(mm)	(mm)	(mm)	(mm)	(mm)
C	7.9	7.9	3.4	54.51	21.1	-2	23.1	9.2	2	15.2	1.5	1027	11	6.7	1.5	29.2	22	24.4	22.7	165
K	7.3	7.2	2.4	78.52	22.4	-6.8	29.2	16.9	1.8	16.9	-3.4	656	8.4	3.2	2.7	22.5	10.8	22.5	12.9	600
M	4.9	6.9	2.2	84.67	21.2	-9.7	30.9	14.4	-1.9	15.8	-5.9	623	7.8	2.9	3.1	21.5	9.6	19.9	11.5	200
S	2.9	8.5	2.5	86.02	20.9	-12.9	33.8	12.6	-3.9	14.2	-8	611	8.1	3	3.1	21.9	9.6	21	11.7	80
A	-0.1	7	2.4	75.15	15.5	-13.3	28.8	8.9	-1.5	10	-9.3	418	6.2	1.8	3.8	16.3	6.2	15.4	8.7	100

MAT = Mean Annual Temperature

MDR = Mean Diurnal Range

Iso = Isothermality

TS = Temperature Seasonality

MTWM = Maximum Temperature of Warmest Month

MTCM = Minimum Temperature of Coldest Month

TAR = Temperature Annual Range

MTWQ = Mean Temperature of Wettest Quarter

MTDQ = Mean Temperature of Driest Quarter

MTWaQ = Mean Temperature of Warmest Quarter

MTCQ = Mean Temperature of Coldest Month

AP = Annual Precipitation

PWM = Precipitation of Wettest Month

PDM = Precipitation of Driest Month

PS = Precipitation Seasonality

PWQ = Precipitation of Wettest Quarter

PDQ = Precipitation of Driest Quarter

PWaQ = Precipitation of Warmer Quarter

PCQ = Precipitation of Coldest Quarter

WTD = Water Table Depth

Supplementary Table SIII.4: Primers and PCR programs used for the two meta-barcoding markers used in the study.

Analyses	16S	18S
Primers	PCR1_515F PCR1_928R	TAReuk454FWD1 TAReukREV3
Sequence of the primers (5' – 3')	GTGYCAGCMGCCGCGGTACCCCGYCAA TTCMTTTRAGT	CCAGCASCYGC GGTAATTCCACTTTCGTT CTTGATYRA
Program of the PCRs	Activation : 10 min – 95°C 30 cycles: 60 s – 94°C 40 s – 65°C 30S – 72°C Final elongation : 10 min – 72°C	Activation : 10 min – 95°C 45 cycles: 30 s – 94°C 45 s – 47°C 60S – 72°C Final elongation : 10 min – 72°C
Remarks	NA	45 cycles needed to obtain even amplification yields. We followed the method of Seppey et al. (2020)

Supplementary Table SIII.5: Hypotheses underlying the structural equation model.

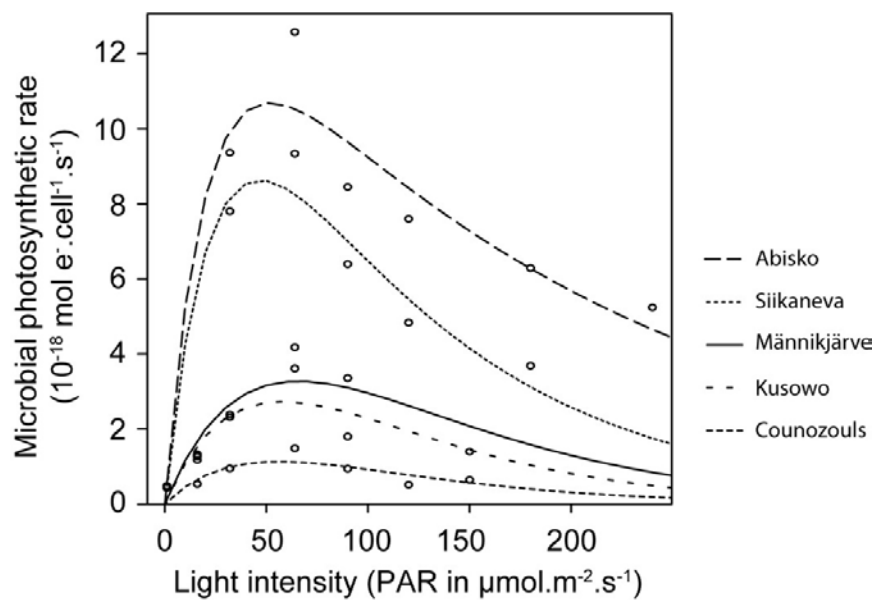
Path	Causal hypothesis
Bac1, Prot1	Changes in the community composition of phototrophic bacteria (Bac1) and protists (Prot1) affect the averaged body size of microbial phototrophs in the community.
Bac2, Prot2	The abundance of phototrophic microbes depends on the composition of their bacterial (Bac2) and protistic (Prot2) community.
Bac3, Prot3	Photosynthetic capacities of phototrophic microbes depends on the composition of their bacterial (Bac3) and protistic (Prot3) communities, through their direct effect on electron transport rates.
Bs	Changes in the body size of phototrophic microbes influence the averaged chlorophyll <i>a</i> content per individual (Kalchev et al., 1996).
Chla	The chlorophyll <i>a</i> content per individual directly affects the electron transport rate of phototrophic microbes.
Et	An increase of phototrophic microbial electron transport rate promotes the total amount of C fixed by phototrophic microbial communities.
Ab1	An increase of phototrophic microbial abundance increases the total amount of C fixed by their community.
Ab2	An increase of phototrophic microbial abundance negatively affects the averaged body size of phototrophs (Huet-Ortega et al., 2012; Padfield et al., 2018).

Supplementary Table SIII.6: Pairwise comparisons of beta-diversity (based on Bray-Curtis dissimilarity) between sites. The lower half of the matrix shows the comparisons based on phototrophic bacteria, while the upper half shows the comparisons based on phototrophic protists. C: COUNZOULS; K: KUSOWO; M: MÄNNIKJÄRVE; S: SIKANEVA; A: ABISKO.

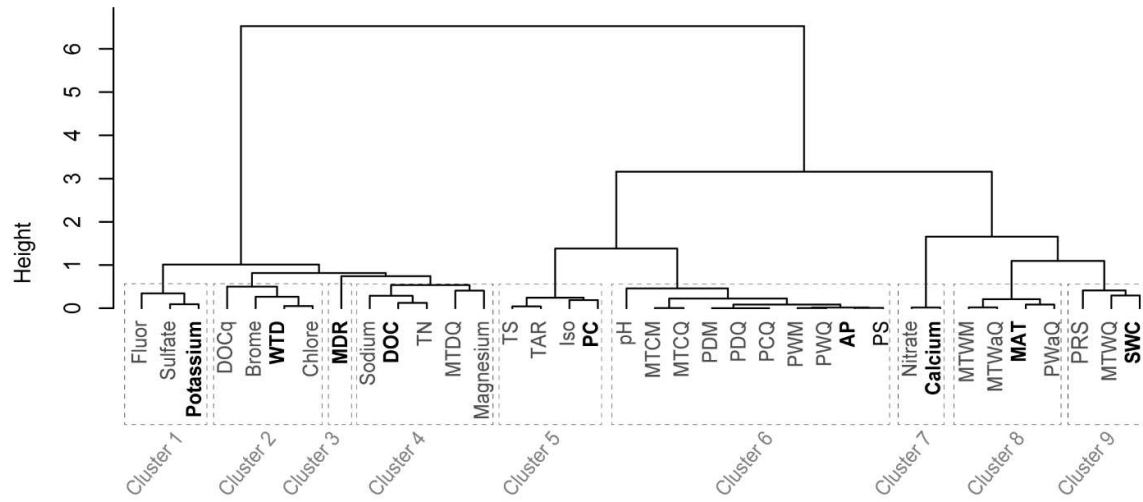
	C	K	M	S	A
C		0.91	0.92	0.84	0.93
K	0.84		0.67	0.77	0.97
M	0.82	0.52		0.7	0.92
S	0.83	0.51	0.4		0.92
A	0.67	0.79	0.8	0.81	

Supplementary Table SIII.7: Parameters used for estimating phototrophic microbial C fixation in peatlands from the northern hemisphere.

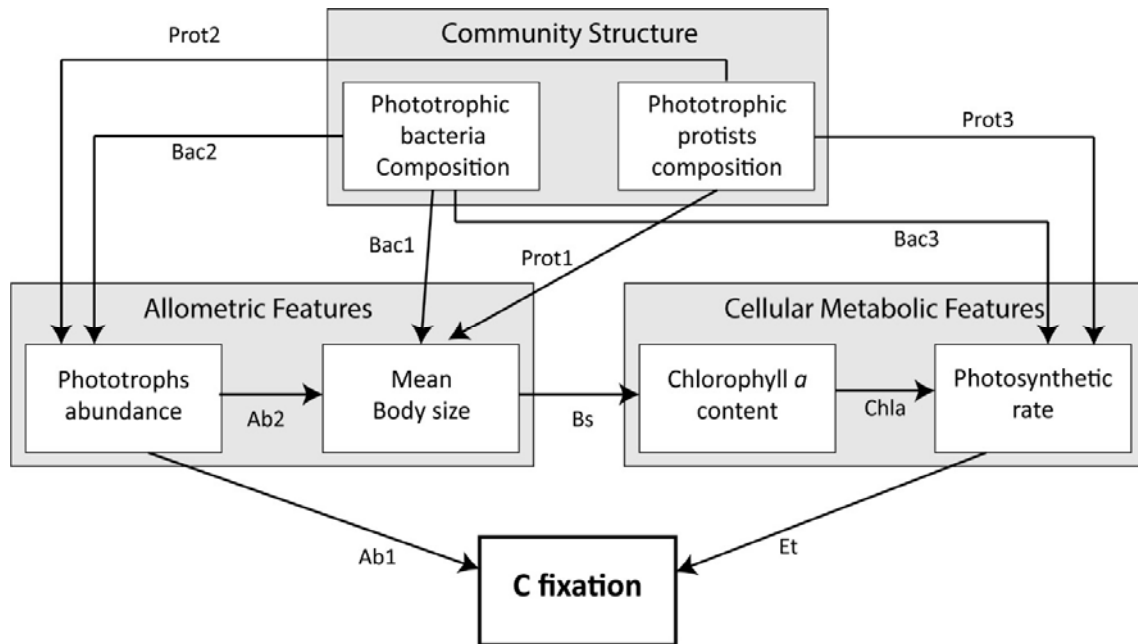
Climate	Total peatland area (10¹¹ m²) (Leifeld & Menichetti, 2018b)	Associated study site	Average microbial C fixation (mg CO₂.h⁻¹.m⁻²) (min – max)	Growing season length (See Methods and Supplementary Fig. S12)	Annual microbial C fixation (MT CO₂.year⁻¹) (min – max)
Subarctic	2.50	Abisko	11.8 (3.3 - 18.9)	120 days; 12h per day	4.2 (1.2 – 6.8)
Boreal	36.09	Siikaneva, Männikjärve	10.8 (2.0 - 53.9)	175 days; 10h per day	68.3 (12.8 - 337.8)
Temperate	1.85	Kusowo, Counozouls	5.2 (1.6 - 22.7)	205 days; 8h per day	1.6 (0.5 - 6.9)
				TOTAL	74.1 (14.5 - 351.6)



Supplementary Figure SIII.1: Light curves of microbial photosynthetic rates (electron transport rate per cell) in the five sites of the study. Microbial communities were extracted from additional *Sphagnum* material, sampled nearby the studied areas.

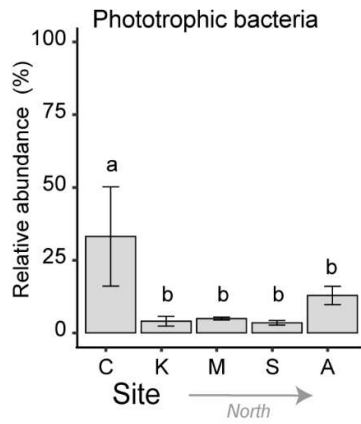


Supplementary Figure SIII.2: Hierarchical clustering of environmental variables. Nine clusters were selected and in each cluster the most representative variable (in bold) was kept for the Generalised Dissimilarity Modelling (GDM). Abbreviations of variables are given in Supplementary Tables 1, 2 and 3.

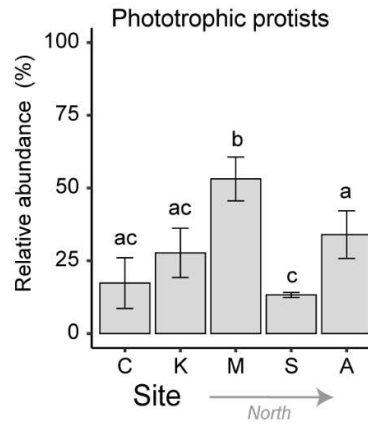


Supplementary Figure SIII.3: A priori conceptual structural equation model (SEM) depicting pathways by which the composition and the abundance of phototrophic microbial communities may affect microbial C fixation. Letters correspond to hypothetical pathways (Table S5).

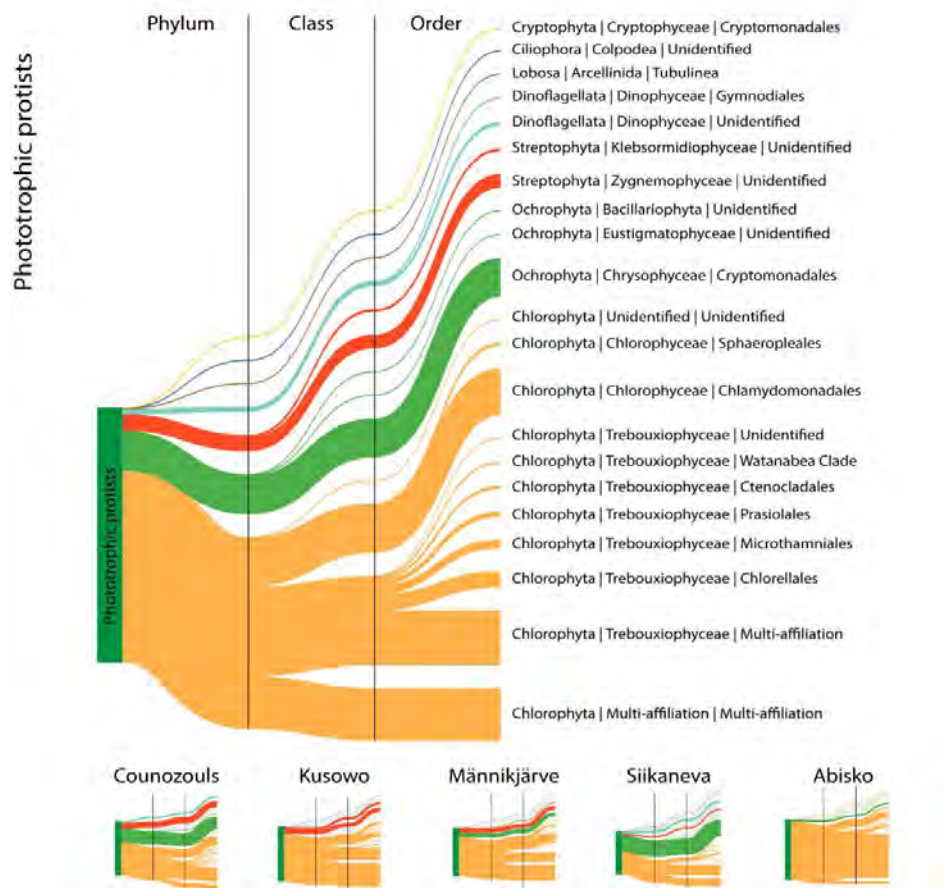
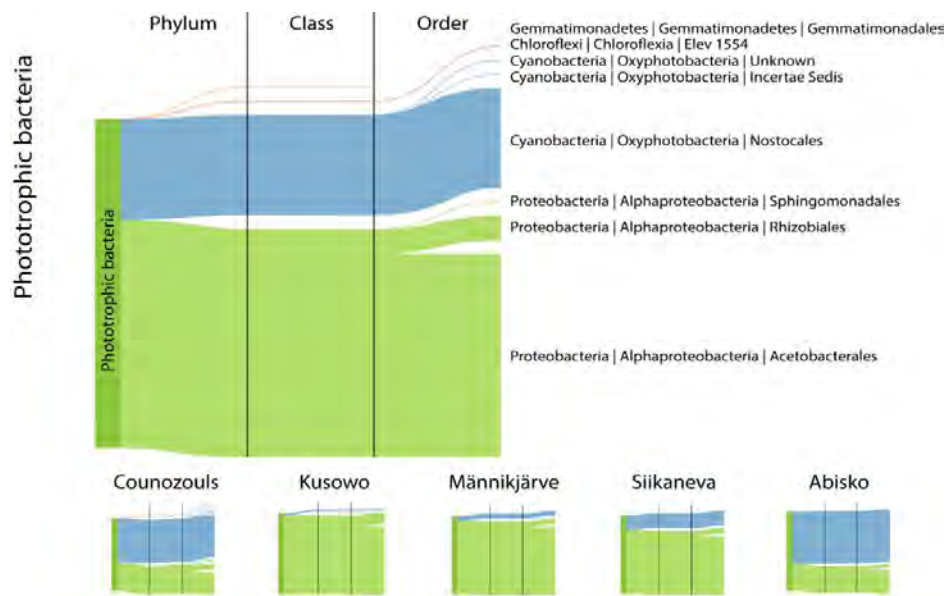
Prokaryotes



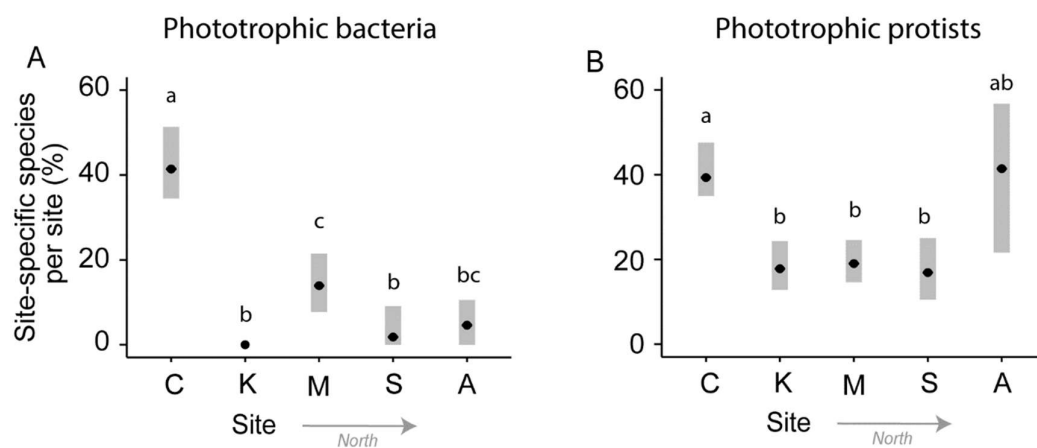
Micro-eukaryotes



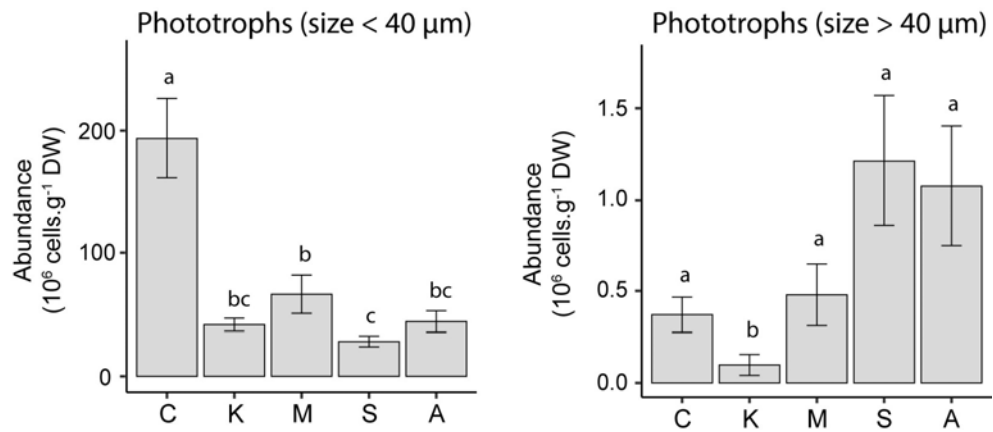
Supplementary Figure SIII.4: Relative abundance of phototrophic bacteria and phototrophic protists, respectively. Error bars present standard error calculated from the five replicates per site ($n = 5$ replicates). Significant differences ($P < 0.05$) are indicated by different letters above bars. C: Counozouls; K: Kusowo; M: Männikjärve; S: Siikaneva; A: Abisko.



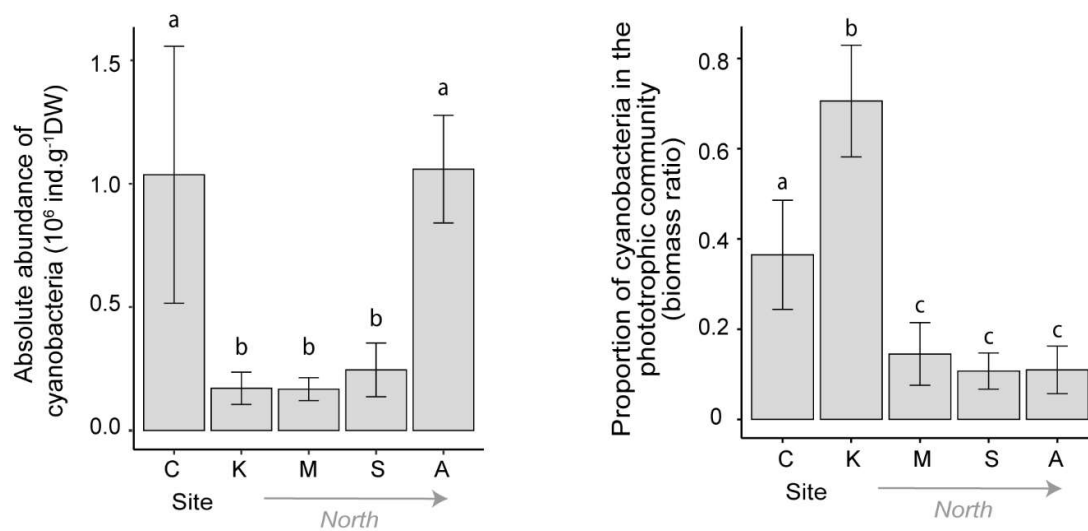
Supplementary Figure SIII.5: Sankley graphs showing the relative abundance of the different taxa of phototrophic bacteria and protists. The width of the branches is proportional to the relative abundance of the taxa. The two main graphs present the average taxonomic composition of phototrophic microbial communities across the five sites.



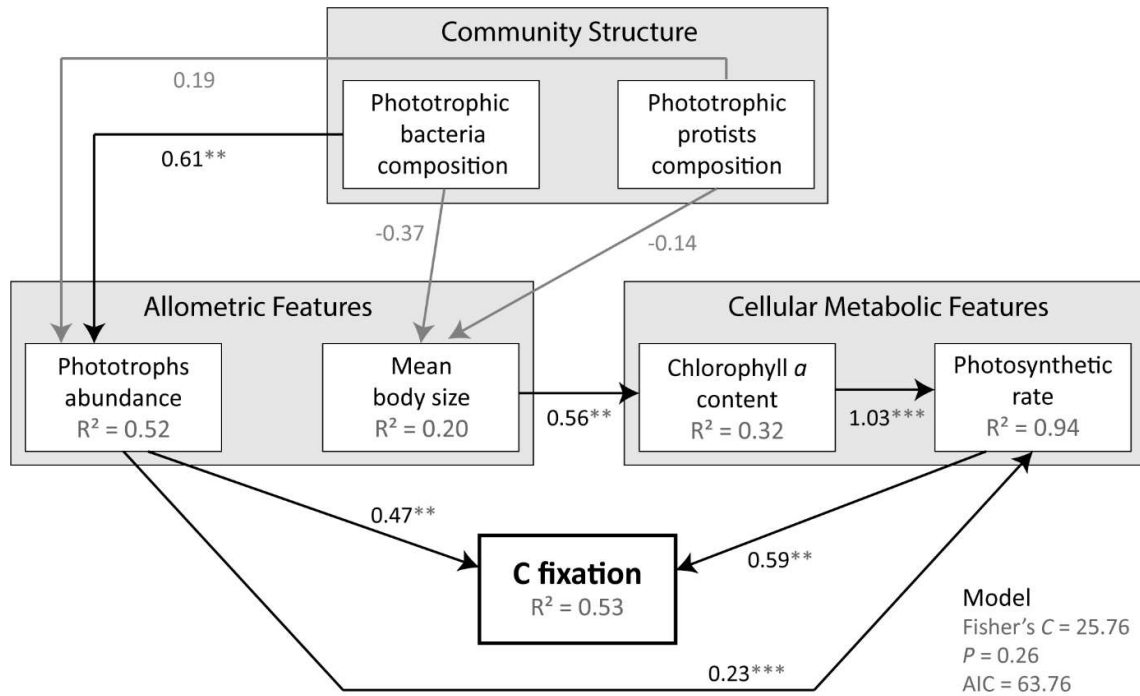
Supplementary Figure SIII.6: Proportion of site-specific OTUs per site for phototrophic bacteria (A) and protists (B). The proportion is expressed as a percentage of the total number of bacterial or protistic phototrophic OTUs per site. Grey bars range between the minimum and maximum values ($n = 5$ replicates), while points represent the mean value in each site. C: Counozouls; K: Kusowo; M: Männikjärve; S: Siikaneva; A: Abisko.



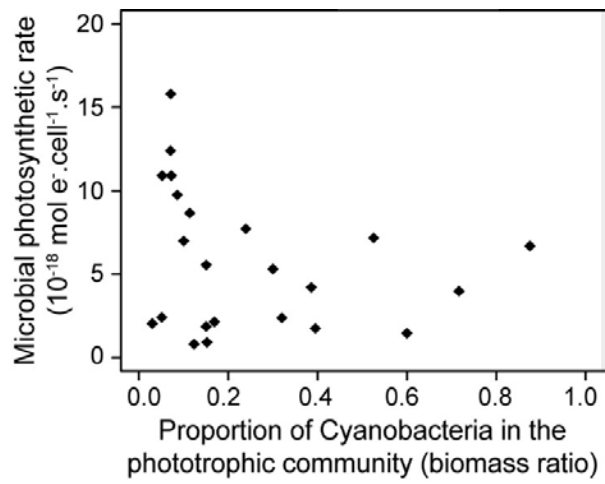
Supplementary Figure SIII.7: Abundance of small phototrophs (body size <math>< 40 \mu\text{m}</math>) and large phototrophs (body size $> 40 \mu\text{m}$) in the five peatlands. Error bars present standard error ($n = 5$ replicates). Significant differences ($P < 0.05$) are indicated by different letters above bars. C: Counozouls; K: Kusowo; M: Männikjärve; S: Siikaneva; A: Abisko.



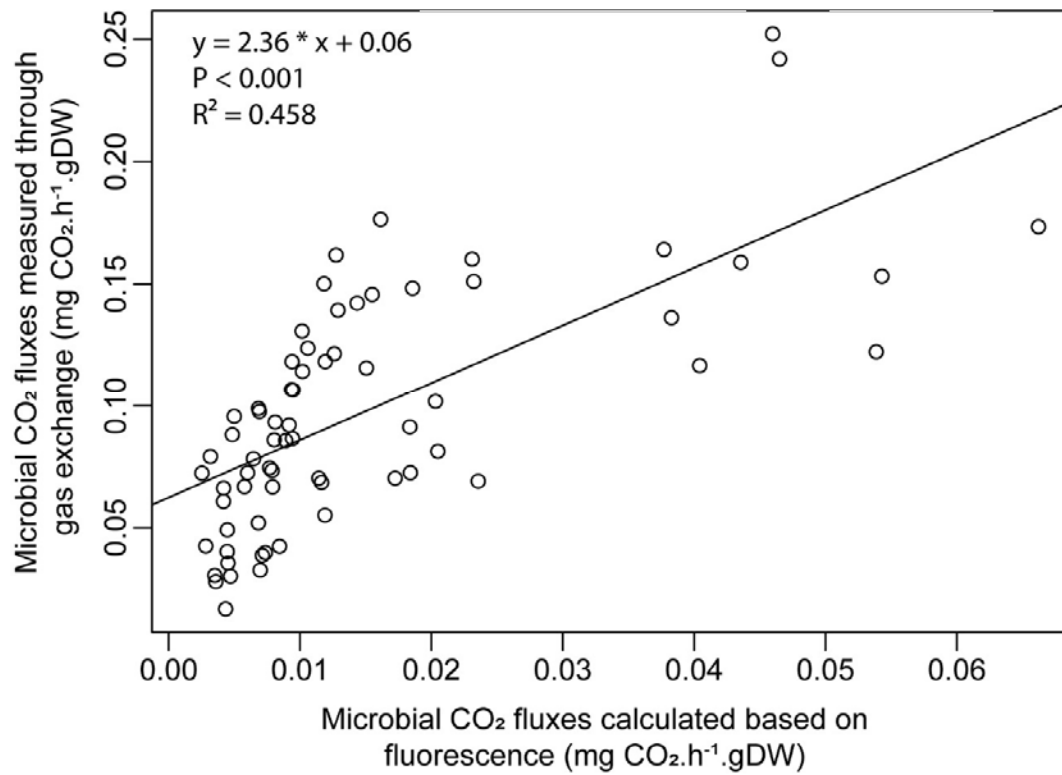
Supplementary Figure SIII.8: Absolute abundance of cyanobacteria and their proportional biomass in the phototrophic community. Error bars present standard error ($n = 5$ replicates). Significant differences ($P < 0.05$) are indicated by different letters above bars. C: Counozouls; K: Kusowo; M: Männikjärve; S: Siikaneva; A: Abisko.



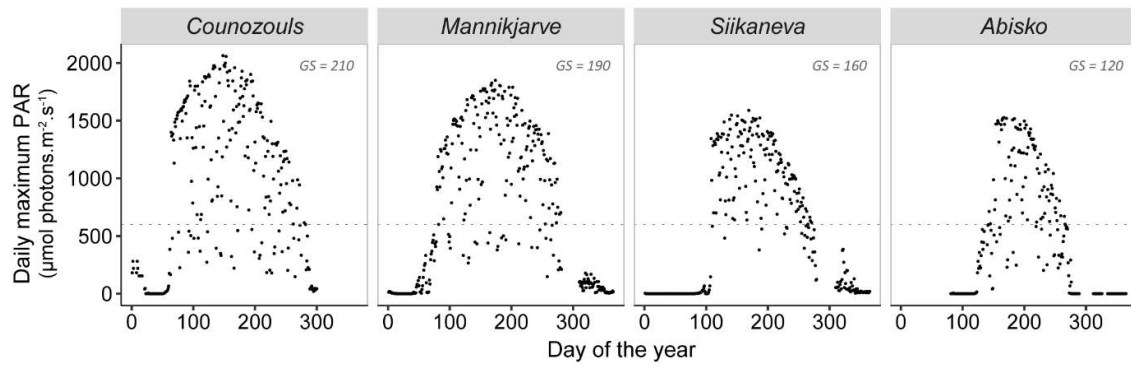
Supplementary Figure SIII.9: Structural equation model (SEM) testing the pathways by which the structure and the abundance of phototrophic microbial communities drive microbial C fixation. Numbers in the boxes indicate the percentage of variance explained by the model (adjusted R-squared), while numbers along the arrows indicate the weight of the path relationship. Black arrows show significant path relationships (* $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$), while grey arrows show non-significant path relationships.



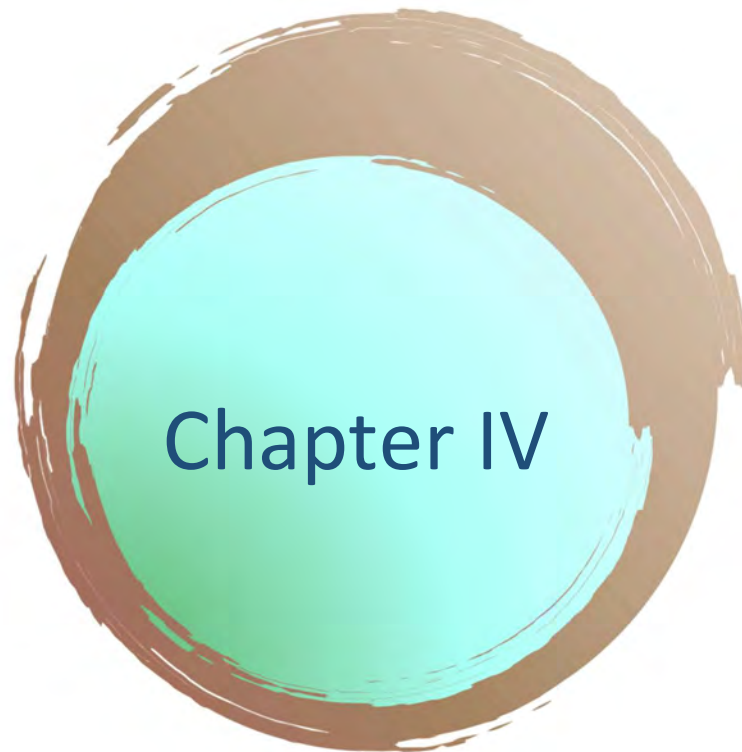
Supplementary Figure SIII.10: Photosynthetic rates of the phototrophic microbial communities in function of the proportion of cyanobacteria in the phototrophic communities.



Supplementary Figure SIII.11: Correlation between microbial CO₂ fluxes measured through gas exchange and calculated based on fluorescence. Data come from another current unpublished study. Microbial CO₂ fluxes were measured from microbial communities sampled in the top three centimeters of *Sphagnum* mats, in the same study sites than the current work.

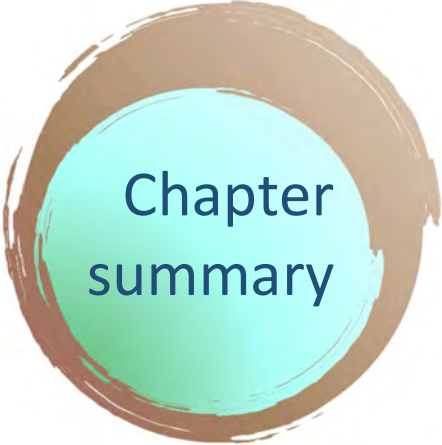


Supplementary Figure SIII.12: Length of the growing season (GS) in Counozouls, Männikjärve, Siikaneva and Abisko, constrained by measurements of daily maximum PAR at the ground surface. Dotted line indicate a PAR value of 600 $\mu\text{mol photons.m}^{-2}.\text{s}^{-1}$. Numbers in the right hand corner indicate the length of the growing season, determined as the number of days between the first and the last day of the year when daily maximum PAR exceeds 600 $\mu\text{mol photons.m}^{-2}.\text{s}^{-1}$.



Chapter IV

Effects of *Sphagnum* leachate on
competitive *Sphagnum* microbiome
depend on species and time



Chapter summary

In the previous chapters, I showed that environmental factors including plant composition and water availability drove the structure of phototrophic microbial communities. Due to confounding effect, I could not disentangle the role of *Sphagnum* species. Yet, *Sphagnum* species can modulate their microbiome. In particular, I showed in collaboration with Anna Sytiuk that *Sphagnum* species can secrete specific chemical compounds (i.e. metabolites) that can regulate the structure and function of microbial assemblages and food webs through anti-microbial effects. Previous studies as well as the results of the preceding chapter show the importance of mixotrophic testate amoebae in driving microbial photosynthesis due to their large body size. However, these organisms can also strongly influence peatland microbial food web structure as top-predators. Because these mixotrophs are key on many aspects of microbial communities functioning in peatlands, I wondered to what extent *Sphagnum* chemicals would affect these microbial species and what would be the consequences for the food web structure.

Using a microcosm experiment and focusing on two competitive *Sphagnum* mosses, I showed that interactions between *Sphagnum* leachates and microbiome were species-specific. More particularly, I found that prolonged exposition of *Sphagnum* microbiome to competitive *Sphagnum* leachate affected the place of mixotrophic testate amoebae in the food web. Some indications suggested that their feeding habits could be affected, shifting toward heterotrophy or autotrophy according to the leachate identity. Overall, the food web structure was destabilised. These results highlight the role of *Sphagnum* mosses in directly shaping their microbial food web, and suggest that *Sphagnum* identity could determine specific top down controls on phototrophic microbes.

Effects of *Sphagnum* leachate on competitive *Sphagnum* microbiome depend on species and time.

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Abstract

Plant specialised metabolites play an important role in soil carbon (C) and nutrient fluxes. Through anti-microbial effects, they can modulate microbial assemblages and associated microbial-driven processes, such as nutrient cycling, so to positively or negatively cascade on plant fitness. As such, plant specialised metabolites can be used as a tool to supplant competitors. These compounds are little studied in bryophytes. This is especially notable in peatlands where *Sphagnum* mosses can dominate the vegetation and show strong interspecific competition. *Sphagnum* mosses form carpets where diverse microbial communities live and play a crucial role in *Sphagnum* fitness by regulating C and nutrient cycling. Here, by means of a microcosm experiment, we assessed to what extent moss metabolites of two *Sphagnum* species (*S. fallax* and *S. divinum*) modulate the competitive *Sphagnum* microbiome, with particular focus on microbial respiration. Using a reciprocal leachate experiment, we found that interactions between *Sphagnum* leachates and microbiome are species-specific. We show that both *Sphagnum* leachates differed in compound richness and compound relative abundance, especially sphagnum acid derivatives, and that they include microbial-related metabolites. The addition of *S. divinum* leachate on the *S. fallax* microbiome immediately reduced microbial respiration (-95%). Prolonged exposition of *S. fallax* microbiome to *S. divinum* leachate destabilised the food web structure due to a modulation of microbial abundance. In particular, leachate addition decreased the biomass of testate amoeba and rotifer predators but increased that of other ciliates with similar feeding habits. These changes did not influence microbial CO₂ respiration, suggesting that the structural plasticity of the food web leads to its functional resistance through the replacement of species that are functionally redundant. In contrast, *S. fallax* leachate neither affected *S. divinum* microbial respiration, nor microbial biomass. We, however, found that *S. fallax* leachate addition stabilised the food web structure associated to *S. divinum* by changing trophic interactions among species. The differences in allelopathic effects between both *Sphagnum* leachates might impact their competitiveness and affect species distribution at local scale. Our study further paves the way to better understand the role of moss and microbial specialised metabolites in peatland C dynamics.

Introduction

Plant species composition and diversity play a fundamental role in regulating ecological processes such as nutrient and carbon (C) fluxes through their linkages with belowground components. Notably, plants are known to put a selective pressure on soil microbes and their activities (Cúcio et al., 2016; Robroek et al., 2015; 2017; Sánchez-Cañizares et al., 2017), and to drive microbial assemblages in soil (Berg & Smalla, 2009; Schlatter et al., 2015; Tkacz et al., 2015). This selective effect is performed by plant-derived chemicals, either through the amount and form of carbon and other nutrients that plants provide to the soil (Cline & Zak, 2015; Huang et al., 2014; Sasse et al., 2018), or through specialised metabolites – i.e. allelochemicals – that directly interact with microbes (Bertin et al., 2003; Musilova et al., 2016; Niro et al., 2016). These plant-derived chemicals allow the establishment of mutual, competitive and defensive relationships between specific plants and microorganisms (Latif et al., 2017), and may have indirect effects on competing plants. Such effects could arise from either direct phytotoxic or stimulatory effects on the microbial community on which competing plants rely for nutrients uptake. This possibility is exemplified by plants that inhibit mutualistic bacteria or fungi that competitive plants require for optimal growth, but that the donor plant does not need (Cipollini et al., 2012). Allelopathy can also modify plant-microbe interactions by favouring growth of pathogenic or parasitic microbes that harm competitive plants (Cipollini et al., 2012; Geisen et al., 2018). Understanding the effects of plant-derived metabolites on the specific plant microbiome as a competitive mechanism is therefore of key importance to understand the dynamics of ecological processes within ecosystems.

The majority of studies on plant-microbial interactions focus on vascular plant-dominated ecosystems, largely ignoring the importance of cryptogams. Yet, cryptogams occur in many terrestrial habitats and contribute significantly to global ecosystem functions such as nitrogen and C cycle (Elbert et al., 2012b). The processes linked to cryptogam metabolites (i.e. regulation of microbial activity, indirect plant competition) in cryptogam-dominated ecosystems remain poorly explored, while they could be rather important for ecosystem functions (Asplund et al., 2013; Asplund & Wardle, 2013). This is especially the case in ombrotrophic peatlands, where cryptogams such as *Sphagnum* mosses can dominate the ecosystem (Yu et al., 2011). *Sphagnum* mosses form expansive carpets that provide a habitat for a large diversity of microbial communities (Gilbert et al., 1998; Jassey et al., 2013, 2015; Bragina et al., 2014; Mieczan et al., 2015a, 2015b). The *Sphagnum* microbiome is structured in a

microbial food web constituted by bacteria, fungi (decomposers), protists (producers, predators, top-predators) and small-sized metazoan (predators, top-predators). The functioning of this *Sphagnum*-associated food web critically determines the cycling of C and nutrients (Jassey et al., 2015) through the microbial loop (Gilbert et al., 1998a) –a trophic pathway through which C and nutrients from organic matter are returned to higher trophic levels through their incorporation into bacterial and fungal biomasses. Empirical observations suggest that the structure and activity of the *Sphagnum* microbiome determine *Sphagnum* fitness (Kostka et al., 2016). For instance, microbial functional guilds such as methanotrophic bacteria, photosynthetic protists and nitrogen-fixing cyanobacteria clearly benefit the host-species by providing a source of C and/or nitrogen that enhances moss production (Jassey et al., 2015; Kostka et al., 2016; Carrell et al., 2019). Hence, it can be argued that any shift in the composition of the *Sphagnum* microbiome can modulate *Sphagnum* productivity and, ultimately, ecosystem C cycling.

Different species of *Sphagnum* coexist in peatlands. Each species has a specific production and performance (Gunnarsson, 2005; Robroek et al., 2007), and each species is associated to a specific microbiome (Opelt et al., 2007; Bragina et al., 2012). It has been observed that *Sphagnum* species often grow in spatially-structured population in response to interspecific competition (Ingerpuu & Vellak, 2013). Apart from environmental effects such as water-table level or niche separation (Bragazza, 1997; Robroek et al., 2007), the mechanisms that drive competition are not well determined. *Sphagnum* exudates can affect the growth of other *Sphagnum* species (Ingerpuu & Vellak, 2013), suggesting that *Sphagnum* metabolites may play a role in interspecific competition. This hypothesis is supported by the fact that *Sphagnum* mosses produce a variety of specialised metabolites (Rasmussen et al., 1995; Opelt et al., 2007; Chiapusio et al., 2018), such as phenolic acid derivatives (Rudolph and Samland, 1985; Rasmussen et al., 1995), with potential allelopathic effects (Verhoeven and Liefveld, 1997). Phenolic acids, particularly sphagnum acid, are highly water-soluble compounds (Rasmussen et al., 1995) and have been long suspected of antimicrobial effects in peatlands (Binet et al., 2017; Verhoeven & Liefveld, 1997). Recent studies further suggest that polyphenol compounds could be an important factor modulating the structure of microbial assemblages in *Sphagnum* peatlands (V. E. Jassey et al., 2013; Jassey et al., 2011a, 2011b). Altogether, these studies indicate an important possible role of *Sphagnum* exudates in affecting peatland microbial activity and suggest their potential implication in interspecific *Sphagnum* competition by alteration of the microbiome, ultimately affecting *Sphagnum*

fitness, peatland primary production and the peatland C cycle. Understanding the role of *Sphagnum* exudates in driving microbial communities is thus crucial to better understand peatland C dynamics.

Here we focus on two widespread *Sphagnum* species, *i.e.* *S. fallax* and *S. divinum*, that often co-occur together, to assess whether *Sphagnum* interspecific competition and ecosystem functioning can be indirectly mediated by a shift in their respective microbiome. We tested how each of these two *Sphagnum* species affected the structure and the functioning of the microbial community associated to the competitive species. Using a reciprocal leachate-transfer experiment, we assessed whether a brief exposition to allochthonous *Sphagnum* leachates (*i.e.* leachates from the competing species) altered the CO₂ respiration of the microbiome. Second, we tested if a prolonged exposition to allochthonous *Sphagnum* leachates altered the microbial food-web structure and functioning, emphasising on microbial activity and C related processes. We hypothesized that: 1) a short-term exposure to allochthonous leachates will inhibit microbial respiration due to species-specific metabolites inhibitory effects, and that this effect is universal across the two species; 2) a prolonged exposure to allochthonous leachate will alter the structure of microbiome causing a decrease of microbial metabolism.

Methods

Field sampling and leachate collection

In April 2015, we collected 15 intact shallow cores (diam. 11 cm; depth 15 cm) of *Sphagnum fallax* and *S. divinum* (30 cores in total) in the Store Mosse National Park, Sweden (57°17'54 N, 14°00'39 E, permit 521-895-2011). Cores were extracted in a habitat that was low in vascular plant cover (< 5%), but occasional specimens were carefully removed after which the cores were placed in PVC pipes (hereafter referred as microcosms) that were open from the top and closed at the bottom. Microcosms were then transported to the laboratory facilities at the Ecole Polytechnique Fédérale de Lausanne, Switzerland, where they were kept in a growth chamber (20°C, 70% RH, 14h/10h day/night photoperiod, PAR intensity 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$) for two weeks to acclimate. During the acclimation period, all microcosms were watered daily with 12 mL of artificial rainwater (Garrels & Christ, 1965), which sufficed to keep water levels at field conditions (-1 cm for *S. fallax* and -3 cm for *S. divinum*). During the acclimation period, we collected the leachates from all microcosms. To do so, we first drained the

microcosms and added fresh artificial rainwater. This was repeated after two days, with the difference that this time all leachate was collected. Leachates from microcosms with the same species were combined in a bulk leachate, resulting in one leachate for *S. fallax* (L_{SF}) and one for *S. divinum* (L_{SD}). After collection, both leachates were filtered at 0.2 μm to remove microorganisms, and frozen (-20°C) until utilisation.

Leachate chemical characterisation

After leachate collection, a set of chemical analyses were performed for both L_{SF} and L_{SD} leachates. The concentrations of dissolved organic carbon (DOC) and nitrogen (DON) were quantified by combustion using a Shimadzu analyser (TOC-V CPH). The quality of dissolved organic carbon was determined by spectroscopy analysis by measuring the absorbance within the range of wavelengths 250-665 nm (Jaffrain et al., 2007). Spectral slopes ($S_{250-665}$, nm^{-1}) were calculated using linear least squares regressions with Ln-transformed absorptions. High $S_{250-665}$ values indicate low molecular weight material and/or decreasing aromaticity of the leachate (Hansen et al., 2016). Leachate phenolic content was determined using the Folin & Ciocalteu's reagent with gallic acid as standard (Jassey et al., 2011a). Phenolic content was expressed as mg of equivalent gallic acid per volume of leachate (mg eq. gallic acid.L $^{-1}$).

A detailed chemical analysis of the metabolites present in *Sphagnum* leachates, *Sphagnum* mosses and bog water was performed using Ultra-High Pressure Liquid Chromatography coupled with High Resolution Mass Spectrometry (UHPLC-HRMS; see details below). To disentangle the provenance of the metabolites (*Sphagnum* versus peat), several comparisons were made. First, we compared leachate metabolic composition to water and methanolic extracts of lyophilized *S. fallax* and *S. divinum* (Jassey et al., 2011). These extracts were prepared by grinding 0.05 g dry weight of lyophilized *Sphagnum* (0-3 cm ; capitulum) in 5 mL of water (mili-Q) or methanol (80/20 methanol/distilled water v/v) using metal ball grinder. We also compared leachate metabolic profiles to the one of the bog water as comparison. *S. fallax*, *S. divinum* and bog water were sampled in the Store Mosse site during the core sampling campaign. All samples were filtered through SPE columns, and directly injected in the UHPLC-HRMS. In total, we analysed seven metabolic profiles through UHPLC-HRMS: the bog water, two *Sphagnum* leachates, two *Sphagnum*-water extracts, and two *Sphagnum*-methanolic extracts.

UHPLC-HRMS Analysis

We qualitatively assessed the metabolic composition of both leachates using High-resolution Mass Spectrometry (MS) and molecular networking. Briefly, chromatographic separation was performed on a Waters Acquity UPLC system interfaced to a Q-Exactive Focus mass spectrometer (Thermo Scientific, Bremen, Germany), using a heated electrospray ionization (HESI-II) source. Thermo Scientific Xcalibur 3.1 software was used for instrument control. The LC conditions were as follows: column, Waters BEH C18 50 × 2.1 mm, 1.7 μm; mobile phase, (A) water with 0.1% formic acid; (B) acetonitrile with 0.1% formic acid; flow rate, 600 μL.min⁻¹; injection volume, 1 μL; gradient, linear gradient of 2–100% B over 6 min and isocratic at 100% B for 0.6 min. An Acquity IClass UPLC photodiode array detector was used to acquire PDA spectra, which were collected from 210 to 450 nm. In positive ion mode, diisooctyl phthalate C₂₄H₃₈O₄ [M+H]⁺ ion (*m/z* 391.28429) was used as internal lock mass. The optimized HESI-II parameters were as follows: source voltage, 4.0 kV (pos); sheath gas flow rate (N₂), 55 units; auxiliary gas flow rate, 15 units; spare gas flow rate, 3.0; capillary temperature, 275.00°C (pos), S-Lens RF Level, 45. The mass analyzer was calibrated using a mixture of caffeine, methionine–arginine–phenylalanine–alanine–acetate (MRFA), sodium dodecyl sulfate, sodium taurocholate, and Ultramark 1621 in an acetonitrile/methanol/water solution containing 1% formic acid by direct injection. The data-dependent MS/MS events were performed on the three most intense ions detected in full scan MS (Top3 experiment). The MS/MS isolation window width was 1 Da, and the stepped normalized collision energy (NCE) was set to 15, 30 and 45 units. In data-dependent MS/MS experiments, full scans were acquired at a resolution of 35 000 FWHM (at *m/z* 200) and MS/MS scans at 17 500 FWHM both with an automatically determined maximum injection time. After being acquired in a MS/MS scan, parent ions were placed in a dynamic exclusion list for 2.0 s.

LC-MS Data Processing

ThermoRAW MS data were converted to the open MS format (.mzXML) using the MSConvert software, part of the ProteoWizard package (Chambers et al., 2012). The converted files were then treated using the MzMine 2.36 software suite. The parameters were adjusted as follow: the centroid mass detector was used for mass detection with a noise level set to 1.0E6 for MS level set to 1, and to 0 for MS level set to 2, respectively. The ADAP chromatogram builder was used and set to a minimum group size of scans of 5, minimum group intensity threshold of 1.0E5, minimum highest intensity of 1.0E5 and *m/z*

tolerance of 8.0 ppm. For chromatogram deconvolution, the algorithm used was the wavelets (ADAP). The intensity window S/N was used as S/N estimator with a signal to noise ratio set at 25, a minimum feature height at 10000, a coefficient area threshold at 100, a peak duration ranges from 0.02 to 0.9 min and the RT wavelet range from 0.02 to 0.05 min. Isotopes were detected using the isotopes peaks grouper with a m/z tolerance of 5.0 ppm, a RT tolerance of 0.02 min (absolute), the maximum charge set at 2 and the representative isotope used was the most intense. An adduct (Na^+ , K^+ , NH_4^+ , ACN^+ , CH_3OH^+ , Isopropanol $^+$) search was performed with the RT tolerance set at 0.1 min and the maximum relative peak height at 500%. A complex search was also performed using $[\text{M}+\text{H}]^+$ for ESI positive mode, with the RT tolerance set at 0.1 min and the maximum relative peak height at 500%. A custom database search was finally performed using the Dictionary of Natural Products 2018 (v. 26.2) database (<http://dnp.chemnetbase.com>), restricted to moss metabolites. Peak alignment was performed using the join aligner method (m/z tolerance at 8 ppm), absolute RT tolerance 0.065 min, weight for m/z at 10 and weight for RT at 10. The peak list was gap-filled with the same RT and m/z range gap filler (m/z tolerance at 8 ppm). Eventually the resulting aligned peaklist was filtered using the peak-list rows filter option in order to keep only features associated with MS2 scans. Full parameters are available as .xml file as supporting information (Sphagnol_profiles_MzMineparams.mzmine).

LC-MAS data analysis: molecular networks generation

In order to further identify compounds in MS dataset, we used the molecular networking (MN) approach that group metabolites by structural similarity (M. Wang et al., 2016). The MN approach is based on the organization and visualization of tandem MS data through a spectral similarity map, revealing the presence of similar MS fragmentations patterns. As structurally related compounds tend to share similar fragmentation spectra, nodes gathered together create clusters of structural analogues. The generated molecular networks were annotated using experimental spectral libraries (GNPS libraries available at <http://gnps.ucsd.edu>) and an in-silico fragmented database of natural products using a previously detailed dereplication strategy (Allard et al., 2016). In the network created, edges were filtered to have a cosine score above 0.65 and more than 6 matched peaks. Further edges between two nodes were kept in the network if and only if each of the nodes appeared in each other's respective top 10 most similar nodes. The spectra in the network were then searched against GNPS'

spectral libraries. The library spectra were filtered in the same manner as the input data. All matches kept between network spectra and library spectra were required to have a score above 0.7 and at least 6 matched peaks. The output was visualized using Cytoscape 3.6 software (www.cytoscape.org). The nodes of the generated networks were colored according to the number of MS/MS triggered in a given sample, thus offering a semi-quantitative information. The size of the nodes was mapped according to the total sum of precursor ions intensities. Molecular networks are available on the GNPS servers at the following addresses:

<https://gnps.ucsd.edu/ProteoSAFe/status.jsp?task=00de48872c8b4d76b108a40fd7b7ea0a>

and <https://gnps.ucsd.edu/ProteoSAFe/status.jsp?task=60f9f10962ae4aa0952a54c9eb9fc21d>.

Experimental setup and measurements

To assess the allelopathic effects of *Sphagnum* leachate addition on potential neighbouring competing species, we set up a targeted reciprocal leachate experiment. We first divided the species-specific mesocosms into two experimental groups. One group, consisting of ten microcosms (five per species), was used to test the instantaneous effect of allochthonous leachate addition on the *Sphagnum* microbiome. The second group, consisting of twenty microcosms (ten per species), was used to test the effect of prolonged exposure to allochthonous leachates.

Instantaneous leachate effects

We sampled 3 g of *Sphagnum* shoots (0-4 cm depth) from all microcosms and placed them in falcon tubes (n = 5). From these shoots, we extracted the microbiome by shaking at 40 rpm for 1.5 h in 30 mL of Mili-Q® water. The extracted microbiome was recovered by filtration at 1 mm. For each microcosm, 0.8 mL of microbial extract was transferred to a Microresp™ (Campbell et al., 2003) 96-deep-well microplate, allocating 8 wells to each microcosm. Subsequently, we added 0.2 mL artificial rainwater solution (+water) to four of these technically replicated microbiomes while the other four microbiomes received 0.2 mL of allochthonous leachates (+leachate). On the whole, this resulted in four incubation treatments, i.e. two for *S. fallax* microbiome (SF microbiome + water and SF microbiome + SD leachate), and two for *S. divinum* microbiome (SD microbiome + water and SD microbiome + SF leachate). After substrate addition (rainwater or allochthonous leachates), the 96-deep-well microplate was sealed with a 96-well detection microplate containing agar gel and cresol red as

indicator dye (Campbell et al., 2003), and incubated at 20°C in the dark. Discoloration of the indicator gel was measured using spectroscopy at 570 nm at irregular intervals (BioTek SynergyMX). The absorbance values were normalised at a given time by the initial absorbance values, after which the percentage of CO₂ released from each well was calculated (Campbell et al., 2003). Values for the four technical replicates were averaged after data-quality check.

In order to understand the effects of leachate composition on microbial respiration, we focused on the effects of *S. divinum* compounds on *S. fallax* microbial CO₂ respiration. We used a fractionation of methanolic extracts of *S. divinum*. Methanolic extracts presented the advantage to be more concentrated than leachates which made the fractionation possible. 3.27 g of the methanolic extract of *S. divinum* were separated by Flash chromatography. Chromatographic conditions: PuriFlash® C18 HQ column (15 µm particle size, 120G), gradient H₂O (+ 0.1% FA)/ MeOH (+ 0.1% FA) (25:75 to 100:0 in 109 min., 100:0 isocratic from 109 to 164 min.), 2 µL (5 mg/mL), flow rate 30 mL/min., UV detection 200, 254, 280 and 366 nm, 18 mL fractions. The 136 resulting fractions were pooled in 23 fractions according to their thin layer chromatography profiles. The 23 fractions were dissolved in dimethyl sulfoxide (DMSO) at a concentration of 10 µg.L⁻¹. As a next step, we incubated 0.8 mL of *S. fallax* microbial extract with the 0.2 mL of all obtained *S. divinum* metabolite fractions using an identical approach as aforementioned (Microresp™). Microbial incubation with DMSO was used as a control. Following the same protocol as previously described, we assessed microbial respiration at irregular intervals.

Prolonged effect of leachates

Ten microcosms from each species were randomly divided into two groups. The first group (n = 5) was watered daily with 12 mL artificial rainwater, and hence served as a control (C). The second group received daily 12 mL of allochthonous leachate; *S. fallax* was water with 12 mL of L_{SD} and *S. divinum* was water with 12 mL of L_{SF}. Essentially this resulted in four experimental treatments: SF-C, SF-L_{SD}, SD-C, and SD-L_{SF}. The experiment lasted three weeks. Due to experimental constraints (i.e. limited leachate availability) we were not able to apply autochthonous leachate addition. The experiment was achieved over a three-week period, which guarantees the microbiome to have turned over multiple times (Schmidt et al., 2007; Schönborn, 1965). Throughout the experiment, the position of the cores

in the growth chamber was spatially randomized and we kept the same conditions applied during the acclimation period.

Microbial biomass and community structure

At the end of the three-week leaching experiment, phospholipids fatty acids (PLFA) biomarkers were used to estimate the biomass of fungi, gram-negative, gram-positive and actinomycete bacteria (Deneff et al., 2009). PLFA were extracted from 0.25 g lyophilized *Sphagnum* shoot over a 12 h period in a solvent phase comprising 3.0 mL 50 mmol.L⁻¹ phosphate buffer (pH 7.0), 3.8 mL chloroform and 7.6 mL methanol (Börjesson et al., 1998). PLFA 19:0 (Larodan, Malmö, Sweden) was added as an internal standard to the phospholipid fraction. PLFA were methylated to form fatty acid methyl esters using 1 mL of 0.2 mol.L⁻¹ methanolic KOH (Chowdhury & Dick, 2012; Sundh et al., 1997) and analysed on a gas chromatograph coupled to a mass spectrometer. Results were expressed as micrograms of PLFA per gram of *Sphagnum* dry mass ($\mu\text{g PLFA.g}^{-1}\text{ DM}$).

The biomass of predators (bacterivores, fungivores and omnivores) such as ciliates, testate amoebae, rotifers and nematodes was estimated using inverted microscopy (Olympus IX71, $\times 400$, Utermöhl method). To this aim, we collected 3 g of fresh *Sphagnum* shoots (0-4 cm depth), fixed them in 20 mL of glutaraldehyde (2% final concentration) and stored at 4 °C in the dark before analyses. Testate amoebae, ciliates, rotifers, and nematodes were extracted from mosses following the method described in Jassey et al. (2011). From a 3 mL subsample, we identified microbial predators with the appropriate taxonomic literature (D. H. Lynn, 2006). The 3 mL aliquots were settled for 1 h in the counting chamber, which was more than enough according to ciliate sinking rates (Claessens & Prast, 2008). Cells were identified and enumerated across 50% of the total chamber area using transects. The abundance of each species was converted into biovolume (μm^3), based on geometrical shapes and dimensions measured under the microscope (length or diameter; width, and height) and then into biomass using conversion factors as given in Gilbert et al. (1998). The biomass data were expressed as micrograms of C per gram of *Sphagnum* dry mass ($\mu\text{gC g}^{-1}\text{ DM}$).

Microbial respiration and enzyme activity

We extracted the microbial communities from each of the 20 microcosms as described above. We incubated the microbial extracts in MicroResp™ with rain water for eight hours, following the previous

protocol. Microbial enzyme activity was quantified in microplates following Jassey et al. (2016). Fluorescence of fluorescein diacetate (FDA), a proxy for total enzyme activity (Green et al., 2006), was monitored spectrophotometrically with an excitation wavelength of 365 nm and emission detection at 450 nm (BioTek, SynergyMX). Spectrophotometric measurements were made every hour during incubation until a plateau was reached. We based the calculation of enzyme activities on incubation times of three hours for FDA hydrolysis. Methodological controls containing boiled enzyme extracts were further assayed. Overall enzyme activity was then calculated by subtracting the mean fluorescence of boiled controls from the mean fluorescence of extracts wells. FDA enzyme activity was converted into $\mu\text{moles per gram dry weight per min}$ ($\mu\text{mol min}^{-1} \text{g}^{-1} \text{DM}$).

Statistical analyses

All statistical analyses were performed in R version 3.5.0 (R Core Team, 2018). Analysis of variance (ANOVA) was applied to test the effects of *Sphagnum* species, leachate treatments and their interaction (fixed effects) on CO₂ release, microbial enzyme activity and microbial biomasses. Prior analyses, we checked the normality and the homoscedasticity of the data; the data were log-transformed when necessary. For time-related measurements (kinetics of microbial respiration) a linear mixed model was used with time, species and treatment as fixed variables and specific microcosm in function of time as a random effect (Pinheiro & Bates, 2000). Similar models were used to assess the effect of each *S. divinum* fraction on microbial respiration. Differences among metabolite relative abundance in both leachates were tested using chisquared-test.

Food web numerical analyses

Food web constructions

To elucidate the effect of prolonged leachate addition on microbial interactions within the *Sphagnum* microbiome, we used a network approach based on the force of trophic interactions among microbial species. For each treatment (i.e. SF-C, SF-L_{SD}, SD-C, SD-L_{SF}), we built an average food web based on the observations from the five replicates. These networks were built in four steps. Firstly, we assigned every species or generic group assessed with PLFA (i.e. gram-positive and gram-negative bacteria, actinomycete, other bacteria, saprophytic fungi, arbuscular mycorrhiza, and diatoms) to a trophic group: decomposers, primary producer, consumer and top-predator. We then identified the feeding

habit of consumers and top-predators (Supplementary table S.IV.1) using microscope observation and literature (Gilbert et al., 2000, 2003; Jassey et al., 2012 b; Mieczan, 2009; Wilkinson and Mitchell, 2010; personam observations). Based on these feeding habits, we constructed a general table of hypothetical trophic links between microbial species and/or groups. We obtained two tables of hypothetical links, one associated to *S. fallax* microbiome, the other associated to *S. divinum* microbiome. Secondly, we used basic rules to transform the general tables of hypothetical links into microcosm-specific tables of effective trophic links. A link between a predator and a prey was considered to be effective in a microcosm (i) if the link existed in the general table of hypothetical links, (ii) if the predator and the prey coexisted in microcosm and (iii) if the predator was less abundant than the prey. Based on previous observations in peatlands (V. E. Jassey et al., 2013; Jassey et al., 2015; Reczuga et al., 2018a), we assumed that predators were always less abundant than bacteria, fungi and algae quantified by PLFA. Thirdly, we weighted the effective trophic links between a predator and a prey by the relative abundance of the predator amongst microcosms of a *Sphagnum* species to take into account the intensity of interactions. For instance, an effective link between a predator and a prey was considered more intense in microcosm A than in microcosm B if the predator was more abundant in microcosm A compared to microcosm B, both microcosms belonging to the same *Sphagnum* species. Finally, we built an average table of links for each treatment by averaging the microcosm-specific tables of weighted links according to their treatments. We only kept links with a weight higher than 0.2 in order to remove weaker interactions (Fig. S.IV.1), assuming that they were unlikely. Such threshold resulted in the removal of c. 20% of weaker links in *S. fallax* and *S. divinum* microcosms.

Food web structure analyses

Networks were then produced using the *igraph* R package (Csárdi & Nepusz, 2006). We extracted the core properties of the webs to evaluate whether substructures responded to leachate addition according to Ma et al. (2019). Each network was then analysed in terms of connectivity (C), density of links within the network (edge D), core size and density of links within the core (Phir). Connectivity was calculated as the number of links divided by the square of the number of species in the network. Density of links within the network was calculated as the number of effective links divided by the number of total possible links. Core size and density of links within the core were calculated as in Ma et al. (2019). Indices of network beta diversity were also calculated between networks (Poisot et al.,

2012) using *betalink R* package (Poisot et al., 2016). Especially, we calculated network beta diversity between average and hypothetical networks (constructed with hypothetical trophic links as explained above) to see if treatments altered the distance with hypothetical networks.

Food web robustness analyses

We tested the robustness and specificity of each network using a series of null models (Robroek et al., 2017; Ma et al., 2019). We used three scenarios to simulate new networks. The first scenario (hereafter R_I) comprised 1000 randomisations of trophic links among microbes whilst keeping the total number of links and species within network intact. The second scenario (hereafter R_R) comprised the removal of trophic links of two species taken randomly, and is based on the observed effect of leachate addition on food web structures (see Results for details). Species removal was repeated until the whole combinations of species removal was reached (i.e. 231 combinations). The last scenario (hereafter R_{IR}) was a combination between R_I and R_R : 30 combinations of two species were randomly chosen based on our observations. For each combination, the links of the two species were removed before proceeding to 100 randomisations of the trophic links within the networks as described above (3000 reshuffled networks in total). On each simulated networks, we calculated structural indices (beta diversity, C , $edgeD$, $Coresize$ and $Phir$) and compared them with the structural indices found in original networks from leachate addition treatments using standardized effect size as described in Robroek et al. (2017). Finally, we proceeded to a targeted species removal within networks based on species that dramatically changed their network position between control and leachate addition treatments (*Hyalosphenia papillo* and *Hyalosphenia elegans* in *S. fallax* networks and *Assulina muscorum* and *Hyalosphenia papillo* in *S. divinum* networks). Starting from the control networks, we proceeded to a target removal of these species when they were brought to network periphery in leachate addition treatments. On the contrary, we proceeded to a replacement of their effective links by their hypothetical links when they were brought to the heart of networks in leachate addition treatments. Again, we measured structural network indices and compared them with the observed structural indices.

Results

Global chemical characterization of *Sphagnum* leachate

Leachate composition was species-specific with global compounds being more concentrated in L_{SF} than in L_{SD}: water-soluble phenolic concentration was higher in L_{SF} (4.87 mg L⁻¹) than in L_{SD} (3.92 mg L⁻¹) as well as DOC (L_{SF} = 39 mg L⁻¹; L_{SD} = 11.55 mg L⁻¹) and DON (L_{SF} = 1.95 mg L⁻¹; L_{SD} = 0.89 mg L⁻¹). The spectral slope (S₂₅₀₋₆₆₅) of DOC was lower in L_{SF} (0.067) than in L_{SD} (0.144), which indicates that the aromaticity and/or molecular weight of L_{SF} was higher than L_{SD}.

According to the metabolite composition, we found that L_{SF} and L_{SD} contained almost the same chemical compounds but in different relative proportions (Fig. IV.1A). L_{SD} (526 metabolites) was slightly richer in metabolites than L_{SF} (516 metabolites); 2% of these leachate-metabolites being species-specific, some of them being present only in L_{SD} (Fig. S.IV.2). Despite similar metabolite richness (Fig. IV.1B), nearly half of the more concentrated compounds (relative abundance > 2.5%) differed between L_{SF} and L_{SD} ($P < 0.01$, Chi-test; Fig. IV.1A). Furthermore, only 25% of leachate-metabolites were common with bog water metabolites. This comparison indicates that bog water and *Sphagnum*-leachates composition is different in terms of molecular compounds. The relative abundance of shared metabolites between *Sphagnum* leachates and bog water also differed ($P < 0.01$, Chi-test) (Fig. IV.1A). Finally, we found according to the molecular network (Fig. S.IV.3) that *Sphagnum* leachates were closely related to water and methanolic *Sphagnum* extracts, which indicates that the metabolites from *Sphagnum* leachates are mostly released by *Sphagnum* mosses and do not come from the peat or vascular plants.

Focusing on metabolites common to methanolic/water extractions and leachates profiles, several annotated metabolites corresponded to aminoacids derivatives. Phenylalanine for example was found to be present in both *Sphagnum* species extract (water, methanolic) and leachates but not in bog water. Typical *Sphagnum* metabolites such as sphagnum acid were found to be present in water and methanolic extracts but not in leachates (Fig. IV.2A). We however detected a derivate of sphagnum acid, sphagnum acid methyl ester, in L_{SD} but not L_{SF}. Finally, we also detected bacteria-related metabolites such as aminobacteriohopane and bacteriohopanetetrol derivatives (Fig. IV.2B). 35-aminobacteriohopane-32,33,34-triol was found to be present in methanolic, water extracts of both species, in the bog water, but only in L_{SD}. Another one, (32,33,34,35-Bacteriohopanetetrol

(21βH,32R,33R,34S)-form 35-O-(6-Amino-6-deoxy-β-D-glucopyranoside)), was detected in leachates, and water/methanolic extracts of *S. divinum* but only observed in the *S. fallax* methanolic extract (Fig. IV.2B).

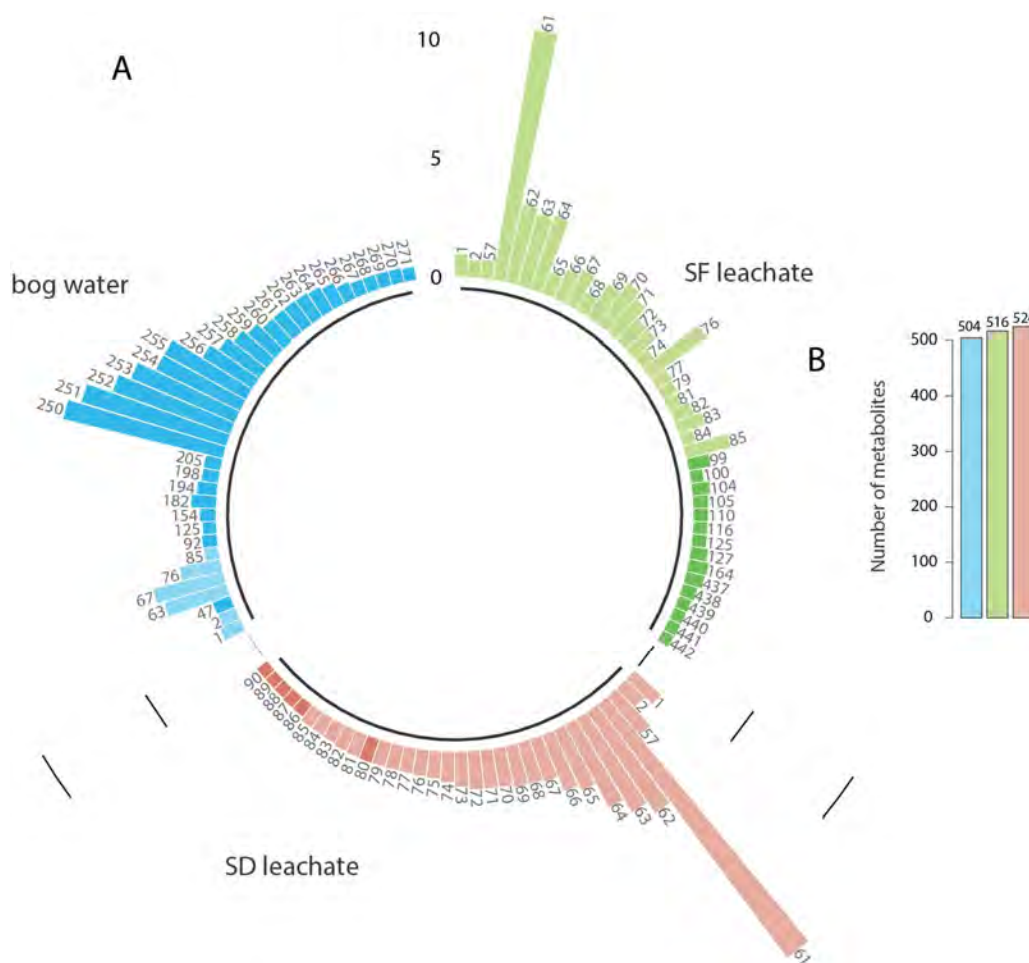
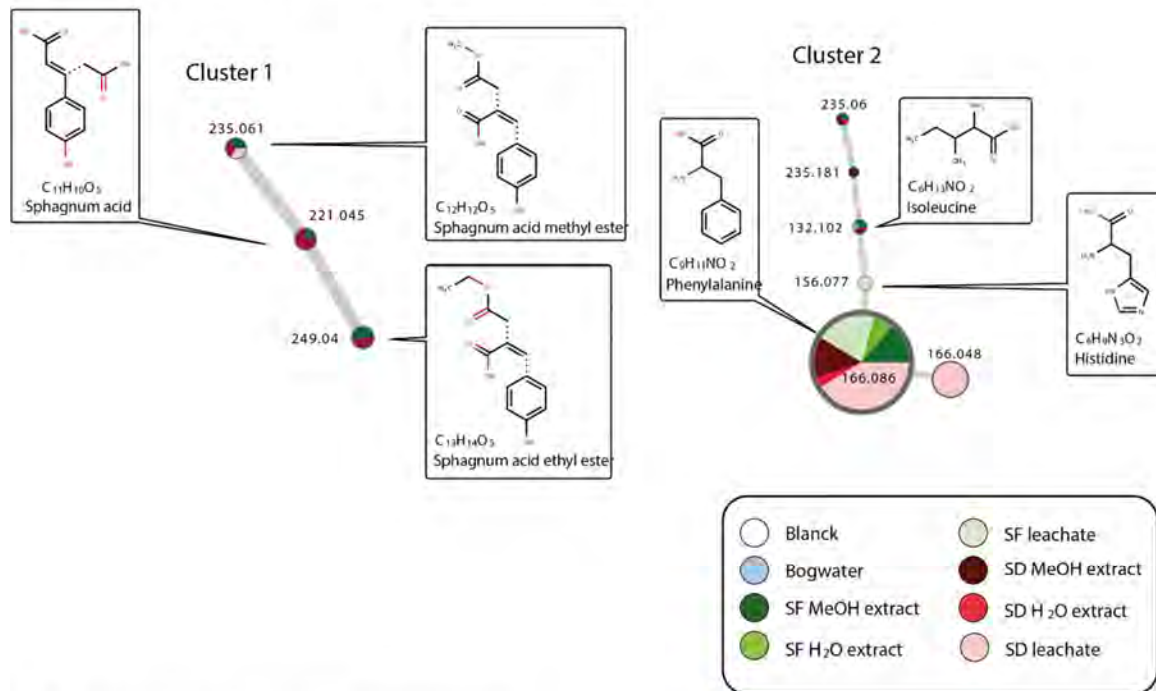


Figure IV.1: Relative abundance of metabolites in SF, SD leachates and bog water (A). Each bar and number correspond to a specific metabolite. For clarity of the graph, only the more concentrated metabolites are presented (relative abundance > 2.5%). Dark-coloured bars refer to metabolites that have a relative abundance higher than 2.5% in the considered extract, but less than 2.5% in other extracts. Total number of metabolites in SF, SD leachates and bog water are presented in (B).

A - Specialized metabolites of the bryosphere



B - Bacterial-related metabolites within the bryosphere

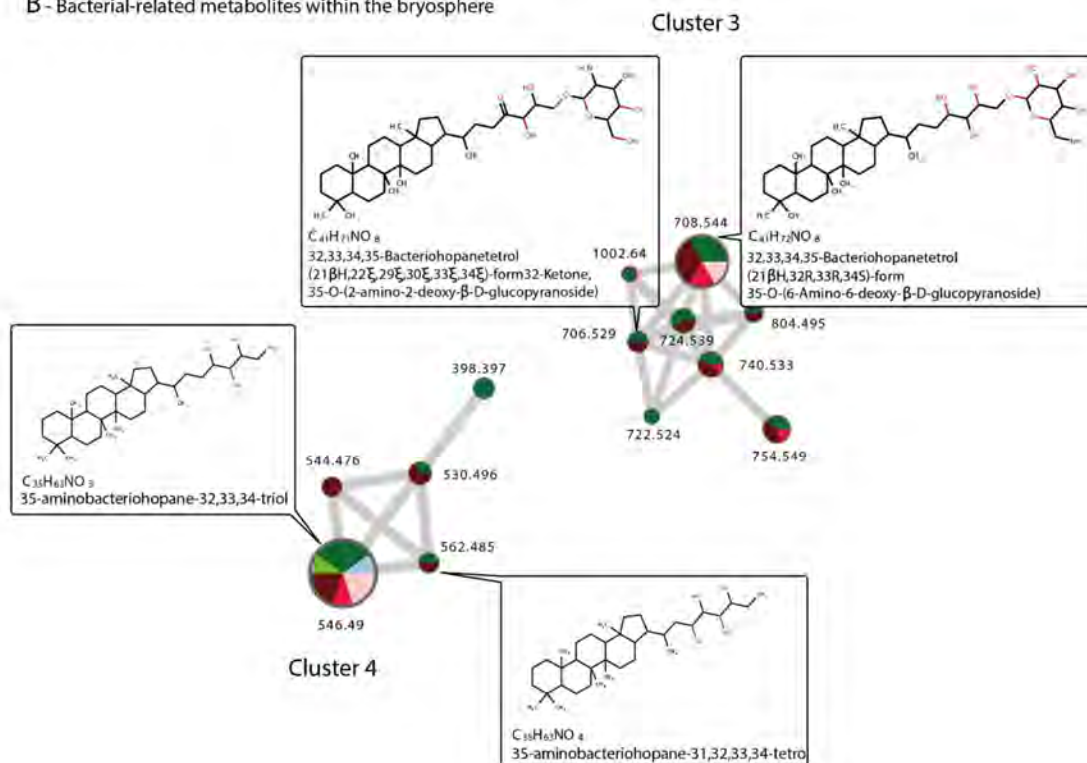


Figure IV.2: Clusters individualized from the massive similarity network (see Fig. S3) and showing identified specialized metabolites found in *Sphagnum* leachates, extracts, and bog water. Metabolites are associated to the bryosphere (A) or to bacteria (B).

Instantaneous effect of an allochthonous leachate addition on microbial respiration

Allochthonous leachates addition effects on *Sphagnum* microbiome CO₂ respiration are time and species-specific ($F_{1,173} = 3.73$, $P = 0.05$). The respiration of *S. fallax*-associated microbiome was strongly inhibited by L_{SD} addition and reached only 5% of the control rates within the first 30 hours ($F_{1,8} = 10.38$, $P = 0.018$) (Fig. IV.3A). This inhibition was, however, time-limited so that after 46 hours of incubation microbial respiration recovered and even released 78% more CO₂ than controls ($F_{1,8} = 3.8$, $P = 0.10$). We did not find an effect of L_{SF} on the microbial respiration of *S. divinum* microcosms ($F_{1,81} = 0.56$, $P = 0.48$) (Fig. IV.3B).

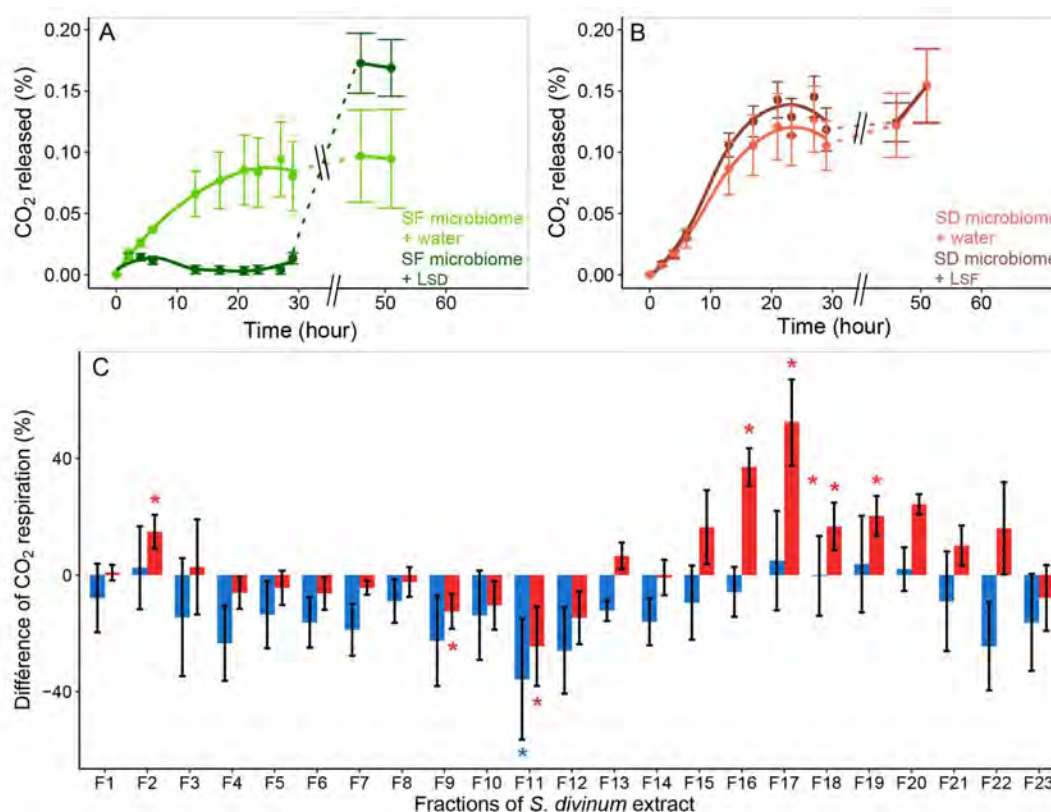


Figure IV.3: Response of microbial respiration to short-term allochthonous leachate addition. The CO₂ released in each well is calculated by normalizing with the initial value and combined according to the treatment. *S. fallax* microbiome (A) were either incubated with water (lightgreen) or with L_{SD} leachate (darkgreen). Similarly, *S. divinum* microbiome (B) was either incubated with water (lightred) or with L_{SF} (darkred). Error bars refer to standard error. Panel (C) shows the difference in respiration of *S. fallax* microbiome after incubation with different fractions of L_{SD} compared to DMSO only (control). Differences are expressed as percentage. Blue bars show differences of respiration after six hours of incubation and red bars after 21 hours of incubation. Error bars refer to standard error and asterisks indicate significant differences with control for each incubation time ($P < 0.05$).

The incubation of *S. fallax* associated microbiome with *S. divinum* metabolic fractions as substrate confirmed the inhibition of microbial respiration on short-term. After six hours of incubation, *S. divinum* metabolic fractions reduced *S. fallax* microbial respiration by 12% on average compared to the DMSO control (Fig. IV.3C). We found that 19 fractions out of 23 induced an inhibition effect on microbial respiration, although only the fraction F11 was significant (-36%, $t = 2.81$, $P = 0.047$). Furthermore, the effect of *S. divinum* fractions varied over time ($F_{23,240} = 1.77$, $P = 0.019$). Indeed, the fractions that had minimal effect after six hours had a positive effect on microbial respiration after 21 h: F2 +15% ($t = 2.53$, $P = 0.045$), F16 +37% ($t = 7.48$, $P < 0.001$), F17 +52% ($t = 4.00$, $P = 0.019$), F18 +17% ($t = 3.14$, $P = 0.021$), F19 +20% ($t = 4.11$, $P = 0.008$), F20 +24% ($t = 5.138$, $P = 0.004$). Overall, 11 fractions out of 23 showed an inhibitory effect after 21 h of incubation, in particular the fractions F11 (-25%, $t = 2.71$, $P < 0.05$) and F9 (-6%, $t = 2.81$, $P < 0.05$).

Effect of a prolonged allochthonous leachate addition on microbial food-web structure and function

By the end of the three-weeks leachate experiment, we did not find differences in CO₂ respiration between the microbial communities that had been exposed every day to allochthonous leachate (L_{SD} and L_{SF} treatment) and those that had been watered only with rain water (C treatment). This result was apparent in the *S. divinum* microbiome ($F_{1,8} = 1.22$, $P = 0.3$) and the *S. fallax* microbiome ($F_{1,8} = 2.68$, $P = 0.14$) (Fig. S.IV.4). Similarly, we did not find any significant effect of treatment on overall enzyme activity (FDA) for both *Sphagnum* species (Fig. S.IV.5).

The analysis of the *Sphagnum* microbiome community composition showed a clear difference in terms of species diversity and species biomass between *S. fallax* and *S. divinum* microcosms. The first two axis of the PCA (Fig. S.IV.6) showed that *Hyalosphenia papilio* (mixotrophic testate amoebae), *Amphileptus* sp. (ciliates), *Lecane quadridentata* and *Polyarthra* sp. (rotifers) were dominating in *S. fallax* microbiome, while *Hyalosphenia elegans* (heterotrophic testate amoebae), *Colurella obtusa* (rotifers) and nematodes dominated the *S. divinum* microbiome. We found that three weeks of allochthonous leachate addition tended to alter the composition of microbial communities in *S. fallax* microcosms, but not in *S. divinum* microcosms (Fig. IV.4). In the *S. fallax* microbiome, we observed a decrease in biomass of some predators, so that the biomass of testate amoebae decreased by 45% ($F_{1,8} = 4.44$, $P = 0.07$) mainly due to a decrease of mixotrophic testate amoebae (-50%, $F_{1,8} =$

3.63, $P = 0.09$). Additionally, the biomass of rotifers decreased by 42% ($F_{1,8} = 2.47$, $P = 0.16$), although these trends were not significant.

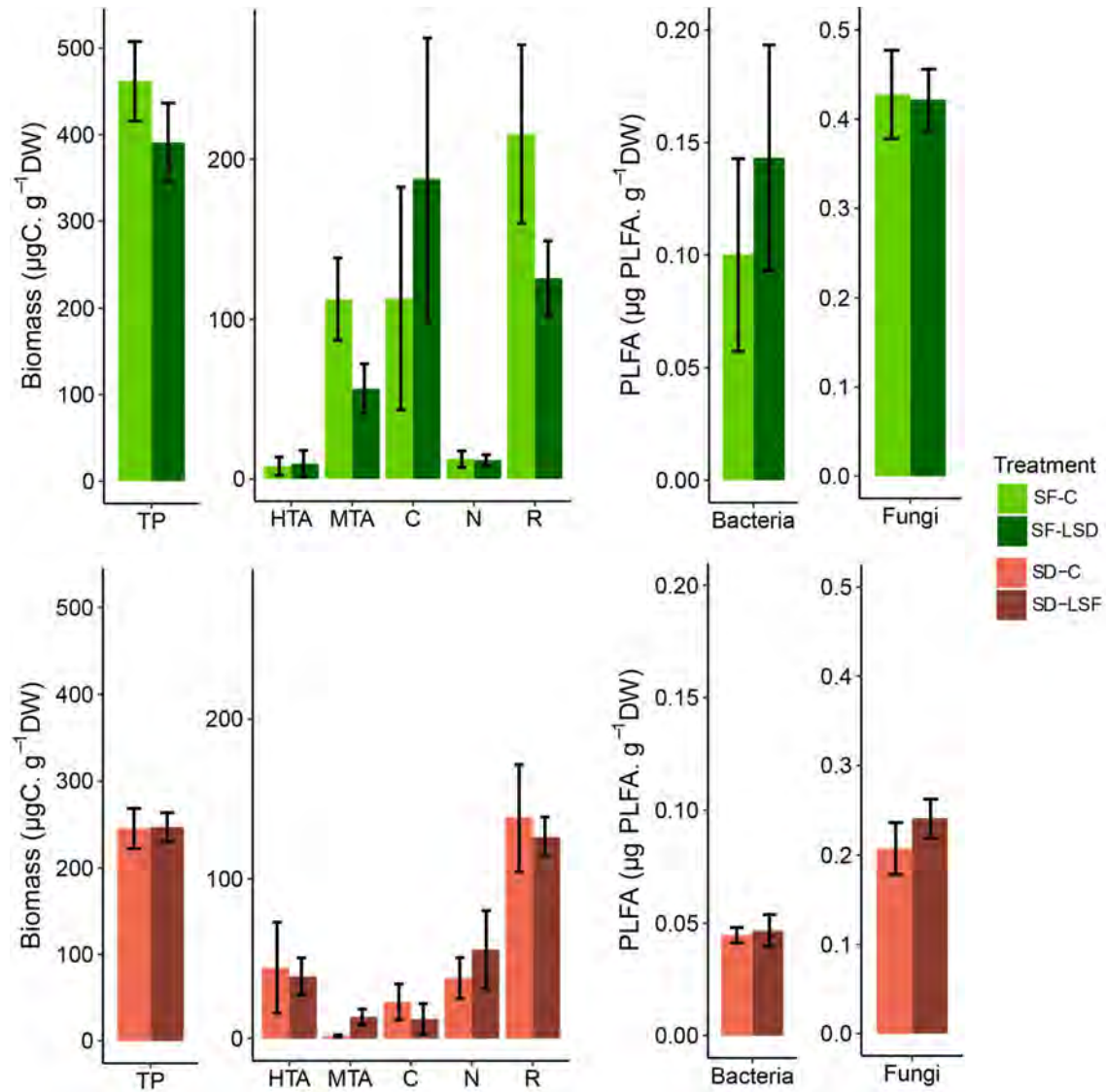


Figure IV.4: Structure of microbiome in *S. fallax* (top) and *S. divinum* (bottom) microcosms after three weeks of daily exposition to rain water (SF-C, SD-C) or allochthonous leachates (SF-LSD, SD-LSF). For each *Sphagnum* species, the two graphs on the left show the predator biomass with TP = total predators, i.e. the sum of HTA = heterotrophic testate amoebae, MTA = mixotrophic testate amoebae, C = ciliates, N = nematodes and R = rotifers. The two graphs on the right show the relative abundance of bacteria and fungi. No significant differences were detected. Error bars refer to standard error.

The addition of allochthonous leachates caused changes in the food web structure, both in *S. fallax* and *S. divinum* microbiome (Fig. IV.5). In the *S. fallax* microbiome, leachate addition led to a 30% decrease in connectivity and link density within the network (Fig. IV.6). Similarly, the networks' core size was reduced from seven species in the SF-C networks to four species in the SF-L_{SD} networks. Interestingly, two of the three species removed from the core were mixotrophs (*Hyalophenia papilio* and *Amphitrema wrightianum*). They were not only pulled away to the periphery of the cores, but they also lost the totality of their trophic links. We further found that SF-L_{SD} network was more different with the hypothetical network than SF-C network as network beta diversity was higher in the first case than in the second one (Fig. IV.6). In *S. divinum* microbiome, we found an opposite effect of allochthonous leachate addition. In particular, we found that core size was doubled in SD-L_{SF} networks (ten species) compared to SD-C networks (five species). Two species, *i.e.* *Amphitrema muscorum* and *Hyalophenia papilio*, that did not have any link in the SD-C network were further integrated to the core. The increasing of core size led to a decreasing of edge density within the core (0.11 and 0.40 in SD-L_{SF} and SD-C networks respectively). Allochthonous leachate addition did not affect neither connectivity and edge density of the networks, nor network beta diversity.

The networks obtained after randomisation and/or random species loss strongly differed from SF-L_{SD} and SD-L_{SF} networks, both in term of network beta diversity and structural indices (SES were strongly different from 0, $P < 0.001$, Fig. S.IV.7). This result was found both in *S. fallax* and *S. divinum* microbiomes, irrespective of the null models tested (Fig. S.IV.7). This indicates that leachate-induced shifts in food web structures are due neither to random changes in interactions nor to random species loss. Finally, the target removal of *H. papilio*, *H. elegans* or both species from SF-C network did not lead to an increased similarity with SF-L_{SD} network (Fig. S.IV.8). On the same way, the addition of hypothetical links of *A. muscorum*, *H. papilio* or both species in SD-C network did not lead to an increased similarity with SD-L_{SF} network (Fig. S.IV.8).

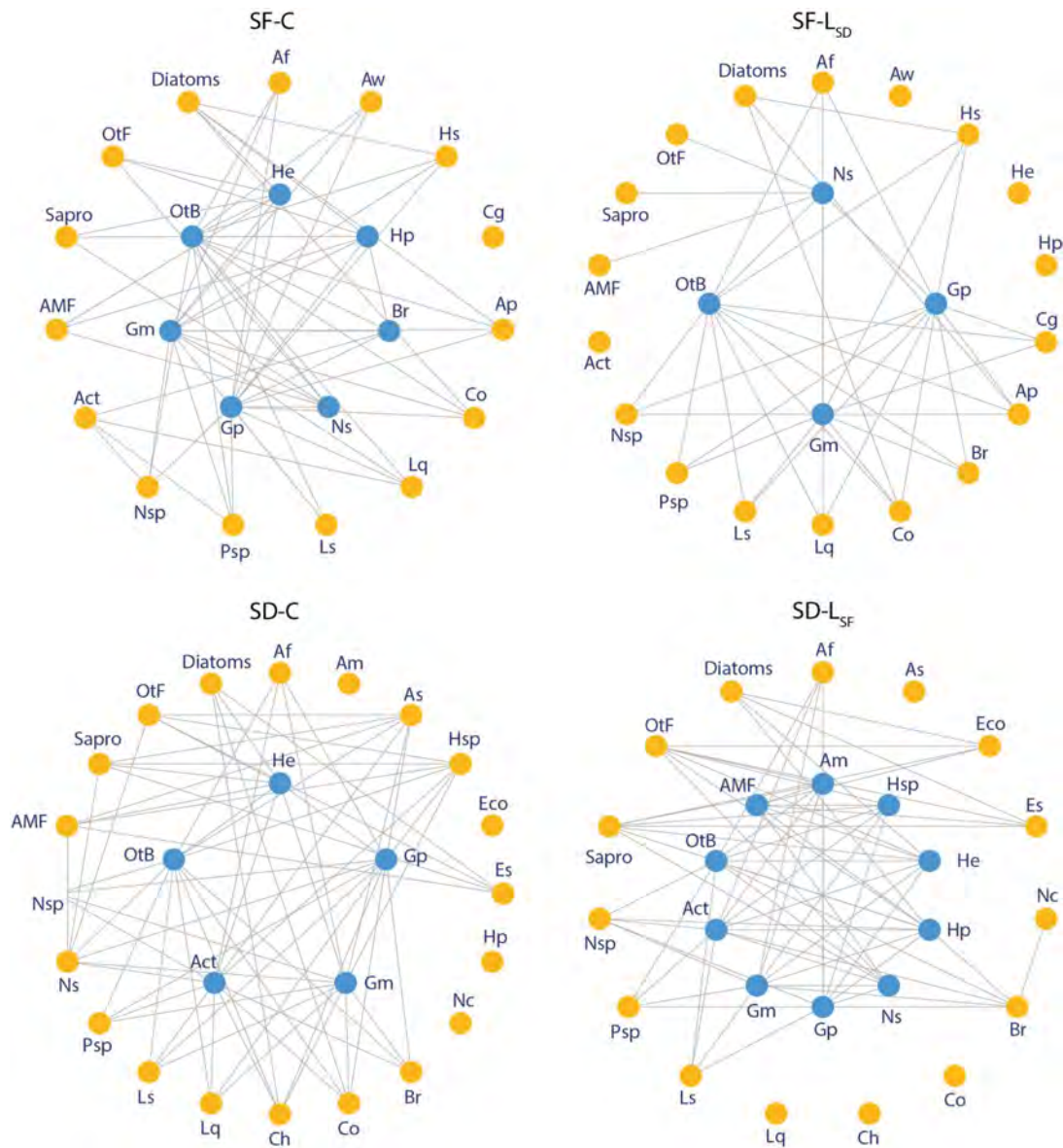


Figure IV.5: Food web structure in SF-C, SF-L_{SD}, SD-C and SD-L_{SF} microbiomes. Each point represent a microbial species or group and is coloured according to its belonging to the core (blue) or to the periphery (yellow) of the network. Trophic links were weighted by the abundance of predators and the 20% weaker links were removed from the network. Abbreviations of names are specified in Supplementary Table S.IV.1.

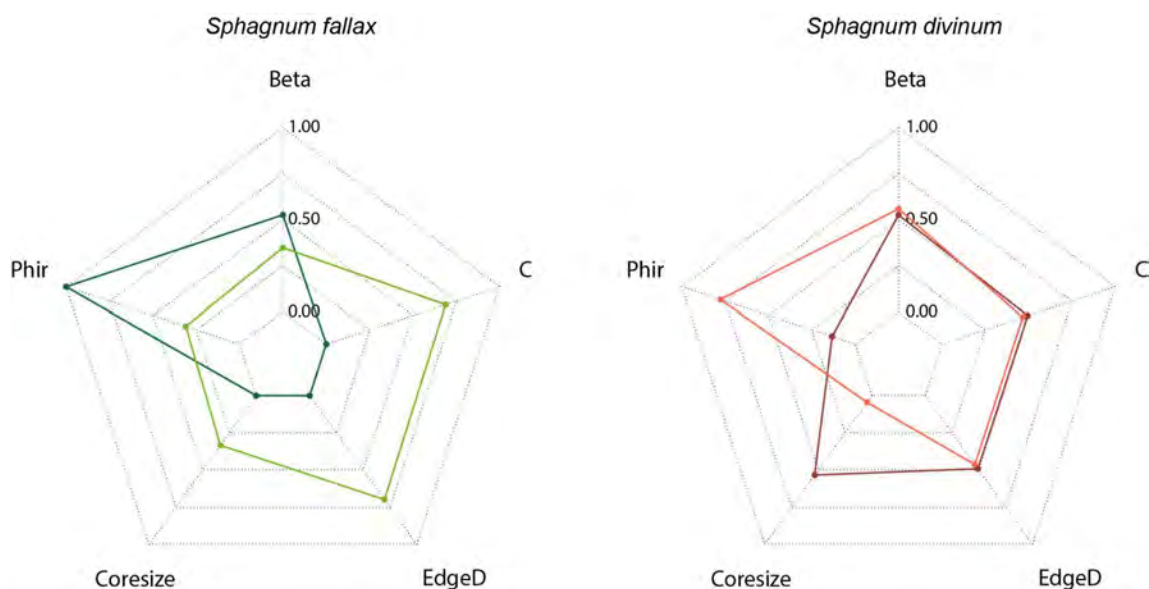


Figure IV.6: Structural indices of SF-C (left, light green), SF-L_{SD} (left, dark green), SD-C (right, light red) and SD-L_{SF} (right, dark red) food web networks. Structural indices comprised connectance (C), edge density within the network (EdgeD), core size, and edge density within the core (Phir). Beta diversity was also calculated with hypothetical networks. Each indice was normalised by its overall range.

Discussion

Sphagnum specialised metabolites have long been suspected to drive microbial processes in peatlands (Verhoeven and Liefveld, 1997; Fenner and Freeman, 2011). In this study, we not only show that *Sphagnum* specialised metabolites comprise a mosaic of microbial and *Sphagnum* compounds, but also that these complex assemblages trigger a set of important changes in the *Sphagnum*-microbiome structure and its functioning. We found that the effects of allochthonous *Sphagnum* leachate addition on competitive *Sphagnum*-microbiome were species-specific with antagonistic responses between *Sphagnum* species. While the addition of *S. divinum* leachates significantly reduced microbial CO₂ respiration and altered the structure of *S. fallax*-associated food web, *S. fallax* leachate addition had only slight effects on *S. divinum* microbiome with no effects on microbial respiration. These results are even more striking by considering that both *Sphagnum* leachates mostly contain similar chemical

compounds but in different proportions, and that the few *Sphagnum*-specific metabolites were poorly concentrated. Furthermore, we found that *Sphagnum* microbiomes strongly differed between species, suggesting that *Sphagnum* leachates target specific microbial species. Species-specificity has been shown as an important factor in plant-plant allelopathic interactions (Inderjit et al., 2011). Indeed, plant species are known to produce different cocktail of specialised metabolites according to their genus and environmental conditions, which can greatly influence their allelopathic interactions. Our results suggest that similar allelochemical mechanisms may exist between *Sphagnum* species and microorganisms. Although we cannot totally exclude that other factors than *Sphagnum* metabolites caused the observed differences in both *Sphagnum* microbiomes, the effect of *Sphagnum* metabolic fractions (Fig. IV.3C) strongly suggests that *Sphagnum* metabolites can be a major driver of microbial CO₂ respiration in peatlands.

Microbial CO₂ respiration

Previous studies found that specialised compounds produced by *Sphagnum* mosses can inhibit bacterial growth (Mellegård et al., 2009) and microbial activity (Freeman et al., 2001; Fenner and Freeman, 2011). In this study, we show that such anti-microbial effects can be found in *Sphagnum* leachates but their magnitude is species-specific and their effects limited in time. Allochthonous leachate addition caused immediate decrease of *S. fallax* microbial respiration since the first exposure, while *S. fallax* leachate addition did not influence *S. divinum* microbial respiration. This result indicates that *S. divinum* leachates exhibit anti-microbial properties that promptly reduce catabolic activities of microbes associated to *S. fallax*, whereas the opposite is not the case. The analysis of *S. divinum* metabolic fractions on the respiration of *S. fallax* microbiome further demonstrates that not all *S. divinum* compounds inhibit microbial respiration. This result is supported by recent findings (Mellegård et al., 2009; Chiapusio et al., 2018) and suggests that anti-microbial effects of *Sphagnum* leachates depend both on metabolic cocktail and on the specific concentration of specialised metabolites (Chiapusio et al., 2018).

The general similarity in the composition of *S. divinum* and *S. fallax* leachates has, however, to be relativized by their low concentration. We cannot exclude that some compounds were under the limit of detection of the UHPLC-HRMS. Nevertheless, slight differences with potential important consequences were found in the composition of both leachates. For instance, sphagnum acid methyl

ester – a derivative from sphagnum acid known for its anti-microbial effect (Verhoeven & Liefveld, 1997) was only found in L_{SD}. Bacteria-related metabolites belonging to the hopane group of pentacyclic triterpenoids and associated to *Rhodopseudomonas* sp. (van Winden et al., 2012) were also only identified in L_{SD}. Molecules of that group are known to have cytotoxic and antibacterial properties (Rohmer et al., 1991, Nagumo et al., 1991). This result is important and indicates that the metabolites secreted by *S. divinum*-associated bacteria could have negative effects on *S. fallax* microbiome. Although further research is needed to specifically identify the compounds with anti-microbial effects in the *Sphagnum*-sphere, our findings bring evidences that *Sphagnum* leachates result from the combined exudation and secretion of metabolites from *Sphagnum* and associated microorganisms. The composition of the resulting chemical assemblage is likely to determine leachate allelopathic potential, and might explain why *S. divinum* leachate has a higher allelopathic effect than *S. fallax* leachate.

Our results indicate that the inhibitory effect of *Sphagnum*-sphere specialised metabolites on microbial respiration in *S. fallax* microbiome is time limited and disappears after two days. Following this inhibition period, microbial respiration recovered at an important rate and the amount of CO₂ respired overtook the one that was respired in control plots. This finding suggests that after the loss of inhibition, the nutrients and the DOC contained in *S. divinum* leachate might have stimulated microbial activity and respiration by supplying easily degradable C to microbes (Robroek et al., 2016). We found that prolonged addition of *S. divinum* leachates on *S. fallax* microbiome did not change microbial respiration despite structural, but functionally redundant changes among the microbial network. This result provides nuance to the traditional assumption that the accumulation of *Sphagnum* specialised metabolites such as polyphenols interferes with microbial catabolic activity in peatlands (Freeman et al., 2001). In our study, microbial enzyme activity and respiration seems to be resilient to prolonged accumulation of *Sphagnum* specialised metabolites due to a selection among microbial species. This suggests that *Sphagnum* leachates may play a role in natural microbial selection (Callaway et al., 2005; Inderjit et al., 2011) and that microbial adaptation within the community can lead to an alleviation of allelopathic effects (Y.-P. Li et al., 2015). Such alleviation effects might have important consequences for the peatland C balance and suggest that a critical re-examination of the mechanisms driven by *Sphagnum* specialised metabolites in peatland C dynamics are urgently needed.

Sphagnum microbiome and microbial networks

Our results show that *S. fallax* and *S. divinum* microbiomes differ and respond differently to allochthonous leachate addition to such an extent that a much stronger impact on *S. fallax* microbiome was observed compared to *S. divinum* microbiome. In both species, allochthonous leachate addition altered the food web structures, but in a different way. In *S. fallax* microbiome, L_{SD} altered the structure of the network through a decreasing of connectivity, edge density and core size. These alterations indicate a destabilisation of the food web, which is reinforced by the fact that L_{SD} addition leads to a disparity with the hypothetical network. In fact, L_{SD} disrupts the intensity of trophic interactions between microbial species through a modulation of microbial abundance and, especially, a decrease of testate amoebae and rotifer abundance. More precisely, we found that mixotrophic testate amoebae, which combine both photosynthesis and predation, were dramatically isolated from the network in SF-L_{SD} treatments. This suggests that the duality in their nutrition does not provide them an advantage to resist to anti-microbial metabolites. It further indicates that *S. divinum* leachates may influence the survival and/or reproduction of mixotrophic testate amoebae, explaining why these species are poorly represented in *S. divinum* microbiome. Garcia-Palacios et al. (García-Palacios et al., 2016) reported similar inhibitory effect of vascular plant polyphenols on specific microbial functional groups such as nematodes in soils. Our findings further point to a novel mechanism by which *Sphagnum* metabolites can have anti-predator effects, in addition to the already recognized anti-bacterial and anti-fungal effects (Verhoeven and Liefveld, 1997; Mellegård et al., 2009; Binet et al., 2017; Chiapusio et al., 2018). In the *S. divinum* microbiome, we found that *S. fallax* leachate addition also altered the food web structure, but with opposite effects compared to *S. fallax*. Particularly, we found that connectivity and core size increased in SD-L_{SF} treatment, which expresses a greater stability in the network (Csete and Doyle, 2004; Liu et al., 2011; Csermely et al., 2013). Therefore, it suggests that L_{SF} did not stress *S. divinum* microbiome but rather benefited and stabilised *S. divinum* associated food web. Those changes in the organisation and the structure of *Sphagnum* food webs show that they are structurally unstable and that a perturbation such as allochthonous leachate addition can quickly change them toward a novel state with novel interactions and species. Simulated targeted removal or addition of the more impacted species in term of abundance or connectivity from control networks gave very dissimilar networks than those found with leachate addition. These findings suggest that, in addition to the direct loss or gain of trophic links, allochthonous leachates strongly modulate the

trophic interactions among non-affected species through cascading effects. However, as mentioned above, the structural changes do not lead to important functional alterations of the microbial food web due to functional redundancies among microbes. These findings suggest that *Sphagnum* associated microbial food web functioning is somehow resistant to allochthonous *Sphagnum* metabolites thanks to structural plasticity. This further indicates that structural plasticity of microbial food webs tends to alleviate the effects of allochthonous leachate on its functioning on long-term. The underlying biochemical mechanisms still have to be elucidated further, but our results underline that notions of perturbation durations are primordial in the comprehension of their effect to peatland C dynamics.

Implications for competition

Plant competitiveness is intimately linked with plant fitness and allocation of resources to different metabolic processes (growth, reproduction, defence, etc.) (Herms & Mattson, 1992). In *Sphagnum*, plant fitness strongly depends on the associated microbiome since microbial activity drives nutrient cycling and production of plant-assimilable nutrients (Weston et al., 2015; Kostka et al., 2016). Hence, by their effects on microbial network structure and functions, allochthonous leachates probably alter *Sphagnum* fitness. For instance, the diminution of mixotrophic testate amoebae in *S. fallax* microbiome following *S. divinum* leachate addition could have decreased *Sphagnum* C uptake (Jassey et al., 2015). Further, the inhibition of microbial catabolic activity immediately after *S. divinum* leachate addition might have temporarily reduced nutrient availability within the *Sphagnum*-sphere. Over a longer time, the functional redundancy of microorganisms suggested that the microbial catabolic activities linked with C cycle were not affected by leachate addition. However, other microbial functions could have been impacted, especially those related to nitrogen or phosphate cycling (Carrell et al., 2019). This hypothesis is supported by Conkle and White (Conkle & White, 2012) who also found an immediate time-limited inhibition of microbial CO₂ respiration by antibiotics in wetland soils with a durable alteration of microbial N₂O respiration and phosphatase activity on longer term. As a consequence, an alteration of *Sphagnum* microbiome could impact *Sphagnum* competitiveness by affecting *Sphagnum* fitness. The increased leachate-resistance of *S. divinum* associated microbiome to allochthonous leachate suggests a better competitiveness than *S. fallax*. This result could have important consequences as it has been showed that hollow species (such as *S. fallax*) lose competitive

strength under global warming (Breeuwer et al., 2008) so that the expected changes in *Sphagnum* distribution under global changes might be intensified by allelopathic mechanisms.

Conclusion

Our findings have important implications for understanding how soil microbial communities respond to plant-associated chemical exudates. Although the exact nature of the metabolites interfering with microbial species still remains unknown, we refined the composition of *Sphagnum* leachates and extracts and showed that they can include microbial products. Further, our data show that addition of allochthonous leachates destabilize microbial network structure, primarily through anti-predators effects, with cascade consequences on microbial functioning and respiration. More research is needed to understand the exact genetic and physiologic mechanisms that define the observed response of microbial species to specialised metabolites. Our data reveal that microbiome alteration can be an important process in interspecific *Sphagnum* competition and indubitably in the C dynamics of peatlands. These findings suggest that facing the vegetation changes in peatlands due to climate warming and drought, specialised metabolites could significantly intervene in defence or offensive mechanisms through their effects on microbial communities.

Acknowledgments

We are indebted to Länsstyrelsen i Jönköpings län and the staff of the Store Mosse National Park, particularly Arne Andersson, Dan Käll, Carina Härlin, and Johan Rova for granting site access (permission 521-895-2011) and make use of the infrastructure of the park. BJMR was supported by a NWO-VENI grant awarded by The Netherlands Organization for Scientific Research (NWO-ALW: 863.10.014) and by the Dutch Foundation for the Conservation of Irish bogs. This research has been funded by the Swiss National Science Foundation through the project SPHAGNOL (grant number: 315260 149807 to LB) and supported by MIXOPEAT project (grant number ANR-17-CE01-0007 to VEJJ) from the French National Research Agency. We are thankful to the two anonymous reviewers for their valuable comments on our manuscript.

Author contributions

VEJJ, BJMR and SH designed and implemented the microcosm study with the help of LB and CS. SH, BJMR and VEJJ sampled the *Sphagnum* cores in the field and collected the leachates. SH and VEJJ collected the samples at the end of the experiment with the assistance of BJMR. SH performed MicroResp, characterized general characteristics of leachates and quantified enzyme activities with the assistance of VEJJ, BJMR, LB and AB. VEJJ analysed the microbial samples under the microscope. PM, SZ, and TS performed LC-MS analyses, peak data processing and molecular networks on *Sphagnum* leachates with assistance of GC and J-LW. SH and VEJJ performed statistical analyses and interpreted the data with assistance of BJMR, PM, LB and AB. SH and VEJJ wrote the paper to which all authors contributed with discussions and/or text.

Table S.IV.1: Feeding habits of consumers and top predators found in *S. fallax* and *S. divinum* microbiomes.

Group	Species	Abbreviation	Feeding habit									
			M	T	R	C	N	A	F	B		
Testate amoebae	<i>Amphitrema flavum</i>	Af	x									x
	<i>Amphitrema wrightianum</i>	Aw	x									x
	<i>Assulina muscorum</i>	Am									x	x
	<i>Assulina seminulum</i>	As									x	x
	<i>Hyalosphenia sp.</i>	Hsp									x	x
	<i>Diffflugia leidyi</i>	DI							x			
	<i>Euglypha ciliata</i>	Eci							x	x		
	<i>Euglypha compressa</i>	Eco							x	x		
	<i>Euglypha strigosa</i>	Es							x	x		
	<i>Heleopera sphagni</i>	Hs	x						x			x
	<i>Hyalosphenia elegans</i>	He							x	x		x
	<i>Hyalosphenia papilio</i>	Hp	x	x	x	x	x	x	x	x	x	x
	<i>Nebela carinata</i>	Nc		x	x			x				
	<i>Nebela militaris</i>	Nm							x	x		x
	<i>Nebela tinctoria</i>	Nt		x	x	x	x	x	x	x	x	x
Ciliates	<i>Cyclidium glaucoma</i>	Cg										x
	<i>Amphileptus procerus</i>	Ap		x					x			
	<i>Paramecium bursaria</i>	Pb	x						x			x
	<i>Paramecium grosse sp</i>	Pg							x	x		x
	<i>Platyophrya sphagni</i>	Ps	x									x
	<i>Uronema sp</i>	Us										x
Rotifers	<i>Bdeloid rotifer</i>	Br										x
	<i>Colurella obtusa</i>	Co							x			x
	<i>Coquille Habrotrocha</i>	Ch							x			x
	<i>Lecane ineris</i>	Li										x
	<i>Lecane quadridentata</i>	Lq										x
	<i>Lepedalla sp</i>	Ls										x
	<i>Polyarthra sp</i>	Psp										x
	<i>Trichocerca sp</i>	Ts										x
Nematodes	<i>Nematode sp 1</i>	Ns									x	x
	<i>Nematodes sp 2</i>	Nsp										x

M = mixotroph; T = eating testate amoebae; R = eating rotifers; C = eating ciliates;

N = eating nematodes; A = algivorous; F = fungivorous; B = bacterivorous.

Supplementary Figures

Figure S.IV.1: Number of links within SF-C, SF- L_{SD} (left), SD-C and SD- L_{SF} (right) networks in function of the threshold chosen to remove weaker links. We kept a threshold of 0.2, consisting in removing 20% of the weaker links.

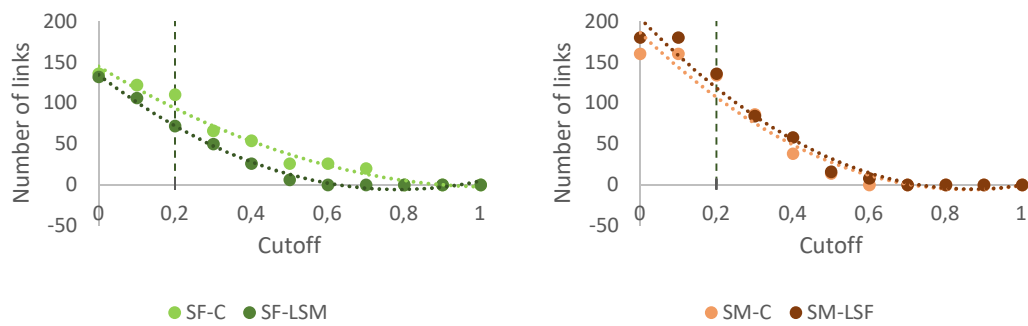
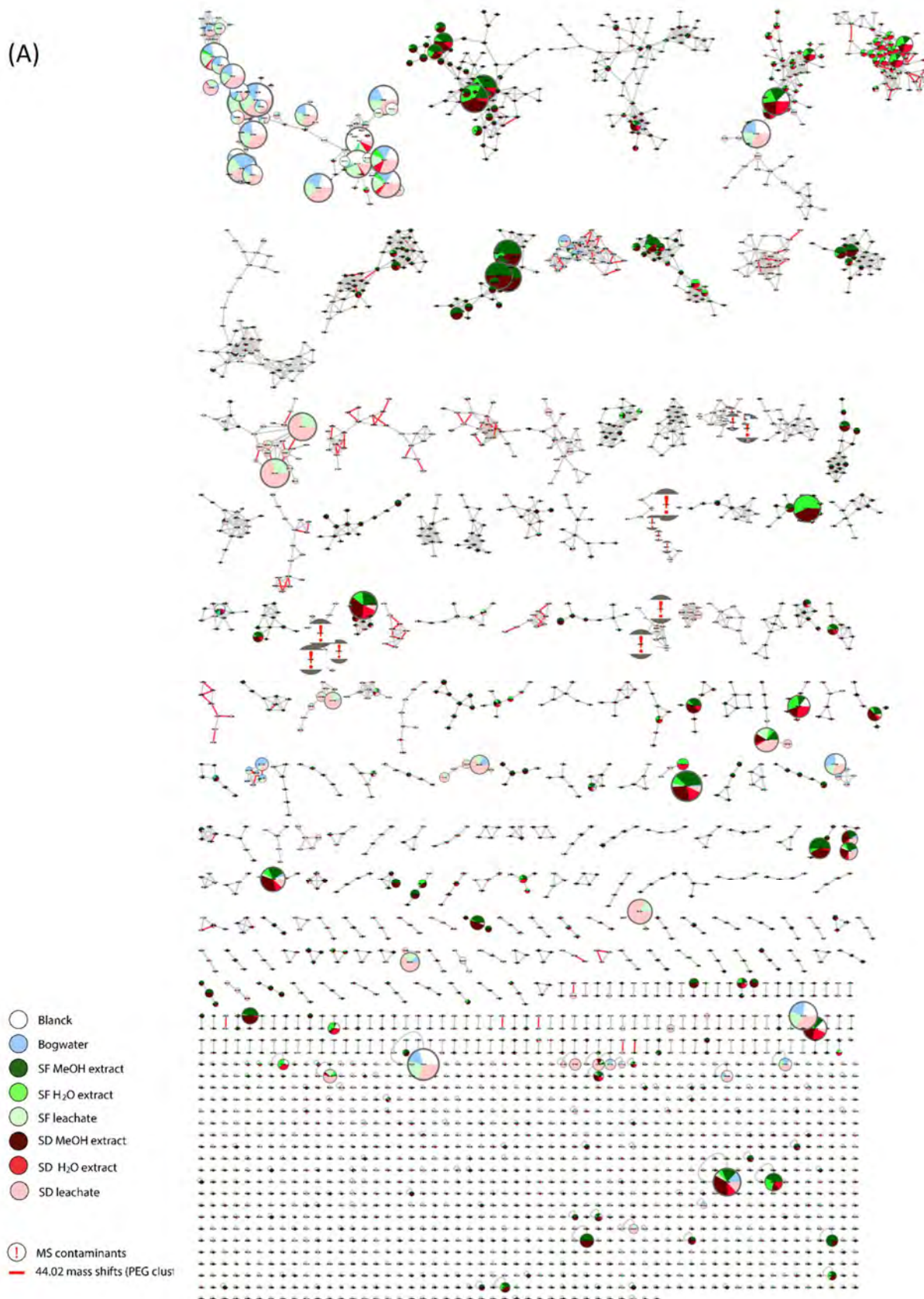


Figure S.IV.3: Molecular network of the metabolites found in *Sphagnum* leachates, methanolic and water extracts, and bog water, with positive (A) and negative (B) analysis.



(B)

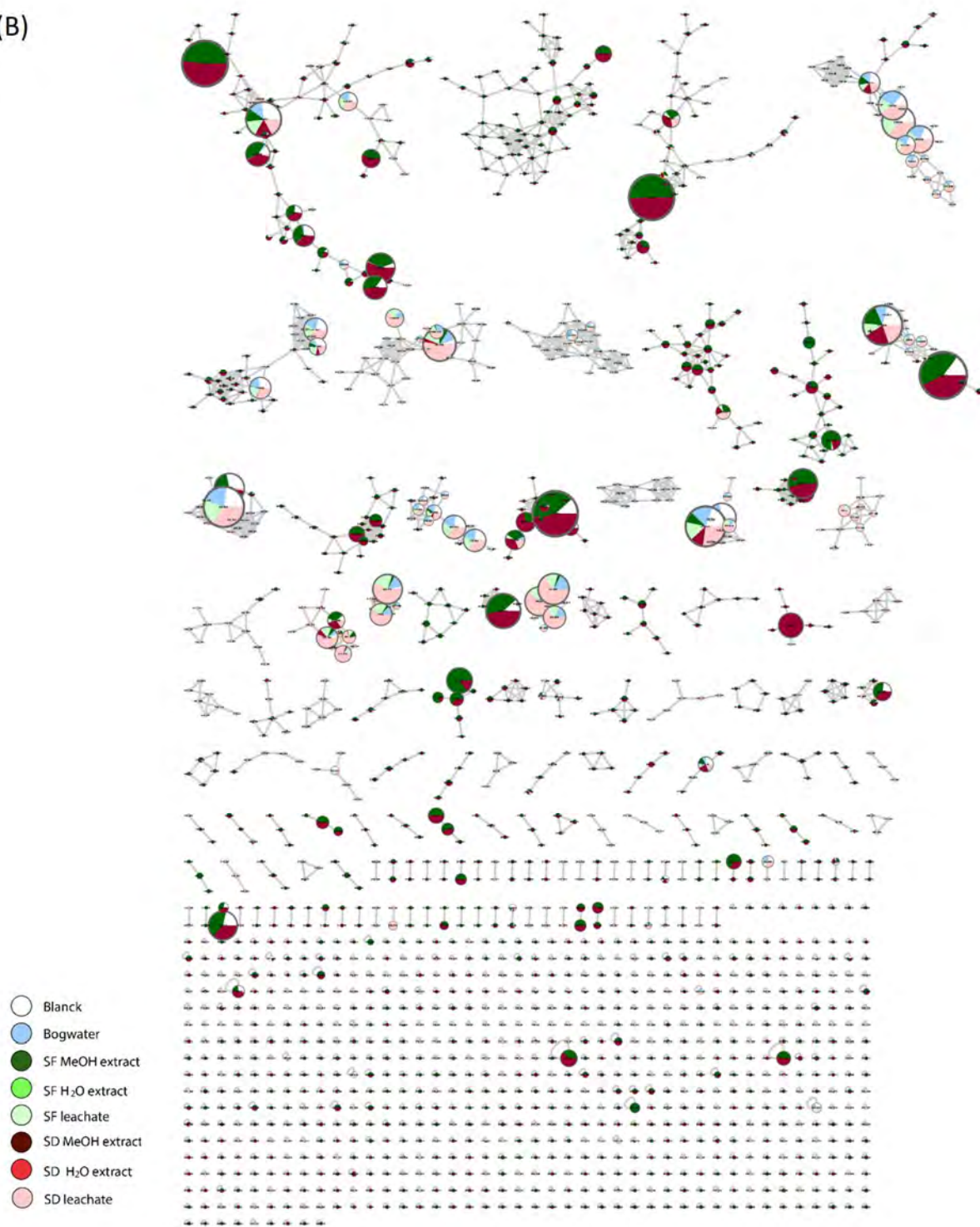


Figure S.IV.4: Respiration of *S. fallax* and *S. divinum* microbiome at the end of the experiment. The microbiomes from each experimental treatment (SF-C, SF-L_{SD} for *S. fallax* and SD-C, SD-L_{SF} for *S. divinum*) were incubated with water. Error bars refer to standard errors. No significant differences were found among treatments (ANOVA).

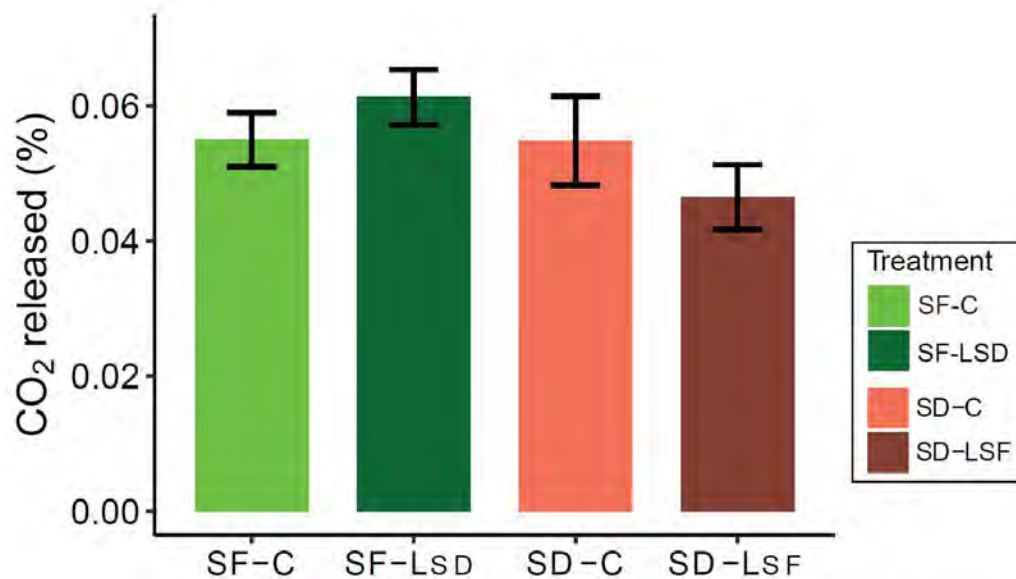


Figure S.IV.5: Overall enzyme activity (FDA) in *S. fallax* and *S. divinum* microcosms at the end of the experiment. Error bars refer to standard errors. No significant differences were found among treatments (ANOVA).

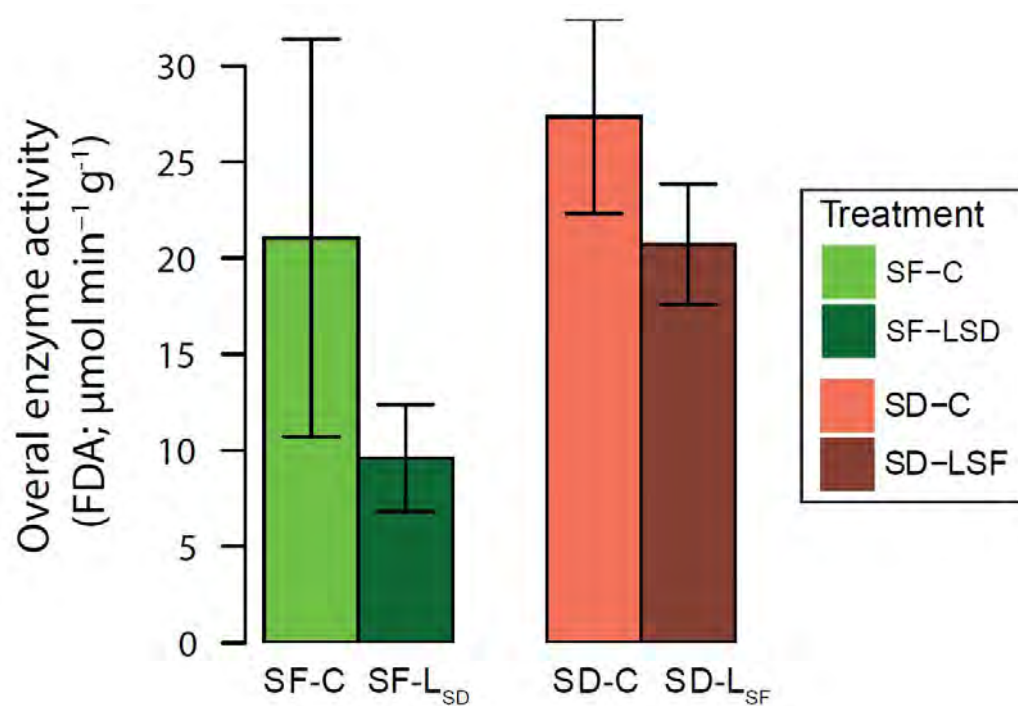


Figure S.IV.6: Principal component analysis of the different species of secondary consumers found in *S. fallax* (green circles) and *S. divinum* (red circles) microcosms after the three-week leachate experiment.

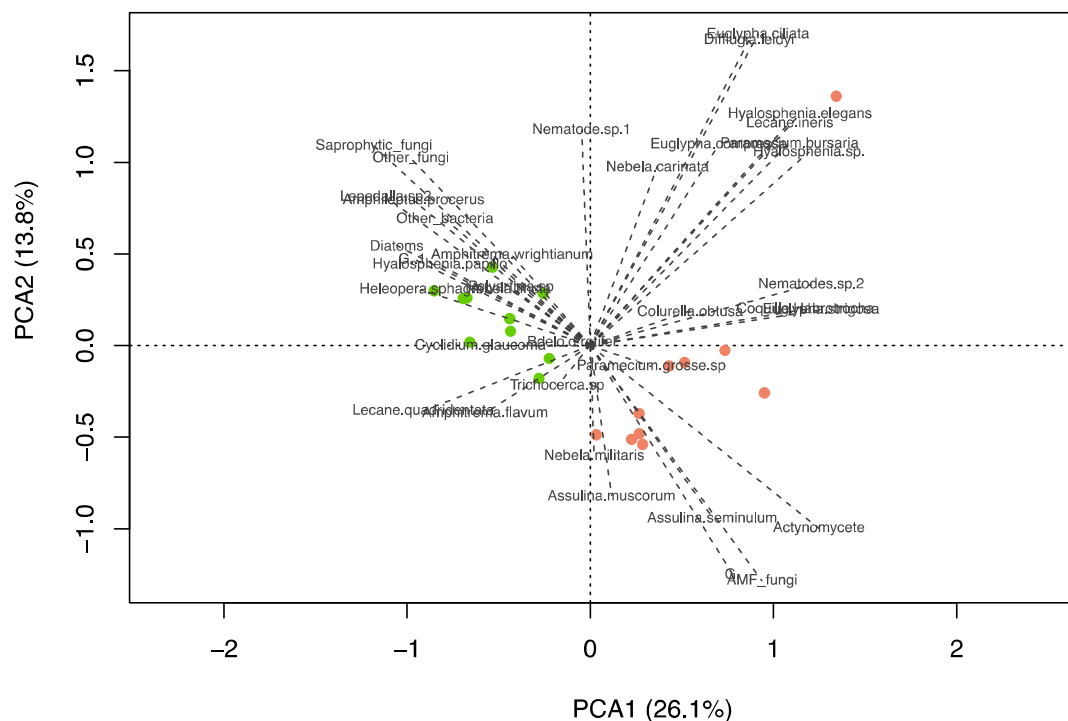


Figure S.IV.7: Differences between modelled trophic networks and leachate addition networks in *S. fallax* (green circles) and *S. divinum* (red squares) microbiomes, expressed as the deviation of the standardized effect sizes (SES) from 0. Modelled networks were simulated following three scenarios (R_I , R_R , $R_{R \times I}$, see methods) and differences between networks were assessed on the five structural network indices: beta diversity with hypothetical networks, connectance (C), edge density within the network (EdgeD), core size, and edge density within the core (Phir).

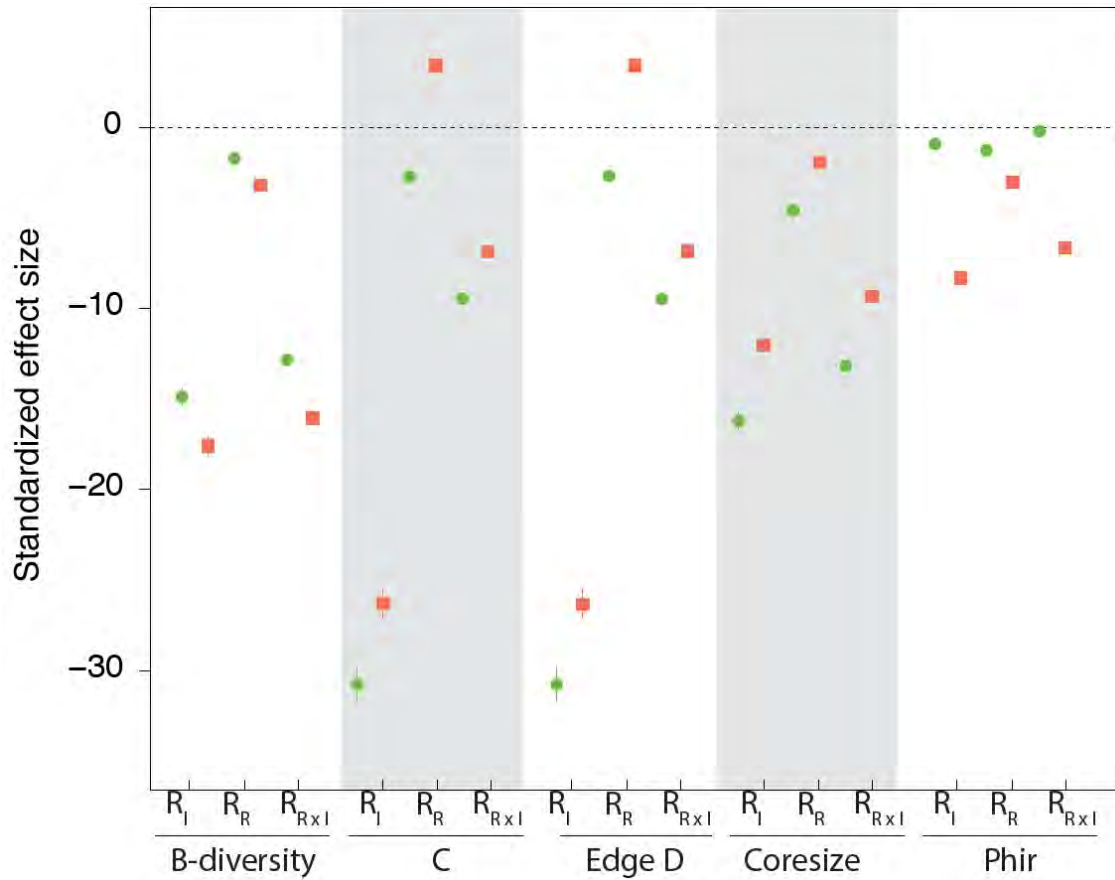
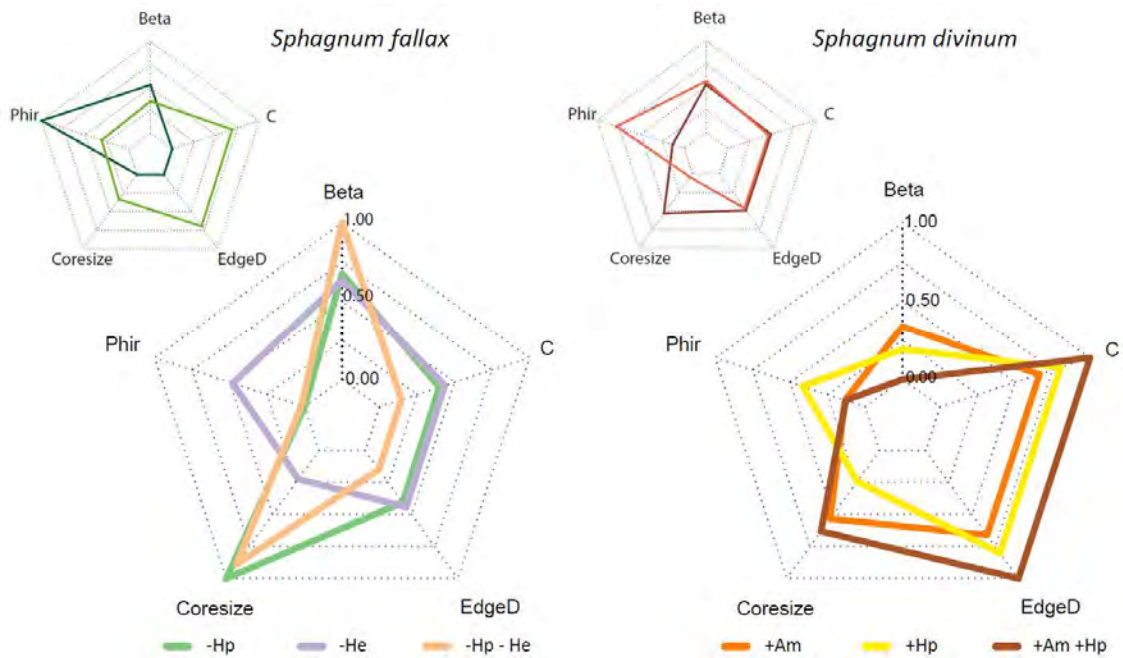
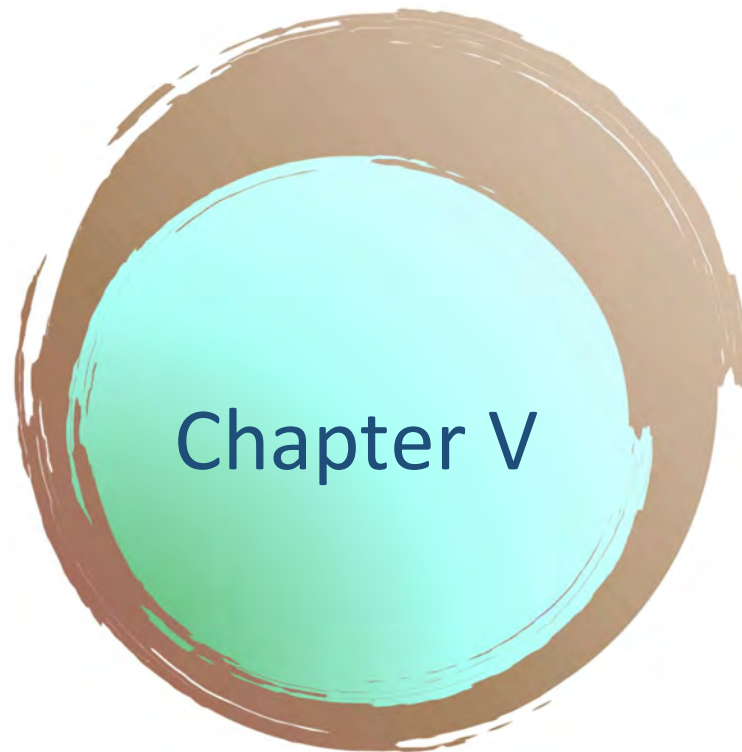


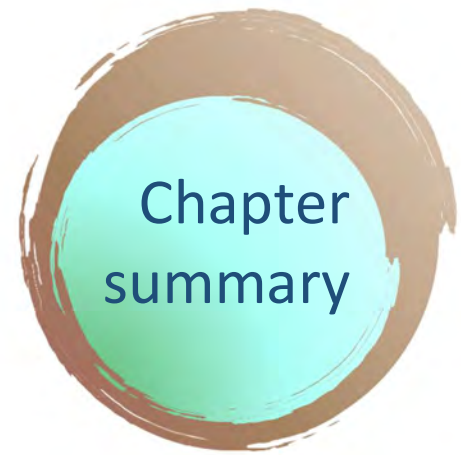
Figure S.IV.8: Structural indices in simulated networks constructed with a targeted removal or addition of key species from control networks. Simulated networks comprised the removal of *Hyalopshenia papilio* (-Hp), *Hyalosphenia elegans* (-He) and both species (-Hp -He) from SF-C network (left); and the addition of *Assulina muscorum* (+Am), *Hyalopshenia papilio* (+Hp) and both species (+Am +Hp) from SD-C network (right). Structural indices from Figure 6 were inserted on side graphs for comparison with the structural indices from networks of SF-C, SF-L_{SD}, (side graph on the left, light green and dark green respectively), SD-C and SD-L_{SF} treatments (side graph on the right, light red and dark red respectively).





Chapter V

Temperature and *Sphagnum* water content mediate microbial photosynthesis response to climate change in northern peatlands



We showed in the previous chapters that phototrophic microbes significantly contribute to the primary production of northern peatlands. These new results disrupt the current view of peatland C dynamic, in which plants are the only suppliers of organic matter to the ecosystem. It suggests that considering phototrophic microbes is necessary to obtain a more precise understanding of peatlands functioning. In particular, including phototrophic microbes in the current view could alter our predictions of peatland C dynamic under climate change. Indeed, the response of phototrophic microbes to climate change might differ from the one of plants, which could induce a reorganisation of the primary production and a change of its levels. The consequences could be dramatic for the peatland C sink, because this function relies on a fragile unbalance between C assimilation and C release.

I therefore believed crucial to explore the response of phototrophic microbes and of their photosynthetic activity to future climates. To explore this question, I simulated a climate change by performing a reciprocal peat monolith transplantation in five peatlands over a 3000 km and 8°C latitudinal gradient. As climate change effects can depend on the seasonality in northern ecosystems, I monitored the becoming of the phototrophic microbial communities over a growing season.

I found that rising temperature tended to increase microbial photosynthesis, but that the effects flipped from strongly positive (+17%) to neutral according to *Sphagnum* water content (SWC). This shows the important role of water availability in addition to temperature for phototrophic microbial activity, further evidencing the vulnerability of peatland C dynamics to changes in temperature and precipitation patterns. I identified two mechanisms through which climate change

affected microbial photosynthesis, through alterations in community structure and abundance. Overall, these results show the importance of phototrophic microbes in northern peatlands, and question our current prediction of peatland C balance and stocks under future global changes.

Temperature and *Sphagnum* water content mediate microbial photosynthesis response to climate change in northern peatlands.

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Abstract

Climate change can alter peatland carbon (C) sink by shifting the balance between C uptake (photosynthesis) and C release (decomposition). The response of northern peatland primary production to climate change has mainly been studied from *Sphagnum* and vascular plant perspectives. Yet, phototrophic microbes are abundant in these ecosystems and significantly contribute to the C uptake. The response of phototrophic microbes and their activity to future climates remains however unclear. To explore this question, we simulated a climate change by performing a reciprocal peat monolith transplantation in five peatlands over a 3000 km and 8°C latitudinal gradient. We monitored the becoming of the phototrophic microbial communities through seasonal measurements of phototrophic microbial abundance, photosynthesis and community structure. We found that, despite their structural differences, the different communities along the gradient responded similarly to climate change. Rising temperature stimulated phototrophic microbial abundance according to water availability. The effects shifted from a strong stimulation (increase of nearly +30% per degree) to an absence of effect as the *Sphagnum* water content (SWC) of peat monoliths switched from intermediate to extremely dry or wet values. Therefore, temperature effects decreased over the growing season, being maximum in spring and nearly non-existent in summer and autumn when *Sphagnum* moisture was either too dry or too moist. Microbial photosynthesis strongly correlated with phototrophic microbial abundance and followed the same evolution. Rising temperature also altered the structure of phototrophic microbial communities, benefitting few OTUs and favouring higher photosynthetic rates. These results indicate that an increase of microbial photosynthesis in peatlands is likely under future climate conditions. They further provide information on how water availability may modulate the effects of climate warming on microbial primary production. Altogether, our results bring a new piece revealing the vulnerability of peatland C dynamics to changes in temperature and precipitation patterns.

Introduction

Primary production converts inorganic carbon (C) into organic compounds and living biomass using light energy through photosynthesis. All life on Earth depends on this C fixation, which feeds higher trophic levels with C and chemical energy. The alteration of primary production by climate change is an important concern, because it could alter the functioning of numerous ecosystems. Depending on the direction of the response, it could also generate positive or negative feedbacks to climate (Matthews et al., 2005; Miller et al., 2007; Reyer et al., 2014). In terrestrial ecosystems, climate change can influence photosynthesis via thermal effects and by altering soil moisture (D'Orangeville et al., 2016; Moyes et al., 2013; Price et al., 2013). Both effects may particularly be important for northern ecosystems where an alternance exists between periods with cool temperatures that limit photosynthesis, and periods with low soil moisture that limit C uptake (Emmingham & Waring, 2011; Madani et al., 2017; K. Zhang et al., 2007). Therefore, climate change may reduce the low temperature constraints on photosynthetic kinetics, but this effect could be mitigated over the growing season by an increase of moisture constraints due to shifts in precipitation patterns (Dai, 2013).

Among terrestrial ecosystems, the response of primary production in northern peatlands could have dramatic consequences for the global climate. Peatland primary production is indeed particularly determining for the global C cycle (Harris et al., 2021): in these ecosystems, C assimilation (photosynthesis) is higher than C release (decomposition and respiration), which leads to a massive storage of soil C, more than 500 Gt over the last thousands years (Clymo et al., 1998; Yu, 2011, 2012). With climate change, a disruption in the balance between C uptake and release could happen and peatlands could contribute to the majority of warming-induced soil C loss over the next century (Crowther et al., 2016). Studying primary production in northern peatlands is therefore of high importance to understand and predict the evolution of peatland C service under climate change (e.g. Basińska et al., 2020; Binet et al., 2017; Breeuwer et al., 2008; Jassey et al., 2018; Robroek et al., 2016).

Primary production in northern peatlands is mainly performed by *Sphagnum* mosses, that can reach a cover of 80-100% (Robroek et al., 2009). It is also performed by vascular plants (Frolking et al., 2010) and more recent research further showed the significant contribution of phototrophic microbes of up to 10% on average (Hamard et al., 2021a; Wyatt et al., 2010). The majority of studies exploring the response of peatland primary production to climate change focused on *Sphagnum* (e.g. Jassey & Signarbieux, 2019; Mäkiranta et al., 2018; Zhang et al., 2020) and vascular plants only (e.g. Dieleman

et al., 2015; Gavazov et al., 2018; McPartland et al., 2020). The response of phototrophic microbes remains under-explored, and so is it for the 10% of C they fix. Yet, the strong effects of climate change on phototrophic microbes in other terrestrial ecosystems (e.g. Gray et al., 2020; Hui et al., 2018, 2021; Rindi, 2011) suggest the possibility of diverse outcomes in peatlands, with changes of phototrophic microbial communities and crucial consequences for the peatland C dynamic.

Phototrophic microbes in northern peatlands show a tremendous diversity of micro-eukaryotic and prokaryotic taxa with numerous traits combinations that represent a continuum between photoautotrophy and photoheterotrophy (Gilbert & Mitchell, 2006a; Hamard et al., 2021a, 2021b; Lara et al., 2011). The community structure of phototrophic microbes, as well as their total abundance and biomass, drives the microbial photosynthetic rates at the ecosystem level (Hamard et al., 2021a, 2021b). Further, the presence of particular taxa can strongly influence photosynthetic rates, as it is the case of mixotrophic testate amoebae due to their large body size (Jassey et al., 2015; Lara & Gomaa, 2015). Few studies showed that peatland phototrophic microbial communities are globally sensitive to climate change and especially to temperature and water availability (Basińska et al., 2020; Reczuga et al., 2018a, 2020). However, short term experiments showed that temperature did not have any effect on peatland algae unless it was combined with changes in nutrient availability (Gu & Wyatt, 2016; Wyatt et al., 2015). Therefore, the response of phototrophic microbial communities and of their diverse taxa to climate change remains elusive (e.g. Elster et al., 2012). A quantification of the response intensity is also still lacking. More importantly, the consequences for microbial photosynthetic rates have hardly been assessed. To our knowledge, it has only been showed that the loss of mixotrophic testate amoebae due to rising temperature could reduce peatland C uptake by more than 10% (Jassey et al., 2015). This gives a glimpse of the potential effect of microbial photosynthesis changes for the peatland C dynamics, and reveals the urgent need to explore further the response of peatland phototrophic microbes and their activity to climate change.

We hypothesized that microbial photosynthesis would respond to temperature and soil moisture changes in peatlands. In particular, we hypothesized that rising temperature would stimulate microbial photosynthesis at the beginning or at the end of the growing season, when low temperatures can be limiting. However, we hypothesised that this effect would become negative under low soil moisture, increasing the constraint on water availability. From the apparent diverse responses of phototrophic microbial taxa to climate change in peatlands (Basińska et al., 2020; Reczuga et al., 2018a,

2020), we further hypothesised that the responses of microbial photosynthesis to climate change would depend on the structure and composition of phototrophic microbial communities. While elevation and latitudinal gradients have long been used as ‘space-for-time’ substitutions to predict how plant and animal communities will respond to climate change (Blois et al., 2013; De Frenne et al., 2013; Nooten & Hughes, 2017), they often failed at teasing out the confounding effects of microbial community composition and abiotic factors on functional processes (Pickett, 1989; Wogan & Wang, 2018). To test our hypothesis while tackling the above-mentioned methodological issues we conducted the largest microbial community transplant experiment to date. We reciprocally transplanted five peat monoliths into five sites across Europe (in total, n = 125) that differ in temperature and precipitation (Fig. V.1A). Our experimental design thus allowed us to quantify the photosynthetic response of five microbial communities to a range of temperature and soil moisture changes that we followed over a growing season.

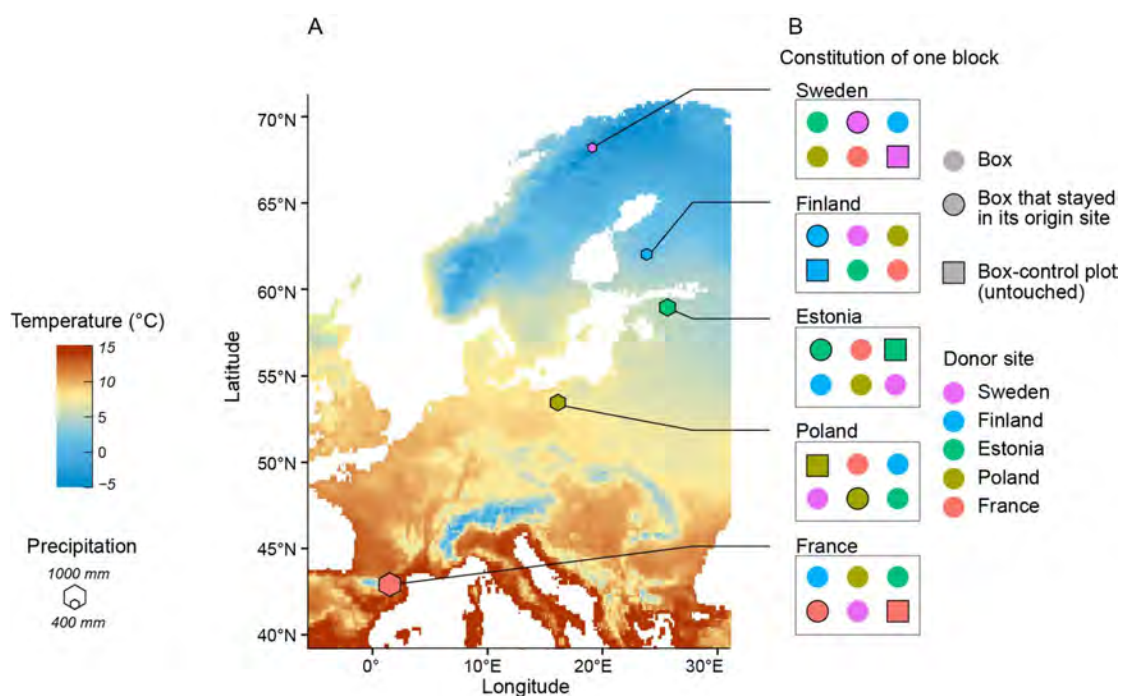


Figure V.1: (A) Location of the sites used for the transplantation, and their annual mean temperature (color) and annual precipitation (dot size) (data extracted from WorldClim, on the period 2000-2018). (B) Schematic constitution of the blocks constituting the different sites.

Experimental procedures

Sites description, reciprocal transplantation and sampling

The five European peatland sites (located in France, Poland, Estonia, Finland and Sweden) were chosen to represent a wide temperature and precipitation range within northern peatland distribution (Fig. V.1A, Fig. V.2A, 2B). A complementary description of the sites is given in the Supplementary Table S.V.1, while a full description can be found in Hamard et al. (2021). On July 2018, we identified five blocks of homogeneous *Sphagnum* carpets (i.e., 5 replicates) in each site. In each block, we cut five *Sphagnum*-dominated peat monoliths (length: 60cm, width: 40cm, height: 30cm) that we placed in plastic boxes. Plastic boxes were sterilised beforehand, and we made holes sealed with 0.45 μm pore nylon mesh in their bottom to allow for transport of water and nutrient while preventing immigration of microbial cells from the bare peat (Allison et al., 2013). In each block, one peat monolith returned in its original place, but in a plastic box, while the four other peat monoliths were transplanted in each of the four other sites in the same block number. The transplantation was therefore reciprocal (Fig. V.1B). In total, there were 25 treatments (five donor sites by five receptor sites) and five replicates, corresponding to 125 boxes. On top of this reciprocal transplantation, we set up in each block one untouched additional plot (length: 60cm, width: 40cm) to control for the box effect (Fig. V.1.B).

In each site, air and soil temperature, photosynthetic active radiation (PAR), and precipitation were recorded continuously every hour using probes linked to a data-logger (METER®). We also monitored soil temperature in the boxes of the block 1 of each site. We calculated average temperature, cumulated precipitation and PAR over a period of 15 days before sampling (Supplementary table V.S.1). We selected 15 days because this period allows the microbiome to have turned over multiple times and therefore drives the community structure at the time of sampling (Schmidt et al., 2007; Schönborn, 1965). We further monitored some edaphic parameters in each box including the dissolved organic C (DOC) and the total nitrogen (TN) measured from *Sphagnum* water extractable organic matter (WEOM), and the *Sphagnum* water content (SWC) of the *Sphagnum* mats, following Hamard et al. (2021a). Finally, we measured pH in the pore water of the boxes.

We collected samples to monitor the abundance and the potential photosynthetic rate of phototrophic microbes at the surface (0-3 cm) of *Sphagnum* in spring (end of April/beginning of May), summer (July) and autumn (October) 2019. Some data were missing in Poland because of the

destruction of few boxes by wild animals, and in autumn in Sweden because of frost precluding any sampling. We measured the diversity of phototrophs only in summer using metabarcoding.

Abundance and photosynthetic rates of phototrophic microbes

To quantify the abundance of phototrophs, five shoots of *Sphagnum* (0-3 cm) were sampled from each box, and preserved in the field in 20 ml formaldehyde (4% final concentration). In the laboratory, we extracted microorganisms from *Sphagnum* tissues following the method of Jassey et al. (2011). Then, we quantified the absolute abundance of phototrophic microbes from microbial extracts by means of flow cytometry following Hamard et al. (2021a). Abundance data were expressed as the number of individuals per g of *Sphagnum* dry weight (DW).

To estimate microbial photosynthesis, we first measured both photosynthesis efficiency and chlorophyll *a* (chl *a*) content of phototrophic microbial communities. Five shoots of *Sphagnum* (0-3 cm) per box were sampled and immersed in 20 ml of demineralized water. Then, we extracted microbial communities in the field by shaking the tubes by hand for 2 min and filtered the microbial extract on nylon filter (100 μm) and a GF/F Whatman® filter (0.7 μm) to recover all phototrophic microbes, as explained in Hamard et al. (2021a). Finally, we measured microbial photosynthesis efficiency using light curves of the quantum yield of photosystem II (Φ_{PSII}) with a Phyto-PAM (Walz, Effeltrich, Germany). Briefly, the filters containing the microbial communities were dark adapted for 30 min in the field, and then exposed to increasing light from 0 to 400 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, while proceeding to the measurements. Following measurements, the filters containing microbes were immediately frozen for further pigments analyses. Back to the laboratory, the microbial pigments were recovered from the filters with a methanolic extraction to measure the chl *a* content of phototrophic microbial communities, as explained in Hamard et al., (2021a). Extracted pigments were quantified through high pressure liquid chromatography (HPLC), following Barlow et al., (1997). Chlorophyll *a* was expressed in ng per g of *Sphagnum* DW.

Chlorophyll *a* content provides an estimate of the photosynthetic machinery of the microbial community, while Φ_{PSII} gives its efficiency to convert light energy in electron flux at a given light intensity. A combination of both chl *a* content and Φ_{PSI} gives an estimation of the effective electron transport rate (ETR) of the microbial community. We calculated light curves of ETR using light curves of Φ_{PSI} as in Hamard et al. (2021a), following Wilken *et al.* (2013) and Falkowski and Raven (2013). From

these curves, we determined the maximum ETR (ETR_{max}), given for a specific light intensity, using the fitPGH function from the Phytotools R package (Silsbe & Malkin, 2015). Finally, we assumed a maximum fixation of 0.25 mol CO₂ per mol of electron (Wilken et al., 2013), and we calculated a C fixation (C_{fixed}) based on the ETR_{max} :

$$C_{fixed} = 0.25 \times ETR_{max}$$

The C fixation is therefore an estimation of maximum or potential photosynthesis given at light optimum. We call it thereafter microbial photosynthesis. It is expressed in mol CO₂.s⁻¹.g⁻¹ *Sphagnum* DW and we converted it into g CO₂.s⁻¹.g⁻¹ *Sphagnum* DW.

Phototrophic community structure

We sampled three *Sphagnum* shoots (0-3 cm) from each box, from which we extracted DNA using the DNeasy PowerSoil Pro Kit (Qiagen). We investigated prokaryote and micro-eukaryote communities through 16S and 18S metabarcoding, using the primers pair PCR1_515F/ PCR1_928R (Y. Wang & Qian, 2009) and TAREuk454FWD1/TAREukREV3 (Tanabe et al., 2016), respectively. The sequencing was performed by the GeT-PlaGe platform (Genotoul, Toulouse, France) with Illumina MiSeq technology and using the V3 chemistry (2x250 bp). The *Sphagnum* sampling, DNA extraction, and polymerase chain reactions (PCR) protocols were performed as described in Hamard et al. (2021a).

Paired-end fastq sequences were analysed using the FROGS pipeline (Find Rapidly Operational Taxonomic Units Galaxy Solution) on the Galaxy platform (Escudié et al., 2018). Paired-end reads were merged using VSEARCH (10% of mismatch; Rognes *et al.*, 2016). Sequences were filtered based on their length and primer mismatches were removed. Sequences were then dereplicated and clustered into operational taxonomic units (OTUs) using the SWARM clustering method with an aggregation distance of three (Mahé et al., 2014). Chimera were identified and removed using VSEARCH. Filters were then applied to remove singletons. The OTUs were assigned at different taxonomic levels using Blast. We used the Silva 138 database (Quast et al., 2013) for prokaryotic assignment and the PR² v4.12.0 database (Guillou et al., 2013) for eukaryotic assignment. After these steps, the 150 samples (125 transplantation samples and 25 box-controls samples) contained 3 157 878 curated prokaryote reads belonging to 3 323 OTUs, and 3 134 161 curated eukaryote reads belonging to 2 126 OTUs.

Further analyses were conducted with the Phyloseq R package (McMurdie & Holmes, 2013). In particular, prokaryotic and micro-eukaryotic sequences were retrieved by removing chloroplast,

mitochondria and plant associated sequences. Microbial phototrophic OTUs were then identified at the genus level. We considered that an OTU was phototrophic if its affiliated genus was referred as photoautotrophic, photoheterotrophic or mixotrophic in the literature (e.g. Jia et al., 2015; Kulichevskaya et al., 2014; Li et al., 1999; Okamura et al., 2009; Yurkov et al., 1993). For the 150 samples, we obtained 98 773 prokaryotic sequences belonging to 113 phototrophic OTUs, and 142 815 micro-eukaryotic sequences belonging to 560 phototrophic OTUs. To alleviate sequencing artefact, we then performed a rarefaction for each sample. We obtained 9 072 prokaryotic sequences (63 per sample) belonging to 85 phototrophic OTUs, and 14 308 micro-eukaryotic sequences (98 per sample) belonging to 411 phototrophic OTUs. Finally, we checked the profiles of the rarefaction curves. They revealed a near saturation at the treatment level (Supplementary Fig. S.V.1), indicating that the majority of the diversity was captured in each treatment.

Numerical analyses

We first tested the box effect on the different environmental and function variables. We compared the values in the box-control plots (plots untouched) with the ones in the boxes that remained in their original sites. We showed that the boxes slightly altered some environmental variables in some sites, such as soil temperature, DOC in WEOM or SWC, but most importantly, they did not alter neither the community structure of phototrophic microbes, nor their photosynthetic rates (Supplementary Table S.V.2).

We then focused on the boxes only. We tested the effects of site (donor site), transplantation (receptor site), and season, including their interactions, on phototrophic features (microbial photosynthesis and abundance) using linear mixed effects (LME) models with the block nested in the donor site and the season as a random effect. Microbial photosynthesis was log-transformed to improve normality. We used similar models to test the effect of air temperature and SWC percentiles (fixed effects) and their interaction on microbial photosynthesis. We also tested the effects of phototrophic abundance on microbial photosynthesis using similar LME models.

Non-metric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity were used to test for structural differences in the micro-eukaryote and prokaryote phototrophic communities of the different treatments (donor and receptor sites). We used the `envfit` function of the `vegan` R package (Oksanen et al., 2013) to fit

and identify the environmental variables that were significantly associated with changes in community structure. Climatic variables were previously averaged over the growing season. Temperature effects on OTU richness, Shannon index and phylogenetic diversity were further tested through LME models, keeping the donor site as a main effect and having the block nested in the donor site as a random effect. We tested the effects of community structure change on microbial photosynthesis using similar LME models. Within the phototrophic micro-eukaryotic communities from each donor site, we further identified the OTUs whose relative abundance significantly correlated with temperature. Finally, we built a LME model to test the combined effect of community structure and phototrophic microbial abundance on microbial photosynthesis, keeping the donor site as a main effect and having the block nested in the donor site as a random effect.

Results

Environmental changes induced by the transplantation

Over the experiment, air temperature differed between sites, ranging on average from 5.7°C in Sweden to 14.2°C in Poland. Although the French site was the southernmost, it was the second colder with 9.6°C on average (Fig. V.2). In spring and autumn, a transplantation toward the southern sites generated a temperature rise (+3°C between Sweden and Poland on average), except in France where temperature were similar to Sweden. In summer, temperature was similar in the three northern sites (14°C) and a transplantation toward the two southern sites induced a 5°C rise (temperature around 19°C) (Supplementary Fig. S.V.2, Supplementary Table S.V.1).

The PAR at the ground surface strongly fluctuated from one day to another, but was similar over the experiment in the four northern sites, around 29 mol photons per square meter and per day (Fig. V.2). It was slightly lower in France (21 mol photons per square meter and per day). In spring, transplantation did not affect PAR. In summer, a transplantation to Poland increased the PAR by 40% by comparison with the other sites, while in autumn a transplantation to France strongly decreased the PAR by 90% by comparison with the other sites (Supplementary Fig. S.V.2, Supplementary Table

S.V.1). We found that air temperature and PAR were significantly correlated ($F_{(1,12)} = 16.72, P = 0.002$), and we therefore focused only on temperature effects for the subsequent analyses.

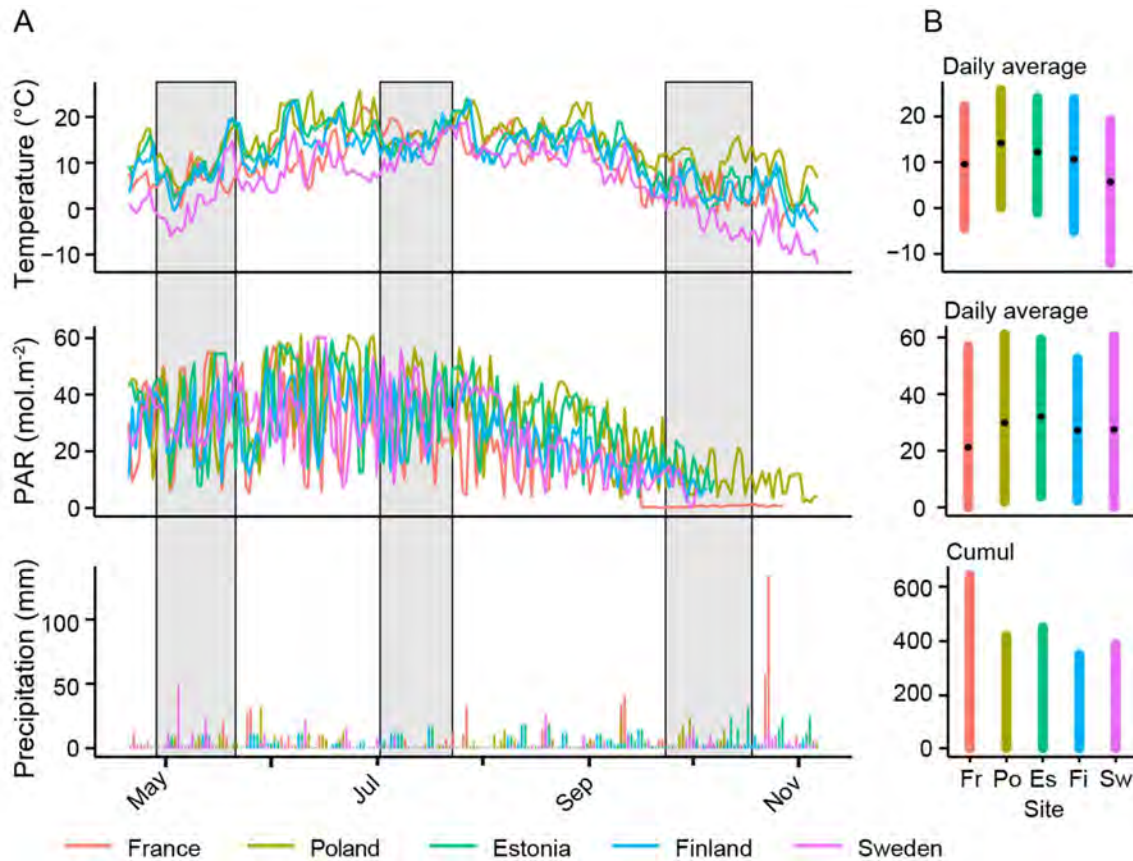


Figure V.2: Daily values of weather variables across sites and seasons (A). Daily values are calculated as the daily average (temperature) or the daily total (PAR, precipitation) of weather variables measured every each hour. Grey areas show the sampling campaigns in spring, summer and autumn. Average of daily temperature and PAR, and cumulated precipitations over the experiment (B). For temperature and PAR, bars extend from the lowest to the highest value, while the black dots show the mean.

Annual precipitations were similar in Poland, Estonia and Sweden (c.a. 450 mm), while the Finnish site was drier (357 mm) and the French site wetter (693 mm) (Fig. V.2). There was no clear latitudinal pattern of precipitation in spring: Poland was the driest site (0 mm), and Sweden the wettest (50 mm), while the other sites had intermediate values. In summer, a transplantation from the centre of the gradient toward its southern and northern ends induced a drying with a loss of nearly 40 mm of rain between Estonia (47 mm) and France (8 mm) or Sweden (5 mm). An opposite pattern was found

in autumn with higher precipitation in Sweden (42 mm) and especially in France (203 mm) compared to the other sites (around 25 mm) (Supplementary Fig. S.V.2, Supplementary Table S.V.1).

The transplantation effects on edaphic variables in boxes were independent from donor sites (Supplementary Fig. S.V.3). We did not identify any clear latitudinal trend of SWC in the transplanted boxes (Supplementary Fig. S.V.3). Similarly, we did not identify clear latitudinal trends of dissolved organic C (DOC) and total N (TN) in the *Sphagnum* WEOM, except for TN in spring, when TN increased along with a transplantation towards the north (Supplementary Fig. S.V.3).

Seasonal and transplantation-induced variations of microbial photosynthesis

The microbial photosynthesis was primarily influenced by the donor site ($F_{(4,252)} = 14.93$, $P < 0.001$) and by the season ($F_{(2,252)} = 19.91$, $P < 0.001$). Each of them explained 17% of the total variation. Regardless of the receptor site and the season, microbial photosynthesis was on average 1.8 and 1.4 times higher in boxes from France ($26 \text{ g CO}_2 \cdot \text{h}^{-1} \cdot \text{g}^{-1} \text{ DW}$) and Poland ($19 \text{ g CO}_2 \cdot \text{h}^{-1} \cdot \text{g}^{-1} \text{ DW}$) respectively, compared to boxes from other donor sites ($14 \text{ g CO}_2 \cdot \text{h}^{-1} \cdot \text{g}^{-1} \text{ DW}$ on average) (Supplementary Fig. S.V.4). In addition, microbial photosynthesis was nearly two times higher in autumn ($26 \text{ g CO}_2 \cdot \text{h}^{-1} \cdot \text{g}^{-1} \text{ DW}$) than in spring and summer ($14 \text{ g CO}_2 \cdot \text{h}^{-1} \cdot \text{g}^{-1} \text{ DW}$ on average) (Supplementary Fig. S.V.4). The transplantation strongly influenced microbial photosynthesis (receptor sites, $F_{(4,245)} = 17.98$, $P < 0.001$). The effect was almost as important as donor site and seasonal effects with 12% of the total variation explained. Moreover, we found that the strength and the direction of the transplantation effects on microbial photosynthesis differed according to the donor site ($F_{(9,224)} = 2.62$, $P = 0.008$) and seasons ($F_{(6,224)} = 5.23$, $P < 0.001$). On average, microbial photosynthesis was the lowest in boxes transplanted to Sweden ($9 \text{ g CO}_2 \cdot \text{h}^{-1} \cdot \text{g}^{-1} \text{ DW}$), and the highest in boxes transplanted to Poland ($28 \text{ g CO}_2 \cdot \text{h}^{-1} \cdot \text{g}^{-1} \text{ DW}$ on average) (Supplementary Fig. S.V.4).

We can explain the transplantation effects by changes in environmental conditions. We indeed found that on average on the three seasons, microbial photosynthesis increased along with increasing mean temperature ($F_{(1,148)} = 13.37$, $P < 0.001$) and cumulative PAR ($F_{(1,148)} = 10.86$, $P = 0.001$) (Fig. V.3A), while precipitation changes had no effect ($F_{(1,148)} = 2.41$, $P = 0.122$; Fig. V.3A). Similarly, we found that neither changes in total nitrogen ($F_{(1,234)} = 0.42$, $P = 0.519$) nor in dissolved organic carbon

($F_{(1,234)} = 0.11, P = 0.740$) affected microbial photosynthetic rates. We however found that changes in *Sphagnum* water content (SWC) had a significant effect ($F_{(1,234)} = 20.77, P < 0.001$).

The temperature effects on microbial photosynthesis were similar for all donor sites ($F_{(4,245)} = 2.01, P = 0.093$), but differed over the seasons ($F_{(2,245)} = 11.30, P < 0.001$). Rising temperature stimulated microbial photosynthesis in spring (+6.4 $\mu\text{g CO}_2\cdot\text{h}^{-1}\cdot\text{g}^{-1}\text{DW}$ per degree on average), and this stimulation disappeared over the seasons (+0.7 $\mu\text{g CO}_2\cdot\text{h}^{-1}\cdot\text{g}^{-1}\text{DW}$ per degree in summer and -0.4 $\mu\text{g CO}_2\cdot\text{h}^{-1}\cdot\text{g}^{-1}\text{DW}$ per degree in autumn) (Fig. V.3.B). Similarly, the SWC effects on microbial photosynthesis were similar for all donor sites ($F_{(4,245)} = 0.26, P = 0.906$) and differed over the seasons ($F_{(2,245)} = 3.98, P = 0.020$). The SWC had no significant effect neither in spring ($F_{(4,112)} = 0.53, P = 0.47$) nor in autumn ($F_{(4,86)} = 3.45, P = 0.07$), while in summer, moister SWC stimulated microbial photosynthesis ($F_{(4,112)} = 4.71, P = 0.03$).

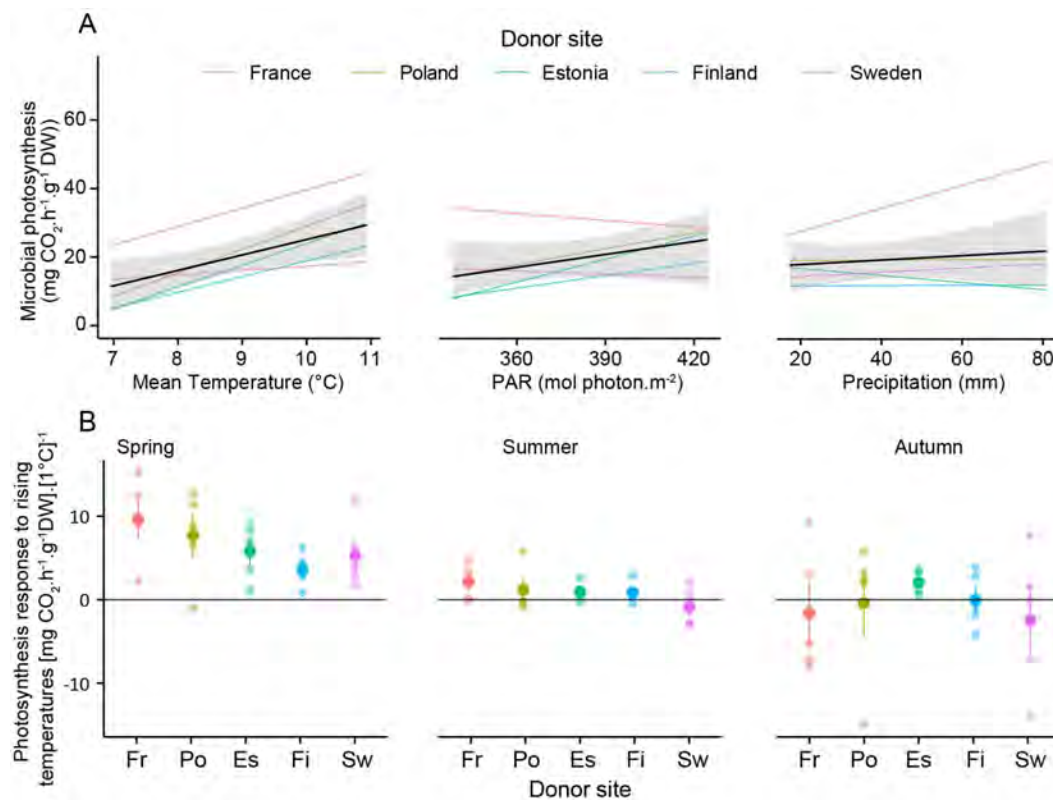


Figure V.3: Effects of temperature, PAR, and precipitation changes on the microbial photosynthesis averaged for the three seasons (A). The coloured lines show the tendencies for each donor sites, while the black line shows the average tendency (linear models). The grey area represents the standard error. Variation of microbial photosynthesis due to rising temperature. Variation rates are calculated for each season and for each donor site and are expressed as the variation of microbial photosynthesis ($\mu\text{g CO}_2\cdot\text{h}^{-1}\cdot\text{g}^{-1}\text{DW}$) per increase of 1°C. Pale dots represent the different replicates, while dark dots present the average. Error bars show the standard error.

Regardless of the season, we explored how the linkages between temperature and SWC changes affected the microbial photosynthesis. We found that rising temperatures had contrasting effects on microbial photosynthesis depending on the SWC ($F_{(1,249)} = 3.67$, $P = 0.050$). In particular, rising temperature increased microbial photosynthesis at intermediate SWC values (mostly 60th and 80th percentiles). In such conditions, an increase of 1°C led to the additional fixation of 4.2 $\mu\text{g CO}_2 \cdot \text{h}^{-1} \cdot \text{g}^{-1} \text{DW}$, stimulating microbial photosynthesis by 17% on average (Fig. V.4A). On the contrary, when SWC was too low or too high (20th and 100th percentiles), rising temperature did not have any significant effect on microbial photosynthesis (Fig. V.4A). This linkage between temperature and SWC was similar for all donor sites ($F_{(4,237)} = 0.71$, $P = 0.589$).

The SWC changes were associated with seasonal variability ($F_{(2,252)} = 93.47$, $P < 0.001$). In particular, SWC took intermediate values in spring (mainly in the 60th and 80th quantiles), while it was drier in summer (mainly in the 20th and 40th quantiles) and wetter in autumn (mainly in the 100th quantile) (Fig. V.4B).

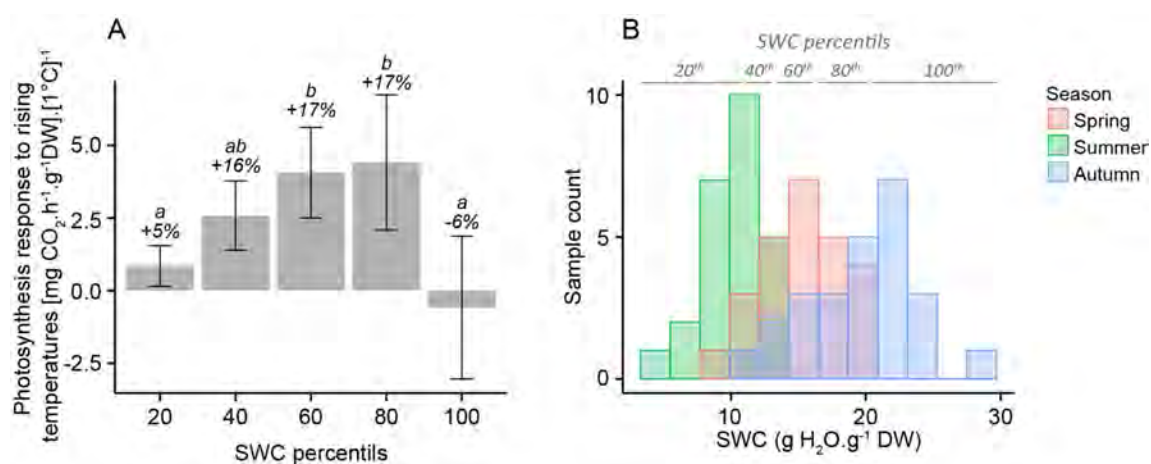


Figure V.4: Effects of rising temperatures on microbial photosynthesis according to the water content of *Sphagnum* mats (SWC) (A), and histogram of SWC across the seasons (B). In (A), error bars show the standard error, while different letters indicate significant differences ($P < 0.05$). Percentages above bars indicate the variation of microbial photosynthesis in the SWC range concerned, for a 1°C temperature increase.

Linkages between microbial photosynthesis and phototrophic microbial community structure

Regardless of the transplantation, phototrophic microbial communities showed different structure according to the donor sites ($F = 3.05$, $P < 0.001$ for micro-eukaryotes and $F = 4.73$, $P < 0.001$ for prokaryotes; Supplementary Fig. S.V.5). One year after the transplantation, both phototrophic micro-eukaryotes and prokaryotes communities still clustered by donor site (NMDS, Supplementary Fig. S.V.6). In total, the donor site explained 21% and 35% of variation in phototrophic micro-eukaryote and prokaryote composition, respectively. Phototrophic microbial communities were nevertheless sensitive to the transplantation, with distinct responses between micro-eukaryotes and prokaryotes. While the transplantation significantly altered micro-eukaryotic communities from all donor sites, it only altered the prokaryotic communities from Sweden (Permanova in Supplementary Table S.V.3). The receptor site explained 9% of variation in phototrophic micro-eukaryote composition, but it only explained 4% of variation in prokaryote composition.

Overall, shifts in phototrophic prokaryote communities did not relate to any of the measured environmental parameter (Supplementary Table S.V.4). However, shifts in phototrophic micro-eukaryote communities were related to temperature ($R^2 = 0.19$, $P < 0.001$; Supplementary Table S.V.4). Temperature effects on phototrophic micro-eukaryote communities were multiple. First, micro-eukaryotic richness correlated negatively with temperature ($F_{(1,112)} = 9.82$, $P = 0.002$), with a similar trend for all donor sites ($F_{(4,112)} = 1.57$, $P = 0.19$). On average, 4.8 OTUs were lost per increase of 1°C. On the contrary, increasing temperature did not significantly affect the Shannon index ($F_{(1,112)} = 2.35$, $P = 0.128$). Second, rising temperature provoked changes in the community structure of phototrophic micro-eukaryotes, as the second axis of an NMDS strongly correlated with temperature ($r = 0.66$, $F_{(1,114)} = 39.69$, $P < 0.001$). More precisely and in total for all communities, over the 411 phototrophic micro-eukaryote OTUs identified, 37 correlated positively with temperature, while 11 correlated negatively. These OTUs belonged to different taxa, mainly Chlorophyta, Ochrophyta and Streptophyta (Fig. V.6). The phylogenetic diversity of the phototrophic micro-eukaryote communities did not correlate with temperature changes ($F_{(1,112)} = 2.09$, $P = 0.151$).

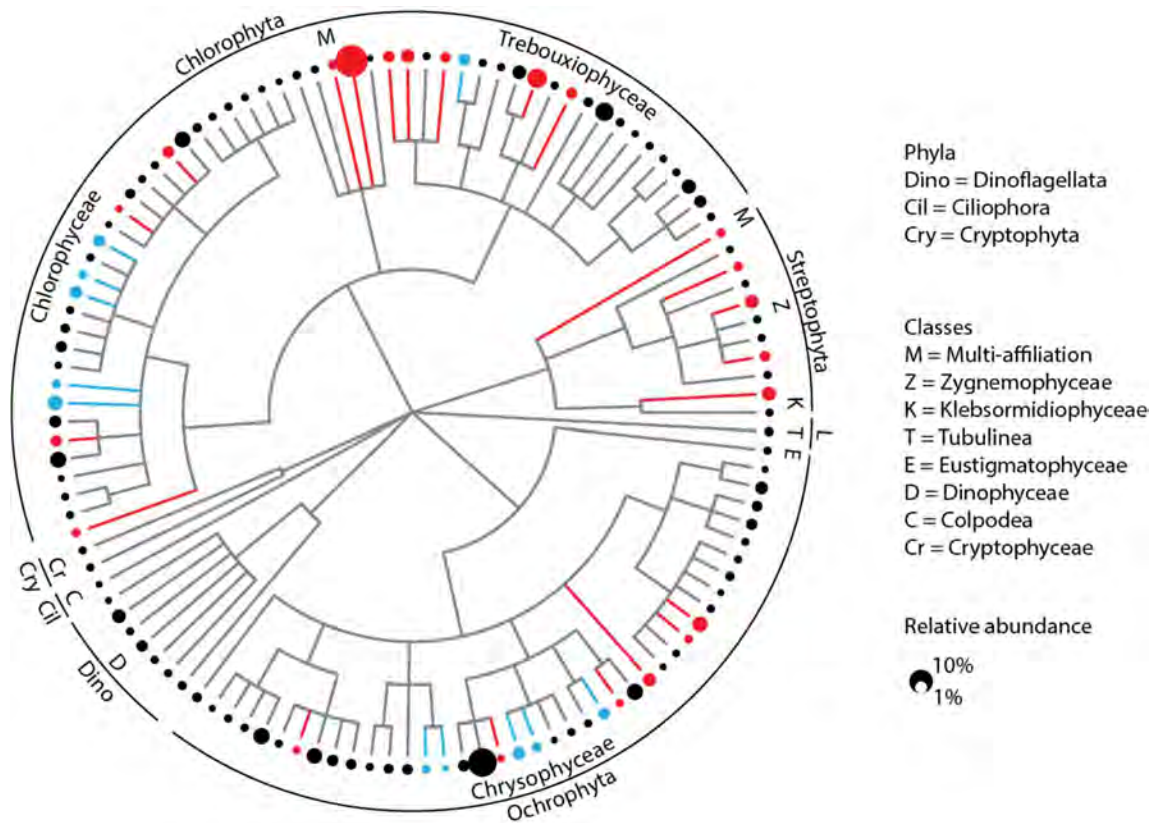


Figure V.6: Taxonomic tree of the most abundant micro-eukaryotic OTUs identified in the boxes (relative abundance > 1%). Red branches show OTUs whose relative abundance is positively and significantly correlated with temperature, while blue branches show significant negative correlation with temperature. Dot size at the end of the branches show the relative abundance of OTUs among all boxes.

The microbial photosynthesis did not correlate with the community structure of phototrophic prokaryotes (NMDS 1: $F_{(1,112)} = 0.01$, $P = 0.975$ and NMDS 2: $F_{(1,112)} = 0.52$, $P = 0.471$). It however correlated with community structure of phototrophic micro-eukaryotes, and especially with the second axis of the NMDS ($F_{(1,114)} = 7.35$, $P = 0.008$). In particular, microbial photosynthesis correlated positively with the relative abundance of the 37 OTUs responding positively to temperature ($r = 0.42$, $F_{(1,112)} = 4.92$, $P = 0.029$), and it correlated negatively with the relative abundance of the 11 OTUs responding negatively to temperature ($r = -0.51$, $F_{(1,112)} = 18.50$, $P < 0.001$). Finally, microbial photosynthesis correlated negatively with the OTU richness of phototrophic micro-eukaryotes ($r = -0.44$, $F_{(1,114)} = 3.92$, $P = 0.050$).

Linkages between microbial photosynthesis and phototrophic microbial abundance

The phototrophic microbial abundance was primarily influenced by the season (explaining 25% of variation, $F_{(2,252)} = 43.08$, $P < 0.001$), then by the transplantation (receptor site explaining 10% of variation, $F_{(4,245)} = 11.62$, $P < 0.001$), and finally by the donor site (explaining 5% of variation, $F_{(4,245)} = 5.69$, $P < 0.001$) (Supplementary Fig. S.V.7). Among the environmental changes induced by the transplantation, we found that phototrophic microbial abundance was significantly and positively correlated with DOC ($F_{(1,245)} = 11.67$, $P = 0.001$) (Supplementary Table S.V.5). Temperature had a strong positive effect but only in spring, increasing phototrophic microbial abundance by 25% per 1°C increase, on average for all donor sites (Supplementary Table S.V.5, Supplementary Fig. S.V.8). Similar to microbial photosynthesis, and regardless of the seasons, rising temperature increased phototrophic microbial abundance only when SWC took intermediate values ($F_{(4,70)} = 2.64$, $P = 0.041$, Supplementary Fig. S.V.9).

The microbial photosynthesis correlated positively with phototrophic microbial abundance ($F_{(1,237)} = 9.77$, $P = 0.002$, $r = 0.25$) for all donor sites ($F_{(1,237)} = 0.55$, $P = 0.699$) and all seasons ($F_{(1,237)} = 1.66$, $P = 0.192$). However, when phototrophic microbial abundance (averaged over the three seasons) and community structure were expressed together as explanatory variables in a LME model, community structure primarily influenced changes in the microbial photosynthesis, explaining 16% of the variation ($F_{(1,109)} = 11.13$, $P = 0.001$). Phototrophic microbial abundance explained only 2% of the variation in this model and lost its significance ($F_{(1,109)} = 3.22$, $P = 0.075$).

Discussion

By conducting a reciprocal transplantation of peat monoliths over a 3000 km and 8°C latitudinal gradient, we were able to simulate a climate change in the range of future IPCC predictions (Masson-Delmotte et al., 2021) and to tease out the different mechanisms through which climate might affect the C uptake of phototrophic microbes in peatlands. We found that the five studied communities along the gradient responded similarly to climate change but that variability in the community structure and the abundance of phototrophic communities influenced the strength of the response. Furthermore, our findings highlighted that the effects of climate warming on microbial photosynthesis flipped from positive to neutral according to *Sphagnum* water content (SWC). These results show the important role of water availability in addition to temperature for phototrophic microbial activity, further evidencing the vulnerability of peatland C dynamics to changes in temperature and precipitation patterns (Barel et al., 2021; Dinsmore et al., 2013; Jassey & Signarbieux, 2019; Nijp et al., 2014).

Despite very different phototrophic microbial communities along the gradient (Supplementary Fig. S.V.5; Hamard et al., 2021a), we observed similar responses of microbial photosynthesis to the transplantation-induced climate changes. This result refutes the hypothesis that climate change effects on microbial photosynthesis depend on the structure of microbial communities. Our results showed that increasing temperature tended to increase phototrophic microbial production in northern peatlands, with a response fluctuating between an absence of effect to a high stimulation (+17% per degree gained). The fluctuation in the response was driven by SWC. In other words, the climate change effects on microbial photosynthesis depended on an interaction between temperature and soil moisture. Similar effects have also been found for other terrestrial primary producers. In particular the effects of climate warming on boreal trees (Reich et al., 2018) or *Sphagnum* species in northern peatlands (Jassey & Signarbieux, 2019) shift from positive to negative as ecosystems transition from rainy to dry periods. As temperature and SWC experience strong natural seasonal variations, we observed that these constraints generated a seasonality in the response of microbial photosynthesis to climate change. In particular, we found that rising temperature stimulated microbial primary production mainly in spring, when SWC had medium values. In summer and in autumn, photosynthesis was constrained by dry or waterlogged conditions, obscuring the effects of temperature changes. Such

seasonal patterns of climate warming on primary production are common in northern ecosystems, where spring beneficial effects are often mitigated later in the season by precipitation patterns with adverse effects (Buermann et al., 2018). These findings further suggest that shifting precipitation patterns in the future, with more drought or less frequent but heavier rainfall (Dai et al., 2018; Fischer & Knutti, 2016; Woodward et al., 2016), could favour dry or waterlogged conditions and reduce the gains of climate warming on microbial photosynthesis in northern peatlands.

While the interdependent effects of temperature and water availability on plant primary production have mainly been studied from physiological perspectives (Jassey et al., 2011b; Reich et al., 2018), the short turnover and growth of phototrophic microbes (Schmidt et al., 2007) suggest that responses of microbial photosynthesis to climate change might also result from community changes. In particular, we identified two mechanisms, common to all sites, by which climate change affected microbial photosynthesis, namely an alteration of the community structure and an increase of phototrophic microbial abundance.

Warming has been reported to shift the composition of soil microbial communities across a wide range of ecosystems, such as forests (Frey et al., 2008), grasslands (Hayden et al., 2012), mountain soils (B. Zhang et al., 2014) or peatlands (Basińska et al., 2020; Jassey et al., 2013; Reczuga et al., 2020). Here we showed that like other microorganisms, phototrophic microbes are sensitive to warming too. We indeed found that climate warming altered the structure of phototrophic microbial communities, affecting more micro-eukaryotes than prokaryotes. This corroborates previous findings about the higher sensitivity to climate change of microorganisms with larger body size (Blankinship et al., 2011). It could suggest that anoxygenic photosynthesis, performed by Proteobacteria, was less affected by climate change than oxygenic photosynthesis. The species turnover driven by climate change affected the primary production of phototrophic microbial communities. In particular, we found that an increase in the relative abundance of some OTUs due to rising temperatures induced an increase of microbial photosynthesis. These OTUs were specific for each donor site. Therefore, it suggests that climate change affected different phototrophic microbial species in each community, but that these species had similar functions. This shows that a decoupling exists between the taxonomic identity and the functionality of microbes (Louca et al., 2018b). In our case, such decoupling is possible because microbial photosynthesis is not monophyletic (Baldauf, 2003; Cardona, 2015) and several microbial

taxa can exhibit similar photosynthetic rates. Further, despite the transplantation-driven community changes, the origin site was still a main factor explaining the community structure of phototrophic microbes. It highlights that the tangled links between *Sphagnum* species and their associated microbial communities (Bragina et al., 2012; Hamard et al., 2019; Opelt, Berg, et al., 2007; Opelt, Chobot, et al., 2007; Sytiuk et al., 2021b) resisted climate change.

The second mechanism by which climate change affected microbial photosynthesis was through a modification of phototrophic microbial abundance. When temperature rose together with intermediate values of *Sphagnum* water content (SWC), phototrophic abundance could expand at the large rate of +30% of phototrophic cells per degree. Microbial photosynthesis positively correlated with phototrophic abundance, following this trend and increasing by 17% in the same conditions. This result suggests that rising temperature could stimulate the apparition of phototrophic blooms in peatlands, especially in spring, with important consequences on microbial primary production. While we identified similar responses for all phototrophic microbial communities along the gradient, the strength of the response differed. For instance, under moist conditions, warming strongly stimulated the abundance of French microbial communities (+9.10⁶ cells per degree, +40%) but had a smaller effect on Swedish communities (+3.10⁶ cells per degree, +15%). We hypothesised that this difference could come from the different phototrophic community structures that might modulate the intensity in the response to climate change.

Overall, our results showed that over a growing season, rising temperature tended to increase phototrophic microbial production in northern peatlands, of up to 17% per degree gained. The predicted temperature increase, between 1.5 and 2.5°C over the mid-century and up to 4°C in northern latitudes (2040-2060; IPCC, 2021), provides a glimpse of the potential changes of microbial photosynthesis in peatlands. This joins the expected tendency for peatland algal production under global change (DeColibus et al., 2017; Ferguson et al., 2021; Wyatt et al., 2012). As *Sphagnum* communities seem to maintain unchanging levels of production in warmed conditions (Jassey & Signarbieux, 2019), it suggests that microbial photosynthesis could contribute more strenuously to peatland primary production, potentially dominating C fluxes during short periods or at least exceeding the contribution of 10% estimated in Hamard et al. (2021a).

The consequences of higher microbial photosynthesis might be pivotal for the peatland C dynamics, although they still remain unclear. Increased microbial photosynthesis could affect peatland microbial food webs (Ferguson et al., 2021), ultimately altering nutrient and C cycling in peatlands (Jassey et al., 2013). More importantly, increased microbial photosynthesis would shift the balance between phototrophic microbial and *Sphagnum* inputs of organic matter in peatlands. While *Sphagnum* are known to produce recalcitrant litter (Hájek et al., 2011), phototrophic microbes in peatlands release a significant part of their photosynthates as extremely labile exudates (Wyatt et al., 2012). These labile compounds stimulate heterotrophic bacteria, causing priming effects, i.e. providing additional energy to invest in the decomposition of more recalcitrant organic matter (Wyatt & Rober, 2020; Wyatt & Turetsky, 2015a). This phenomenon could be exacerbated by positive feedbacks, as increased microbial photosynthetic activity and abundance could lead to a competition with *Sphagnum*, either for nutrients or light, which could result in a reduction of photosynthetic tissues in *Sphagnum* (e.g. Limpens et al., 2003; Szymeja et al., 2010). A parallel has to be done with vascular plants: their growth and cover increase under climate change supports C uptake through photosynthesis, but also compete with *Sphagnum* and stimulates heterotrophic decomposition of peat C due to the release of labile rhizosphere exudates (Gavazov et al., 2018). Therefore, similar to vascular plants, increased microbial photosynthesis under climate warming may affect and weaken the C storing function of peatlands.

Conclusion

As a conclusion, we show in this study that the responses of microbial photosynthesis to climate change is seasonal, with the benefits of rising temperature being modulated by water availability. We identified two mechanisms driving these changes: first, a warmer climate altered the community structure of phototrophic microbes, benefitting a higher primary production, and second, rising temperature induced a higher abundance of phototrophic microbes under moist conditions. We acknowledge that we estimated the community structure of phototrophic microbes only in summer, but that the community structure might have changed throughout the growing season (Reczuga et al., 2020). Therefore, the seasonal variation of microbial photosynthesis response to warming might result from community structure changes in addition to abundance changes. These two mechanisms focus

on community alteration, but climate change might also affect the individual physiology and metabolic rates of phototrophic microbes. While a temperature alteration of the photosynthetic metabolism of phytoplankton and soil cyanobacteria has been demonstrated (M. Behrenfeld, 2011; Lange et al., 1998), further measurements would be needed to evidence this phenomenon in peatlands.

Overall, and on average on the growing season, we found that rising temperature increased microbial photosynthesis. While we did not realise a budget of this gain throughout a year, our results show that this phenomenon can be intense, reaching high levels of photosynthesis stimulation. Over a year, the photosynthetic gains might be enforced because climate warming is likely to extend the growing season northern systems, increasing the period of microbial photosynthetic activity. Although higher photosynthetic levels are thought to reduce CO₂ atmospheric levels, we suggest here that increased microbial photosynthesis could have opposite effects in northern peatlands. Phototrophic microbes could indeed destabilise peat organic matter and stimulate decomposition through the release of labile exudates. If verified, this phenomenon could bring a dramatic positive feedback to climate change. Altogether, our results highlight the urgent need to focus more intensely on the unseen phototrophic microbes, to improve our knowledge on the peatland C balance and stocks under future global changes.

Acknowledgments

This work was supported by the MIXOPEAT project (Grant No. ANR-17-CE01-0007 to VEJJ) funded by the French National Research Agency. We gladly acknowledge the support from the *Genome & Transcriptome* platform of Genopole Toulouse (Genotoul) where environmental DNA sequencing was performed, and from the Bioinformatics platform of Genotoul from which we used computing clusters to perform DNA bioinformatic analyses. We thank the *Plateforme Analyses Physico-Chimiques* from the Laboratoire Ecologie Fonctionnelle et Environnement (Toulouse) for their analyses (water extractable organic matter).

Supplementary materials

Supplementary Tables

Table S.V.1: Coordinates of the five sites and their weather conditions over the experiment and fifteen days before the seasonal samplings in spring, summer and autumn.

	France	Poland	Estonia	Finland	Sweden
Coordinates	42°41'16 N 2°14'18 E	53°48'48 N 16°35'12 E	58°52'30 N 26°15'04 E	61°50'00 N 24°11'32 E,	68°20'54 N 19°04'09 E
Weather indexes	<i>Mean Temperature: Cumulated PAR: Precipitation:</i>	<i>Mean Temperature: Cumulated PAR: Precipitation:</i>	<i>Mean Temperature: Cumulated PAR: Precipitation:</i>	<i>Mean Temperature: Cumulated PAR: Precipitation:</i>	<i>Mean Temperature: Cumulated PAR: Precipitation:</i>
Over the experiment	9.6°C 4027 mol.m ⁻² 693 mm	14.2°C 5672 mol.m ⁻² 453 mm	12.2°C 6099 mol.m ⁻² 479 mm	10.6 °C 5157 mol.m ⁻² 357 mm	5.7°C 5224 mol.m ⁻² 437 mm
Spring	5.3°C 483 mol.m ⁻² 31 mm	6.6°C 450 mol.m ⁻² 0 mm	6.7°C 422 mol.m ⁻² 40 mm	5.9°C 423 mol.m ⁻² 21 mm	4.1°C 458 mol.m ⁻² 50 mm
Summer	18.5°C 506 mol.m ⁻² 8 mm	19.3°C 744 mol.m ⁻² 23 mm	13.9°C 496 mol.m ⁻² 47 mm	14.1°C 496 mol.m ⁻² 30 mm	14.0°C 550 mol.m ⁻² 5 mm
Autumn	2.1°C 14 mol.m ⁻² 203 mm	7°C 113 mol.m ⁻² 29 mm	5.3°C 186 mol.m ⁻² 23 mm	4.6°C 140 mol.m ⁻² 20 mm	2.8°C 130 mol.m ⁻² 42 mm

Table S.V.2: Effect of the plastic boxes on several variables measured in the peat monoliths of the different sites. Shaded cells show significant effects ($P < 0.05$), while the percentage indicates the increase or the decrease of the value compared to untouched plots. WEOM: Water extractable organic matter, DOC: Dissolved organic carbon, N: nitrogen, SWC: *Sphagnum* water content.

	France	Poland	Estonia	Finland	Sweden
Soil temperature	t = 2.47, P = 0.01 (+0.1°C)	NA	t = 9.79, P < 0.001 (-0.3°C)	t = 0.47, P = 0.64	t = 3.36, P = 0.001 (+0.1°C)
DOC in WEOM	F = 2.54, P = 0.12	F = 0.35, P = 0.56	F = 5.11, P = 0.03 (+43%)	F = 7.69, P = 0.01 (+62%)	F = 0.09, P = 0.76
Total N in WEOM	F = 1.54, P = 0.22	F = 13.24, P = 0.001 (-51%)	F = 3.84, P = 0.06	F = 0.21, P = 0.65	F = 0.01, P = 0.91
pH	F = 0.26, P = 0.78	F = 0.35, P = 0.71	F = 1.47, P = 0.30	F = 8.47, P = 0.06	F = 1.35, P = 0.32
SWC	F = 96.08, P = 0.002 (+25%)	F = 6.17, P = 0.02 (-24%)	F = 3.50, P = 0.07 (-11%)	F = 7.28, P = 0.01 (+26%)	F = 4.21, P = 0.06
Algal abundance	F = 11.58, P = 0.002 (-39%)	F = 0.03, P = 0.87	F = 4.77, P = 0.04 (+31%)	F = 0.58, P = 0.45	F = 0.10, P = 0.75
Community structure of phototrophic micro-eukaryotes	F = 1.15, P = 0.31	F = 0.73, P = 0.74	F = 0.72, P = 0.75	F = 0.98, P = 0.43	F = 0.89, P = 0.59
Community structure of phototrophic prokaryotes	F = 1.41, P = 0.19	F = 0.90, P = 0.51	F = 0.36, P = 0.85	F = 1.90, P = 0.11	F = 1.30, P = 0.27
Microbial photosynthesis	F = 0.89, P = 0.36	F = 0.23, P = 0.64	F = 0.55, P = 0.59	F = 1.36, P = 0.28	F = 0.62, P = 0.44

Table S.V.3: Transplantation effect on the community structure of phototrophic micro-eukaryotes and prokaryotes originating from the different donor sites. Values show the result of PERMANOVA analyses, based on Bray-Curtis dissimilarity. Shaded cells show significant effects of the transplantation ($P < 0.05$).

		Donor site				
		France	Poland	Estonia	Finland	Sweden
		Phototrophic micro-eukaryotes				
Receptor site	Global	$R^2 = 0.22$, $P = 0.010$	$R^2 = 0.25$, $P = 0.012$	$R^2 = 0.23$, $P = 0.047$	$R^2 = 0.30$, $P = 0.001$	$R^2 = 0.28$, $P = 0.001$
	France		$F = 2.27$, $P = 0.018$	$F = 1.52$, $P = 0.114$	$F = 2.92$, $P = 0.012$	$F = 2.26$, $P = 0.049$
	Poland	$F = 1.61$, $P = 0.093$		$F = 1.23$, $P = 0.251$	$F = 1.71$, $P = 0.091$	$F = 2.61$, $P = 0.009$
	Estonia	$F = 1.46$, $P = 0.099$	$F = 1.12$, $P = 0.321$		$F = 1.72$, $P = 0.067$	$F = 1.67$, $P = 0.111$
	Finland	$F = 1.72$, $P = 0.095$	$F = 1.44$, $P = 0.134$	$F = 1.33$, $P = 0.194$		$F = 2.29$, $P = 0.016$
	Sweden	$F = 1.80$, $P = 0.015$	$F = 1.99$, $P = 0.027$	$F = 1.39$, $P = 0.183$	$F = 1.19$, $P = 0.271$	
		Phototrophic prokaryotes				
Receptor site	Global	$R^2 = 0.22$, $P = 0.101$	$R^2 = 0.24$, $P = 0.061$	$R^2 = 0.25$, $P = 0.104$	$R^2 = 0.16$, $P = 0.674$	$R^2 = 0.40$, $P < 0.001$
	France		$F = 2.22$, $P = 0.069$	$F = 0.70$, $P = 0.680$	$F = 0.92$, $P = 0.455$	$F = 3.74$, $P = 0.035$
	Poland	$F = 1.50$, $P = 0.136$		$F = 0.99$, $P = 0.379$	$F = 1.08$, $P = 0.280$	$F = 3.97$, $P = 0.016$
	Estonia	$F = 0.72$, $P = 0.805$	$F = 1.33$, $P = 0.288$		$F = 0.47$, $P = 0.845$	$F = 6.84$, $P = 0.007$
	Finland	$F = 1.95$, $P = 0.040$	$F = 1.30$, $P = 0.208$	$F = 0.90$, $P = 0.426$		$F = 5.66$, $P = 0.006$
	Sweden	$F = 1.53$, $P = 0.111$	$F = 2.06$, $P = 0.066$	$F = 1.40$, $P = 0.261$	$F = 0.61$, $P = 0.97$	

Table S.V.4: Significance between environmental parameters and transplantation-induced shifts in the community structure of phototrophic eukaryotes and prokaryotes from the different donor sites. Only P values lower than 0.1 are shown, NS for non significant is mentioned otherwise. Shaded cells show significant effects ($P < 0.05$). DOC: Dissolved organic carbon, TN: Total nitrogen, SWC: *Sphagnum* water content.

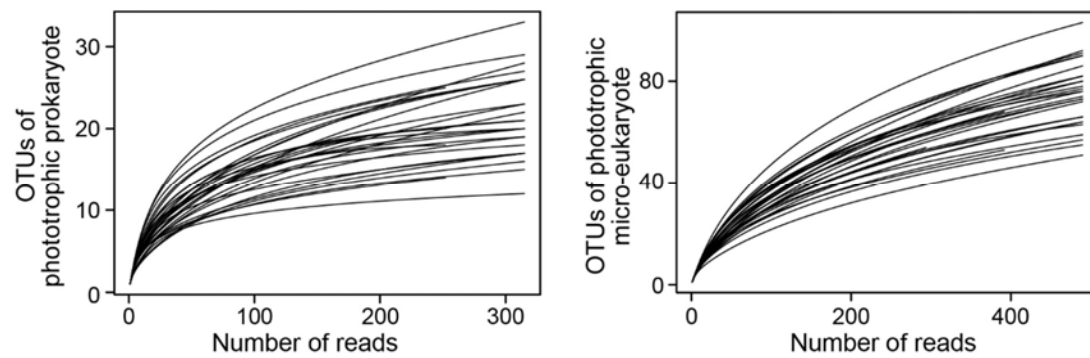
	Donor site					
	All origins	France	Poland	Estonia	Finland	Sweden
	Phototrophic micro-eukaryotes					
Temperature	R ² = 0.19 P < 0.01	R ² = 0.30 P = 0.02	R ² = 0.42 P < 0.01	R ² = 0.33 P = 0.020	R ² = 0.57 P < 0.01	R ² = 0.71 P < 0.01
Precipitation	NS	R ² = 0.27 P = 0.03	R ² = 0.21 P = 0.08	NS	R ² = 0.24 P = 0.07	NS
PAR	NS	R ² = 0.24 P = 0.05	R ² = 0.27 P = 0.04	NS	NS	NS
DOC	NS	NS	NS	NS	NS	NS
TN	NS	NS	NS	NS	NS	NS
SWC	R ² = 0.04 P = 0.07	NS	NS	R ² = 0.21 P = 0.09	R ² = 0.30 P = 0.03	NS
	Phototrophic prokaryotes					
Temperature	NS	NS	R ² = 0.27 P = 0.04	R ² = 0.25 P = 0.05	NS	NS
Precipitation	NS	R ² = 0.43 P < 0.01	NS	NS	NS	NS
PAR	NS	R ² = 0.34 P = 0.01	R ² = 0.21 P = 0.09	NS	NS	NS
DOC	NS	NS	NS	NS	NS	R ² = 0.29 P < 0.03
TN	NS	NS	NS	NS	R ² = 0.44 P < 0.01	NS
SWC	NS	NS	R ² = 0.47 P < 0.01	NS	NS	NS

Table S.V.5: Results of LME models in which microbial phototrophic abundance was explained by a combination of donor site, season, and environment variable. Donor site and season effects were significant ($F = 4.59$, $P = 0.007$; and $F = 36.96$, $P < 0.001$, respectively). The bloc nested in season and donor site was considered as a random effect.

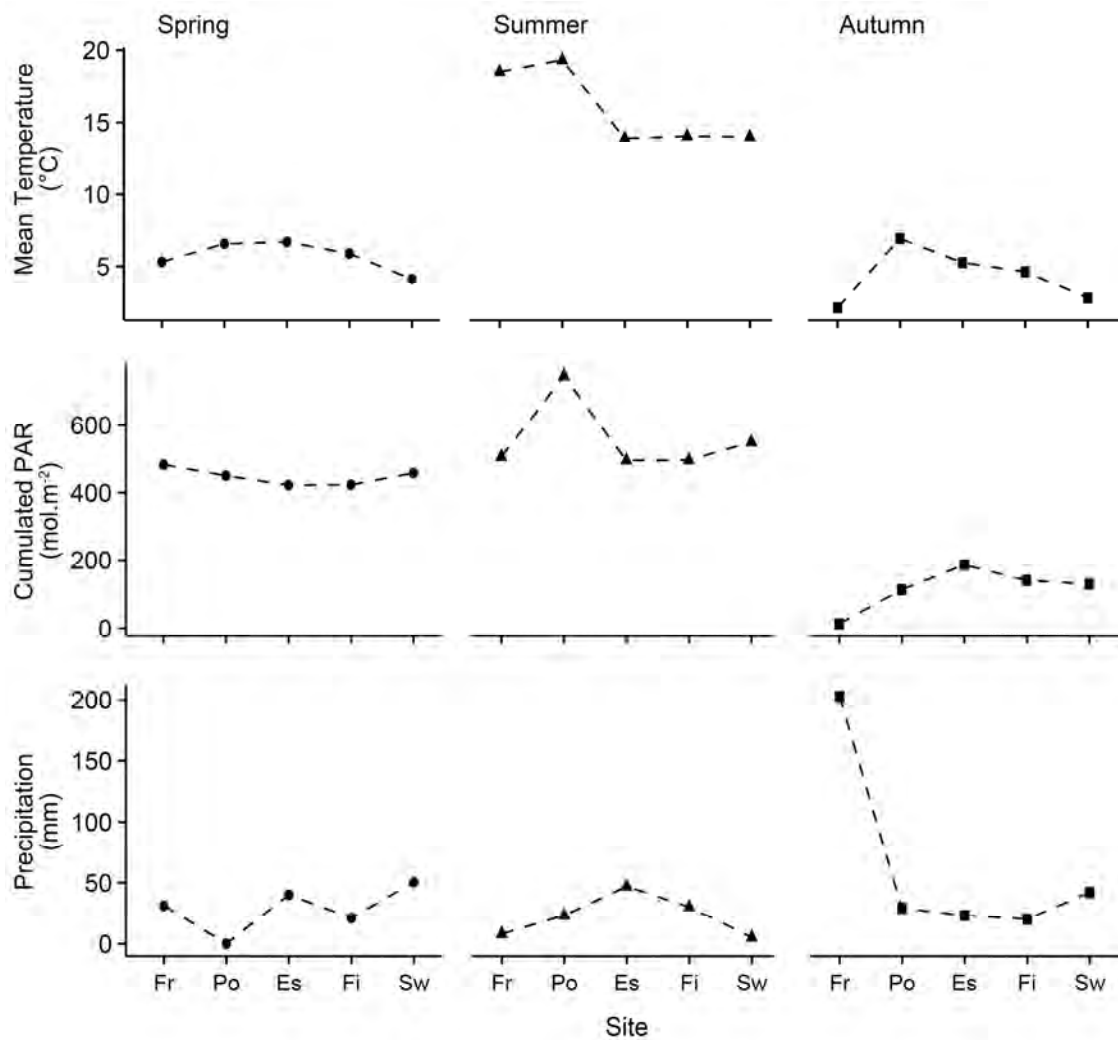
	Environmental variable	Donor site: Environmental variable	Season: Environmental variable	Donor site: Season: Environmental variable
Temperature	$F = 1.83$, $P = 0.178$	$F = 0.49$, $P = 0.687$	$F = 12.44$, $P < 0.001$	$F = 1.02$, $P = 0.413$
Precipitation	$F = 2.66$, $P = 0.105$	$F = 0.70$, $P = 0.548$	$F = 5.93$, $P = 0.003$	$F = 2.33$, $P = 0.035$
DOC	$F = 11.67$, $P = 0.001$	$F = 1.46$, $P = 0.226$	$F = 0.98$, $P = 0.374$	$F = 0.70$, $P = 0.647$
TN	$F = 2.58$, $P = 0.110$	$F = 1.02$, $P = 0.383$	$F = 2.95$, $P = 0.055$	$F = 0.28$, $P = 0.945$
SWC	$F = 0.15$, $P = 0.697$	$F = 1.14$, $P = 0.332$	$F = 0.98$, $P = 0.375$	$F = 1.03$, $P = 0.404$

Supplementary Figures

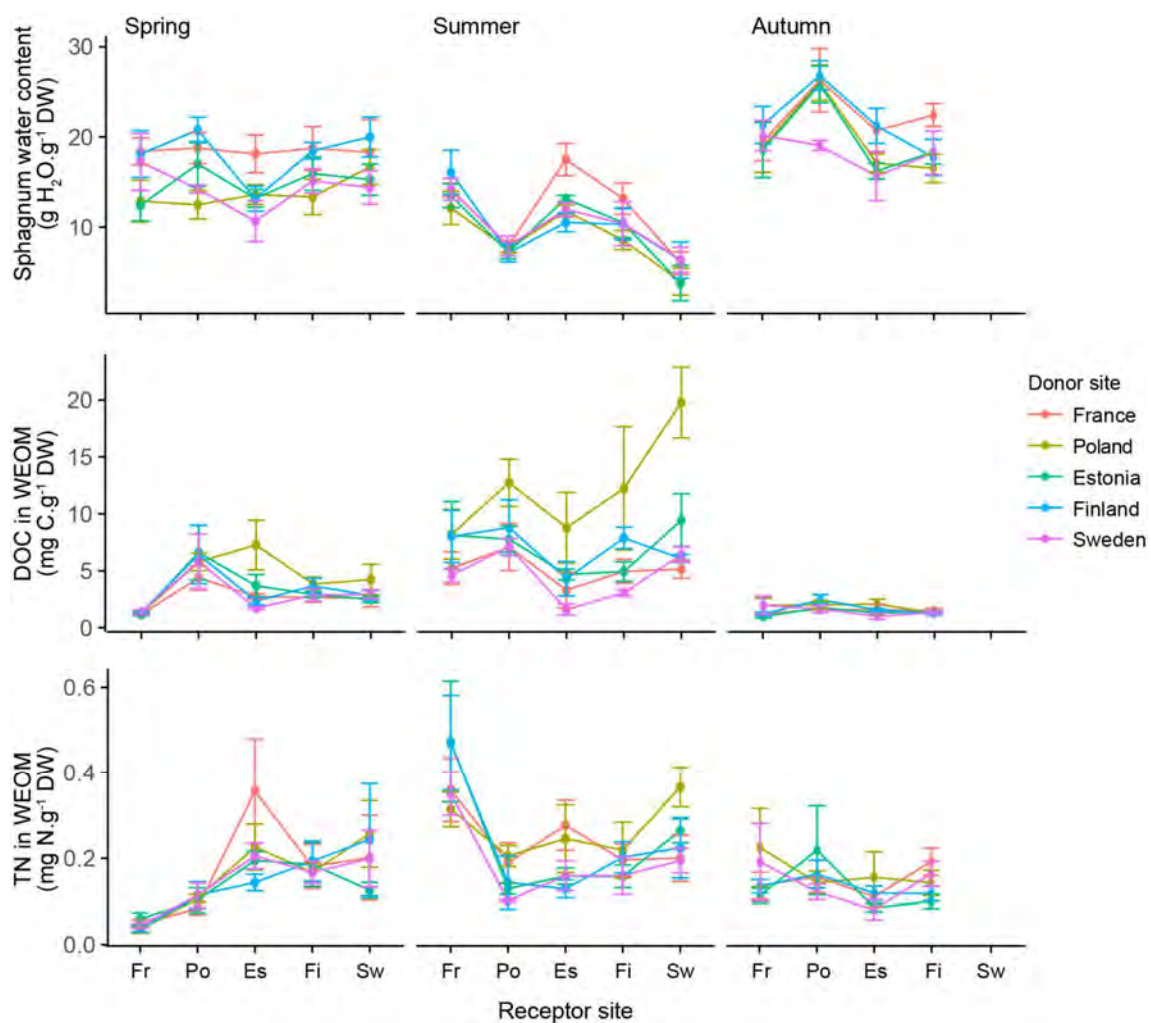
Supplementary Figure S.V.1: Rarefaction curves of phototrophic microbial sequences after normalisation of the number of sequences, for phototrophic prokaryotes (left) and phototrophic micro-eukaryotes (right). One rarefaction curve is associated to one of the 30 treatments (the 25 transplantation treatments, plus the five box-control treatments).



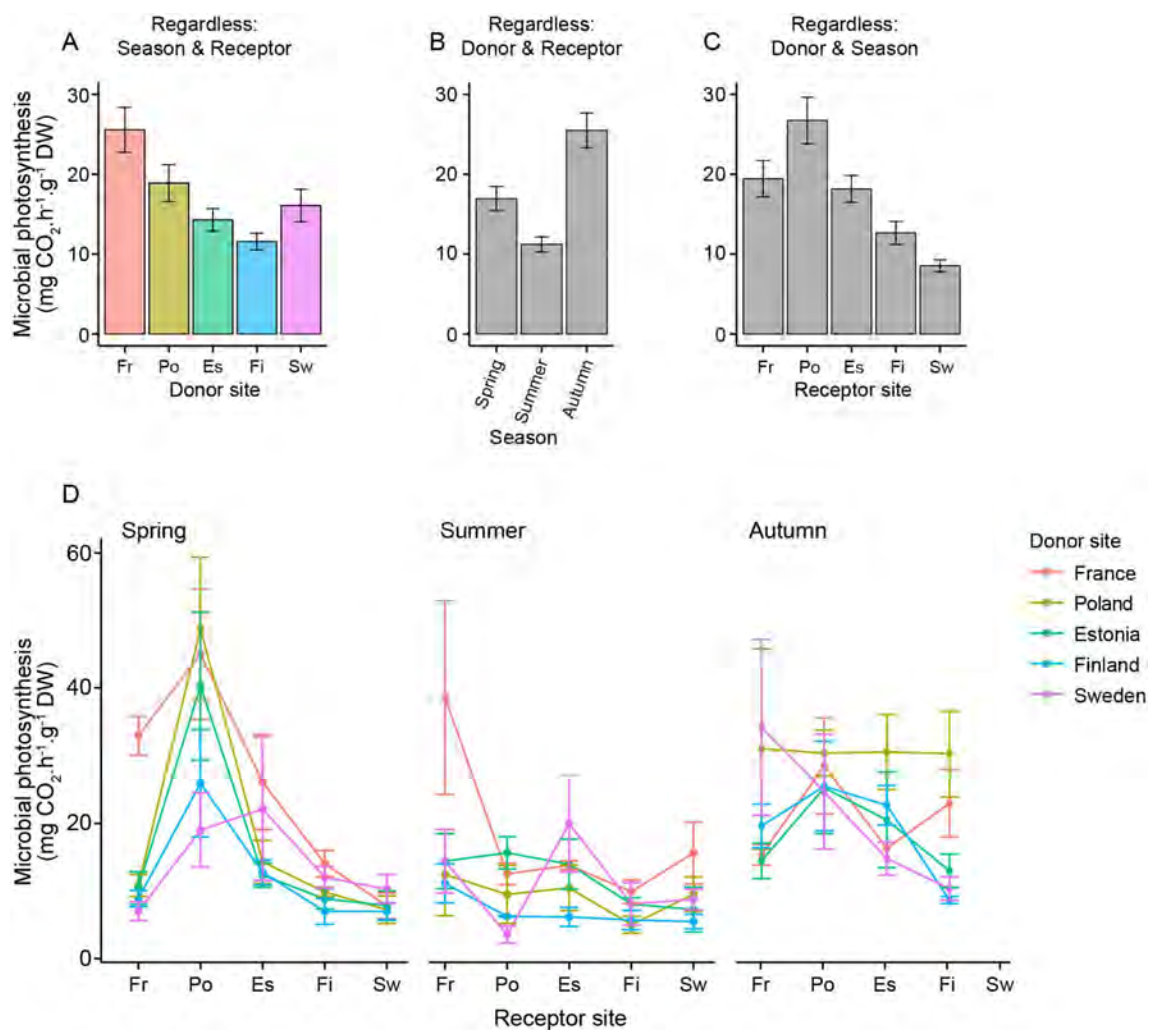
Supplementary Figure S.V.2: Weather indexes measured in each sites during the 15 days before each seasonal sampling.



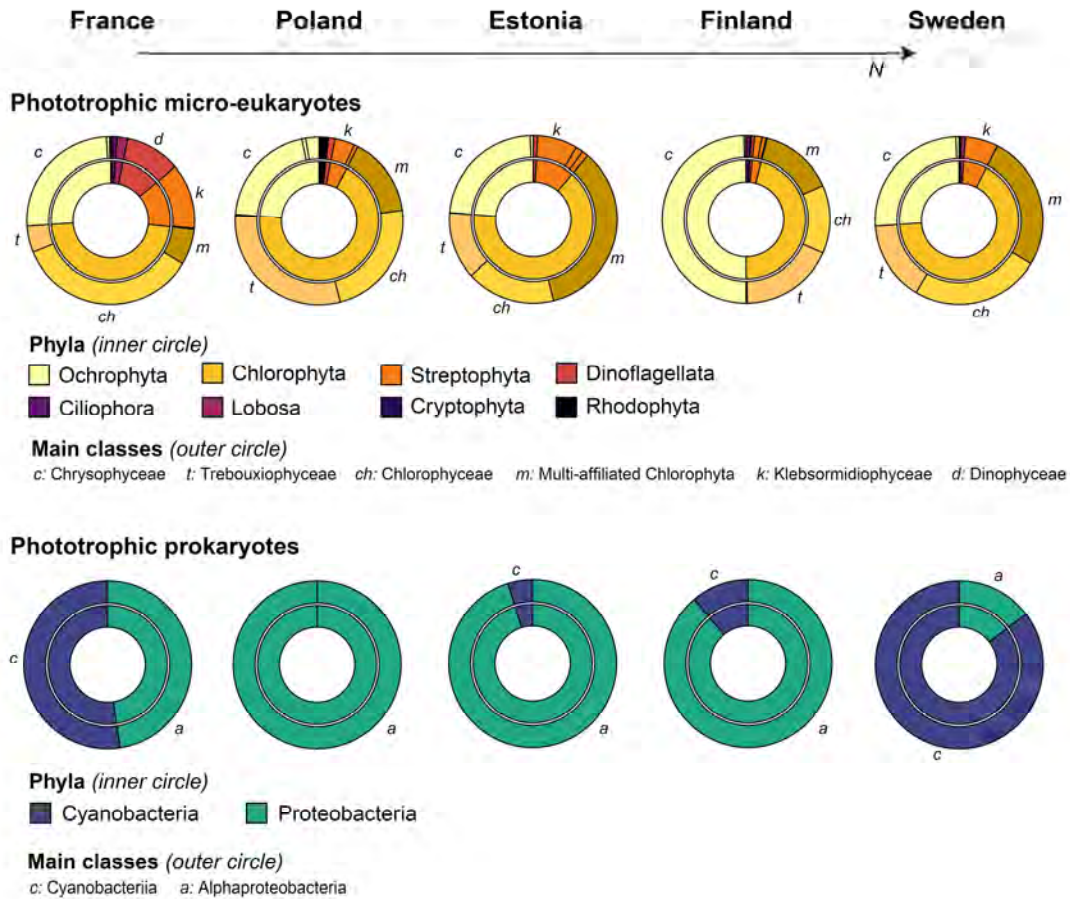
Supplementary Figure S.V.3: Edaphic parameters measured in the different boxes (colours: donor site, x-axis: receptor site) and in the different seasons. Error bars present standard error.



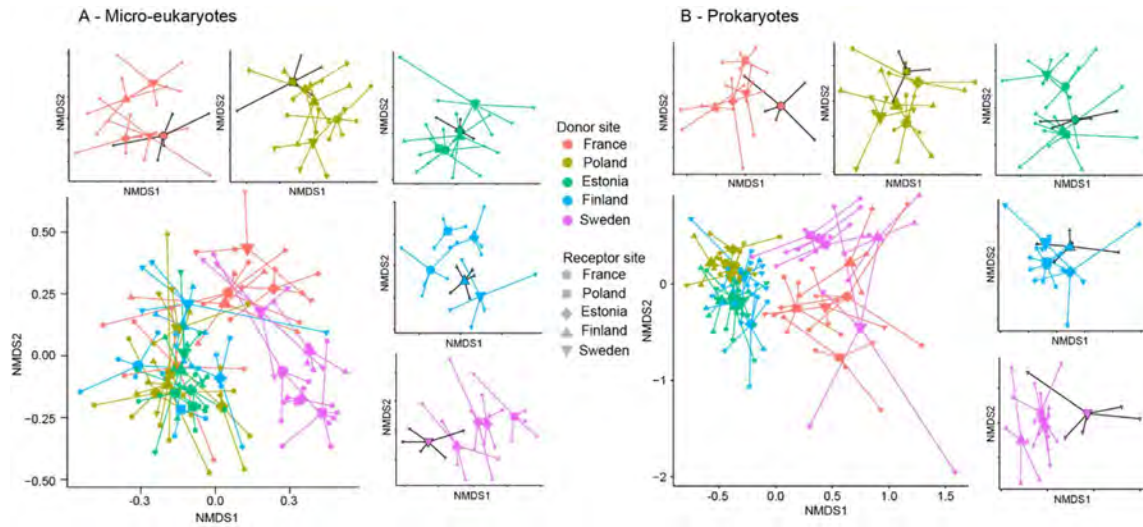
Supplementary Figure S.V.4: Microbial photosynthesis in the different boxes, averaged by donor site (A), by season (B) and by receptor site (C), and complete data set across seasons (D). In (D), colours represent donor site while x-axis represent receptor site. Error bars present standard error in all graphs.



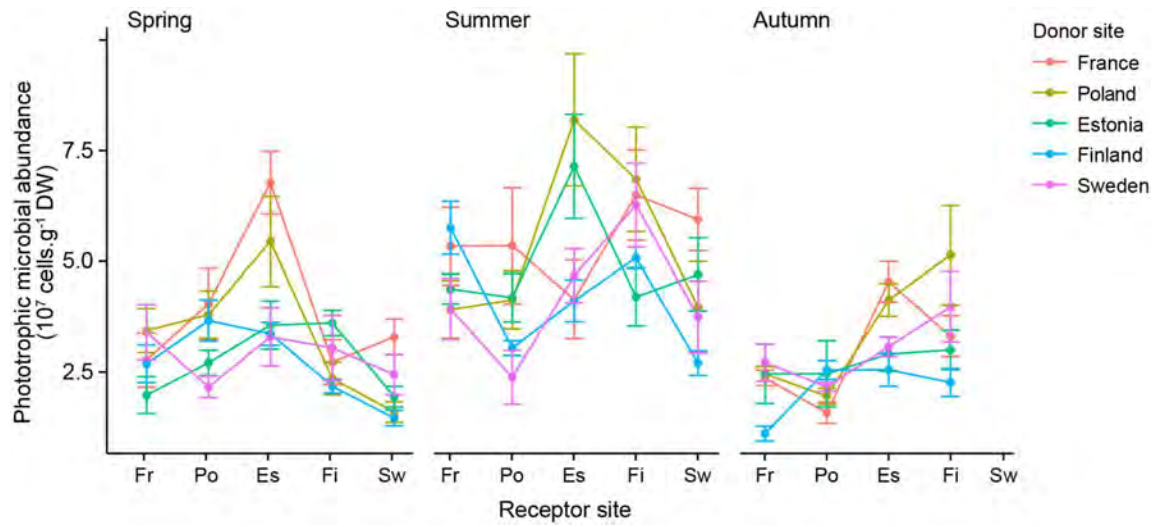
Supplementary Figure S.V.5: Community structure of phototrophic micro-eukaryotes (top) and phototrophic prokaryotes (bottom) in the different donor sites regardless transplantation. The inner and outer circles show the relative abundance of the taxa at the phylum and class level, respectively.



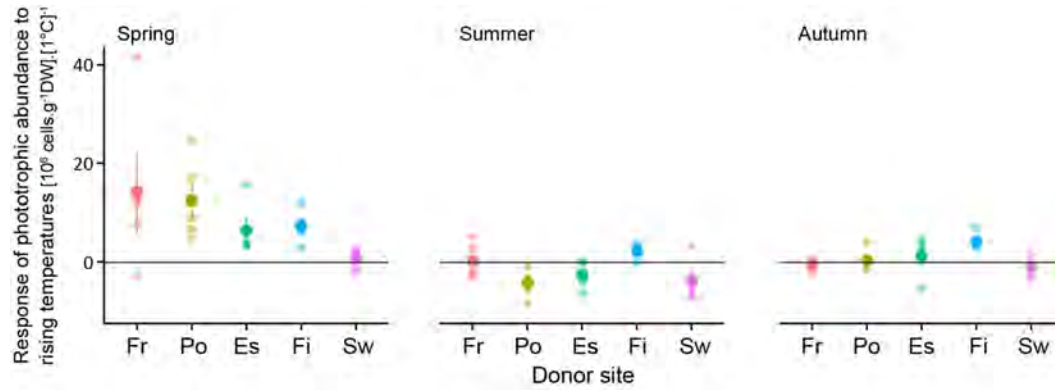
Supplementary Figure S.V.6: Non-metric multidimensional scaling (NMDS) of phototrophic micro-eukaryotes (A) and phototrophic prokaryotes (B). Dots are coloured by donor site, shaped by receptor site and they represent the community in a box. Small dots are clustered per treatment (combination of donor site and receptor site) around a larger dot, the centroid of the treatment. For both micro-eukaryotes and prokaryotes, smaller panels show an insight of the NMDS per donor site. Clusters outlined by black show the boxes that remained in their donor site.



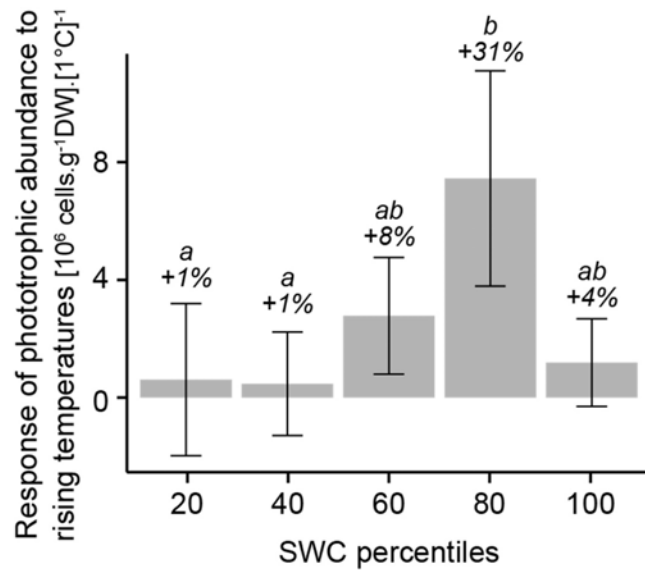
Supplementary Figure S.V.7: Phototrophic microbial abundance in the different boxes (colors: donor site, x-axis: receptor site) and in the different seasons. Error bars present standard error.



Supplementary Figure S.V.8: Variation of phototrophic microbial abundance due to rising temperature. Variation rates are calculated for each season and for each donor site and are expressed as the variation of phototrophic microbial abundance (10^6 cells.g⁻¹DW) per increase of 1°C. Pale dots represent the different replicates, while dark dots present the average. Error bars show the standard error.



Supplementary Figure S.V.9: Effects of rising temperatures on phototrophic microbial abundance according to the water content of *Sphagnum* mats (SWC). Error bars show the standard error, while different letters indicate significant differences ($P < 0.05$). Percentages above bars indicate the variation of phototrophic microbial abundance in the SWC percentile concerned, for a 1°C temperature increase.





Chapter VI

General Discussion

Phototrophic microbes are abundant primary producers in northern *Sphagnum*-dominated peatlands, but their functional role in the ecosystem C dynamic remains unknown. A comparison with recent estimates in other terrestrial ecosystems suggests that phototrophic microbes could fix significant amounts of C in peatlands. Taking into consideration this unexpected C flux could thus advance our understanding of the peatland C cycle, in which C sequestration relies on a fragile balance between C assimilation and release. Any modification or disruption in this balance, for instance brought by phototrophic microbes, could have a dramatic effect on peatland C dynamic, ultimately altering peatland C stocks. Taking into consideration phototrophic microbes could therefore alter current predictions of peatland C sink under climate change scenarios.

In this context, the general aim of this work was to estimate:

- 1) the importance of phototrophic microbes in peatlands and their contribution to peatland primary productivity;
- 2) the importance of interactions between *Sphagnum* and key species of phototrophic microbes (mixotrophic testate amoebae), and the consequences for the microbial food-web structure;
- 3) the consequences of the response to climate change of phototrophic microbial diversity and photosynthesis for peatland primary productivity.

The first question is essentially addressed in the second and third chapters. The chapter IV aims to answer the second question, while the third question is addressed in chapter V. This discussion aims to synthesise and compare the results obtained in the different chapters in order to draw general conclusions and to propose research perspectives to complete and refine this thesis work.

1. Phototrophic microbial communities in *Sphagnum*-dominated peatlands

Owing to their potential contribution to the global C cycle, microbial phototrophic communities of terrestrial ecosystems have received increasing attention in the past decade (Elbert et al., 2012; Jassey et al. 2022). In particular, many studies focused in ecosystems with few or no plants, where phototrophic microbes dominate the C fluxes (e.g. Anesio et al., 2009; Maier et al., 2018). More recently, global biogeography of phototrophic microbes and estimates of their activity have been done in the different terrestrial biomes (Cano-Díaz et al., 2020; Jassey et al., 2022; Oliverio et al., 2020). However, most of these studies overlooked northern peatlands. Here, my studies highlight the significant role of phototrophic microbes in *Sphagnum*-dominated peatlands, and therefore contribute to the global knowledge of phototrophic microbial significance in terrestrial ecosystems.

Relative and absolute abundance of phototrophic microbes in northern peatlands

An important result of my studies is the extremely high relative abundance of phototrophic microbes in the *Sphagnum* microbiome, rivalling that of the main phototrophic microbial hotspots found among terrestrial ecosystems (Fig. VI.1). My findings show that 70% (44% – 88%) of the protist sequences belong to phototrophic organisms in surface peatlands. This is much higher than in any other terrestrial biome, where phototrophic organisms do not exceed 20% of the protist community (Oliverio et al., 2020). Further, among Cyanobacteria, I found that 56% (14% - 97%) of the sequences were phototrophic which is similar to drylands (60%) where phototrophic microbes are key organisms (Büdel et al., 2016). These results strongly suggest that peatland *Sphagnum* mats and their capitula are hotspots for phototrophic microbial communities and, consequently, that phototrophic microbes dominate microbial processes at the surface of peatlands in the photic zone. Corroborating our findings on the relative abundance, I found that *Sphagnum* capitula were inhabited by an extremely high absolute abundance of phototrophic cells, with on average $3.9 \cdot 10^7$ cells.g⁻¹ DW ($1.5 \cdot 10^7$ – $9.3 \cdot 10^7$). Though this abundance is in the same magnitude than what is measured in other peatlands

(Greenwood & Lowe, 2006; Rober et al., 2014), it is much higher than what can be found in other terrestrial ecosystems ($5.7 \cdot 10^5$ cells.g⁻¹ DW on average, Fig. VI.2). The reasons for these different patterns are twofold. First, northern peatlands are moist ecosystems, with a high water table and the presence of hyaline cells in *Sphagnum* that maintain moist conditions. This environment thus offers suitable conditions for phototrophic microbial growth: water availability is indeed a key driver of phototrophic microbial abundance (Jassey et al., 2022). Second, *Sphagnum* is a porous material with a low density, around 0.015 g.cm⁻³ on average, while by comparison the density of most soils is typically 100 times higher, around 1.3 g.cm⁻³ (Rai et al., 2017). This means that light can penetrate deeper in the porous *Sphagnum* than in soils, and further, that one gram of *Sphagnum* dry weight represents a high volume, offering a large area for microbial development.

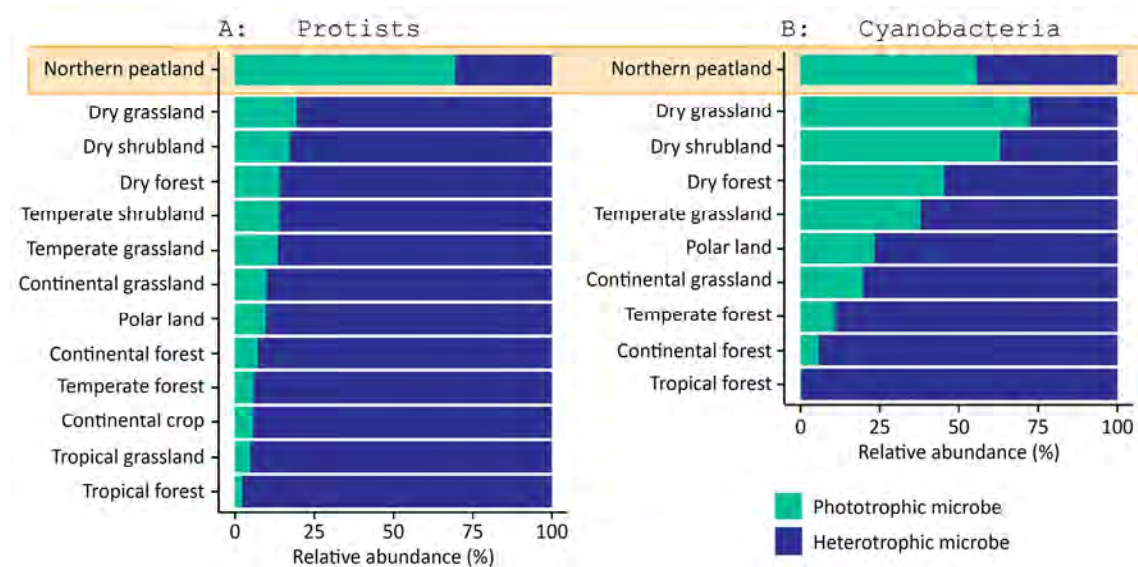


Figure VI.1: Relative abundance of phototrophic organisms among protists and Cyanobacteria in my studies (northern peatlands) by comparison with other biomes (data synthesis from Cano-Díaz et al., 2020; Oliverio et al., 2020 and Hamard et al., 2021a, 2021b).

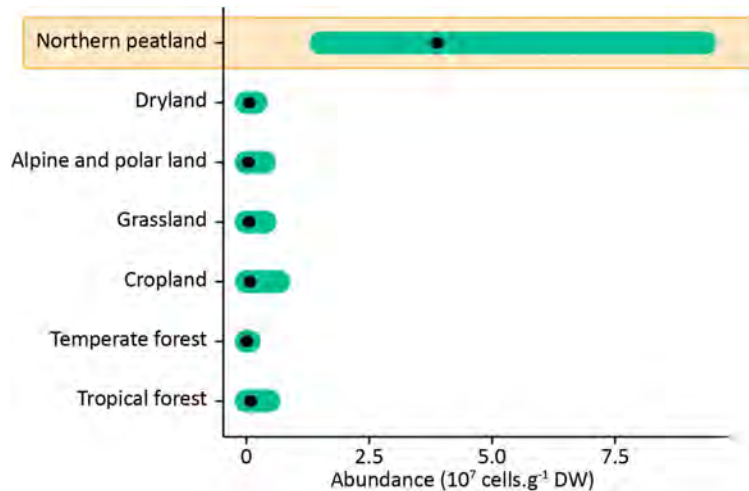


Figure VI.2: Absolute abundance of phototrophic microbes in my studies (northern peatlands), by comparison with other biomes (data synthesis from Jassey et al., 2022 and Hamard et al., 2021a, 2021b).

Diversity and environmental drivers of phototrophic microbial communities

In addition to their striking abundance, I found that that phototrophic microbes were diverse in northern peatlands, with the presence of hundreds of different micro-eukaryotic and prokaryotic phototrophic OTUs. Briefly, the six major micro-eukaryote groups in which photosynthesis has been identified on Earth were represented. Regarding the class level, the taxonomic composition of phototrophic protist in peatlands was not drastically different from the one of the other biomes, though being richer in Zygnemophyceae, Chrysophyceae and Cryptophyta (Fig. VI.3). Concerning the phototrophic prokaryotes, I identified the presence of four out of the seven existing phyla (Cyanobacteria, Proteobacteria, Chloroflexi and Gemmatimonadetes). Firmicutes and Acidobacteria were also present, but the taxonomic affiliation did not allow disentangling if the OTUs were phototrophic or not. I did not evidence the presence of Chlorobi (green sulphur bacteria) although they have already been reported in peatlands (Urbanová & Bárta, 2014, 2016). Chlorobi are anaerobic microbes and they might locate deeper in the *Sphagnum* mat.

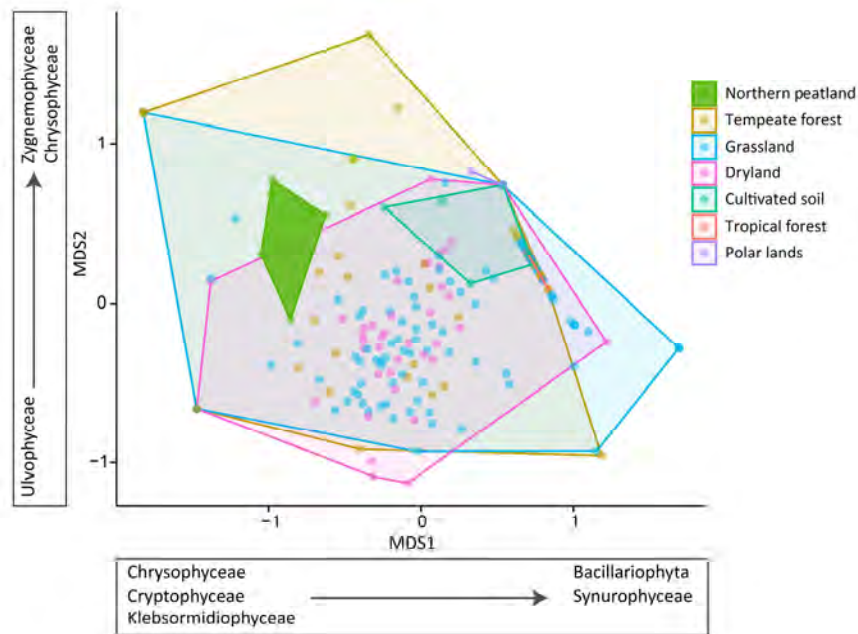


Figure VI.3: Non-metric multidimensional scaling of phototrophic micro-eukaryote communities at the class level in my studies (northern peatlands, green) by comparison with other biomes (data synthesis from Oliverio et al., 2020 and Hamard et al., 2021a, 2021b).

I found that the community structure of phototrophic microbes varied at both local and continental scales. Interestingly, geographic distance was not a driver of this variation, as communities encountered among the different microhabitats of a same site (within a hundred of meters) showed a similar variation of diversity than the habitats encountered along a 3000 km latitudinal gradient (Fig. VI.4). Simply, the environmental factors varying along the local or continental gradients were not the same (shadow/water table depth in the first case; and plant composition/water availability in the second case), and the species responding to the environmental changes differed according to the local or continental gradient. This is observable in an NMDS ordination where the inter-site diversity expresses on the x-axis, while the intra-site diversity expresses on the y-axis (Fig. VI.4). When the NMDS is done at higher taxonomic levels (phylum, class, order), the response of community structures to gradients disappears. This suggests that the response of phototrophic microbes to environmental variations is not driven by the phylogeny, but rather depends on each species. Similarly, I found that rising temperature affected the community structure of phototrophic microbes without affecting their

phylogenetic diversity: the community changed with an effect on specific species independently of their phylogeny.

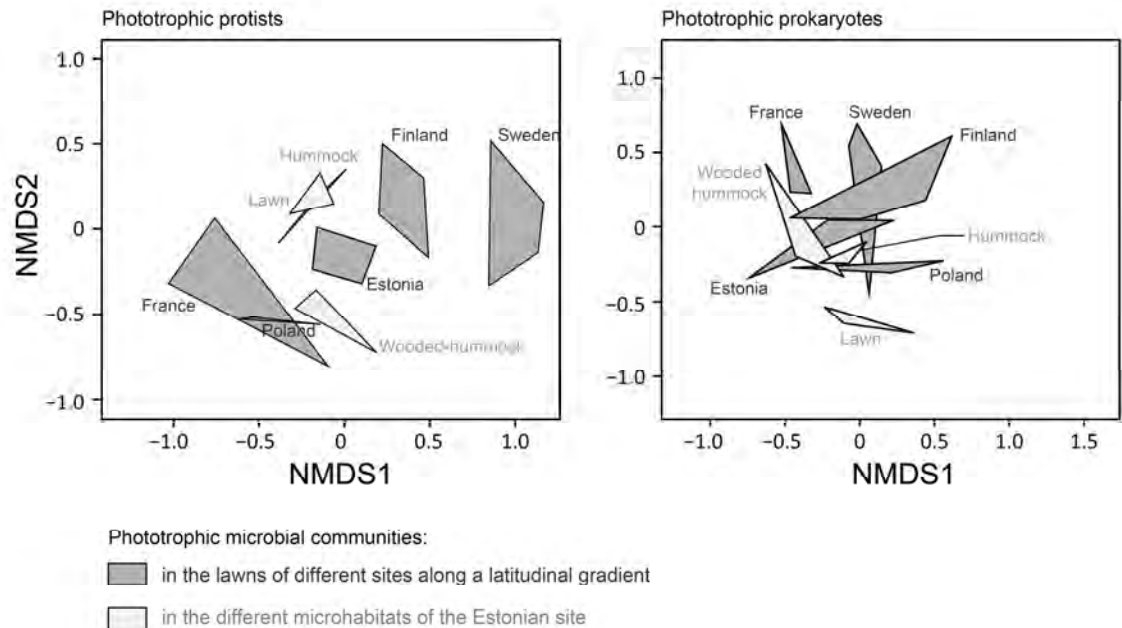


Figure VI.4: Non-metric multidimensional scaling of phototrophic protist and phototrophic prokaryote communities, along the microhabitat gradient (chapter II) and the latitudinal gradient (chapter III) (data synthesis from Hamard et al., 2021a, 2021b).

Structure-function relationships among phototrophic microbial communities

The phototrophic taxa identified exhibited diverse photosynthetic pathways, some being not purely photoautotrophic, combining mixotrophy or photoheterotrophy. I therefore expected that the phototrophic community composition and structure would affect the microbial photosynthetic rates at the community level, due to the presence of taxa photosynthesising more than others. I found that microbial photosynthesis did not significantly vary between the communities of the different sites along the latitudinal gradient, despite strong structural changes (Hamard et al., 2021a). Yet, microbial photosynthesis significantly varied among the microhabitats of a same site (Hamard et al., 2021b). These results highlight a decoupling between the taxonomic identity and the functionality of phototrophic microbes, suggesting that several microbial taxa can exhibit similar photosynthetic rates.

This is possible because microbial photosynthesis is not monophyletic (Baldauf, 2003; Cardona, 2015). Such decoupling between structure and function is frequent among microbial communities (Louca et al., 2018). These results further suggest that the microbial photosynthetic levels are determined by other factors than community structure and could imply environmental factors such as light, nutrient resources or grazing pressure as it is the case in aquatic environments (e.g. Di Pippo et al., 2012; Mackey et al., 2009). In particular, *Sphagnum* plays an important role because it shapes the environment of microbial communities. Its mat density determines the amounts of hyaline cells and the volume of favourable environments for microbial growth. I found from my studies a significant positive relation between microbial C fixation and *Sphagnum* mat density (Fig. VI.5). It suggests that *Sphagnum* density could be one of the limiting environmental factors determining microbial productivity through the microbial load found in the ecosystem, and independently of the phototrophic community structure. It could also explain why C fixation was similar in the same type of habitats (lawns) even if they were geographically distant, and changed only along with microhabitats, when *Sphagnum* mat density changed.

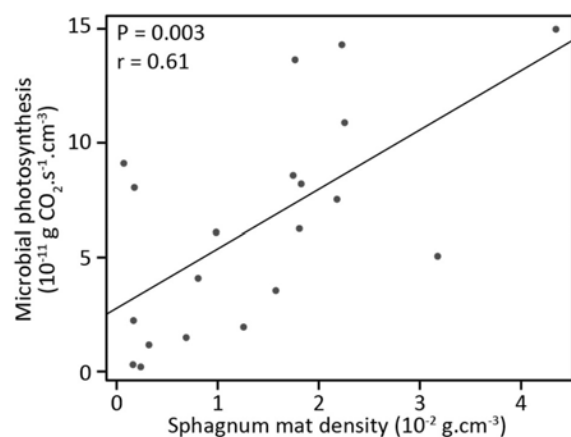


Figure VI.5: Correlation between microbial photosynthesis and *Sphagnum* mat density (data synthesis from Hamard et al., 2021a, 2021b).

These results of a decoupling between phototrophic microbial structure and function are nevertheless questioned by the transplantation experiment (chapter V). In this experiment, I found that the community structure of phototrophic microbes was affected by climate changes, as well as microbial C fixation. In particular, I found that the microbial C fixation correlated with the relative abundance of some phototrophic species, suggesting that these species played a key role in the microbial primary productivity. Similarly, a comparison between tropical and northern peatland bryosphere showed that microbial photosynthesis efficiency correlated with cyanobacterial abundance (Hamard et al., under review), highlighting the role of community composition in driving microbial C fixation.

Altogether, these results show that the structure-function relationships among phototrophic microbes are complex. My studies bring new insights for understanding such complexity, though the jigsaw puzzle is far from being complete and other studies are needed to refine these findings. Further, other aspects could complicate the structure-function relationship. In particular, phototrophic microbes can show an intra-specific variability (e.g. Brandenburg et al., 2018; Godhe & Rynearson, 2017; Long & Hay, 2006), which can be exacerbated by environmental factors and that can have a repercussion on ecosystem functioning (Des Roches et al., 2018). For instance, in marine environments the populations of specific Rhodophyta or diatoms present different photosynthetic potential according to the location or the season of sampling (Godhe & Rynearson, 2017; Ursi et al., 2003). The feeding habits of mixotrophic species can change under climate change, becoming more heterotrophic with rising temperature (Wilken et al., 2013). In this thesis, I did not focus on the intra-specific variability of phototrophic microbes in peatlands and its consequences for the community primary production. Yet, the fourth chapter bring some insight on the potential effects of environmental changes on mixotrophic testate amoebae traits. In this experiment, I showed that the *Sphagnum* microbial food web was affected by *Sphagnum* leachate. In *S. fallax* food web, the testate amoeba *Hyalosphenia papilio* was a core species, a top-predator with multiples trophic links. The addition of *S. divinum* leachate displaced *H. papilio* from the core of the food web, thus removing its trophic links. It

suggests that the addition of *S. divinum* leachate altered the feeding habit of *H. papilio* from a more heterotrophic to a more autotrophic feeding habit, possibly due to the loss of species in the system. This result shows that biotic factors such as *Sphagnum* species identity could affect the functional traits of phototrophic microbes in peatlands.

2. Primary productivity of phototrophic microbial communities

Levels of primary productivity and contribution to peatland C uptake

I found that phototrophic microbes had a potential fixation of $0.20 \mu\text{gC}\cdot\text{h}^{-1}\cdot\text{cm}^{-3}$ on average ($0.03 - 1.00 \mu\text{gC}\cdot\text{h}^{-1}\cdot\text{cm}^{-3}$). My estimations are in the range of previous results in peatlands. They are a bit higher than those found by Gilbert et al. (1998; $0.07 \mu\text{gC}\cdot\text{h}^{-1}\cdot\text{cm}^{-3}$ ($0.01 - 0.013 \mu\text{gC}\cdot\text{h}^{-1}\cdot\text{cm}^{-3}$) in *Sphagnum*-dominated peatlands and lower than the values obtained in a fen ($0.47 - 2.48 \mu\text{gC}\cdot\text{h}^{-1}\cdot\text{cm}^{-3}$) by Wyatt et al. (2012). The differences could come from the conditions of sampling that were different between the studies. I indeed found that microbial primary productivity varied with microhabitats, seasons or latitude. Microhabitats explained the highest part of this variation (45%), followed by seasonality (30%) (Fig. VI.6). Phototrophic microbes had unexpectedly a higher primary productivity in microhabitats distant from the water table and under dense plant cover (in hummocks and wooded-hummocks). I also showed that microbial photosynthesis peaked in autumn, being up to two times higher than in spring or summer. In the third chapter, I roughly estimated that phototrophic microbes would fix a global amount of *ca.* 75 MT C per year in northern peatlands, upscaling data sampled in lawns and in summer. Altogether, my different studies suggest that this global amount is most probably underestimated as higher microbial photosynthetic rates are found in other microhabitats and in other seasons. Just by considering a two-fold C fixation in autumn, this estimation would increase by 15%, around 85 MT C fixed per year. No data describes the global repartition of northern peatland microhabitats, preventing any further refining of the estimation.

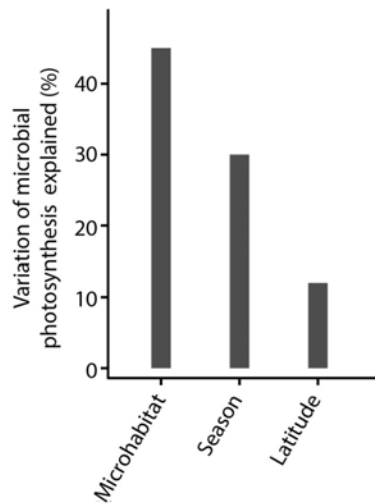


Figure VI.6: Variation of microbial photosynthesis observed in my studies, explained by spatial (microhabitat and latitude) and temporal (season) factors.

In the study of *Sphagnum*-dominated peatlands, Gilbert et al. concluded that microbial primary production was negligible compared to plant primary production, representing less than 1% of peatland C uptake (Gilbert & Mitchell, 2006). My results lead to a different conclusion. When I compare microbial photosynthesis with *Sphagnum* photosynthesis— the main primary producer in peatlands— I found that phototrophic microbes fix on average 9% (4% - 12%) of the total bryosphere C fixation (Fig. VI.8A). I believe that such contribution is significant and has a key role in the peatland C dynamic, as suggested by recent studies in fens (Ferguson et al., 2021; Wyatt & Turetsky, 2015). This microbial contribution of 9% to ecosystem C fixation is a typical value compared with the ecosystems of other biomes (Fig. VI.7), where phototropic microbes contribute on average to 6% of C uptake (Jassey et al., 2022). I acknowledge that my estimations of microbial contribution to C uptake were done in one microhabitat (lawns) at one date (one day in summer) and therefore require further data to better estimate annual microbial primary productivity in peatlands. For instance, I compare microbial C uptake to *Sphagnum* only and overlooked vascular plants. Although vascular plants are unevenly distributed in peatlands they significantly contribute to primary productivity and therefore might affect microbial contribution to peatland C uptake. Further studies will be necessary to refine

my estimates, over a full year and in different microhabitats. Still, despite these caveats, my findings show that microbial contribution is significant and could reach high levels under particular conditions, for instance in autumn or in hummocks, where microbial photosynthesis peaks unlike *Sphagnum* photosynthesis.

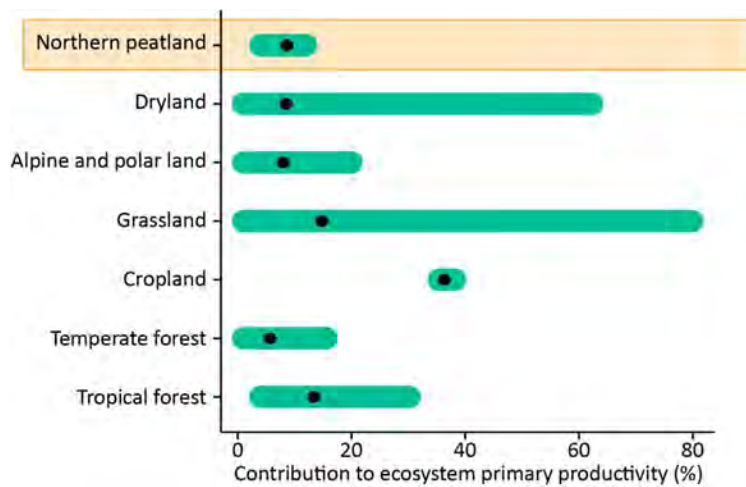
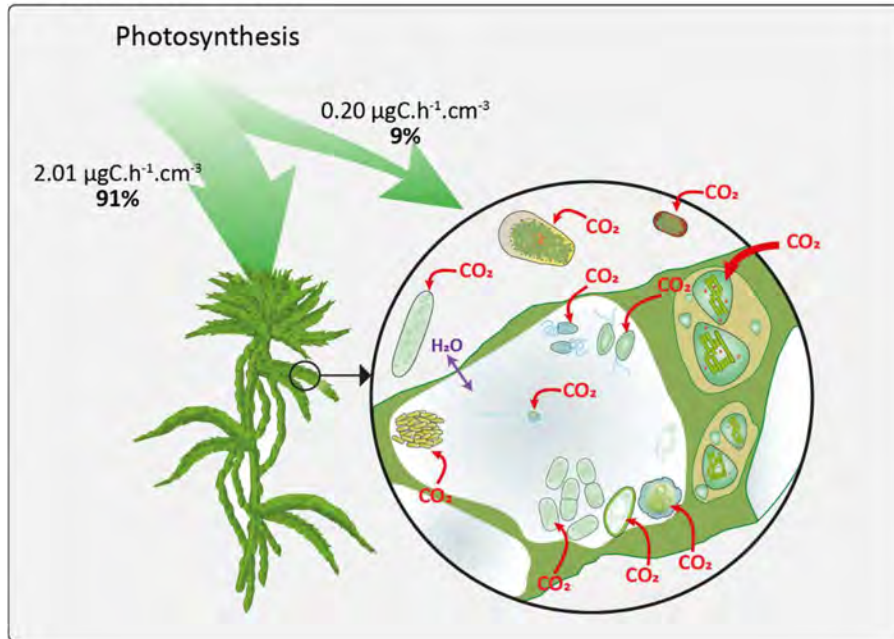


Figure VI.7: Phototrophic microbial contribution to ecosystem primary productivity in my studies (northern peatlands) by comparison with other biomes (from Jassey et al., 2022).

A: PROPOSED VIEW



B: PROPOSED VIEW WITH CLIMATE CHANGE

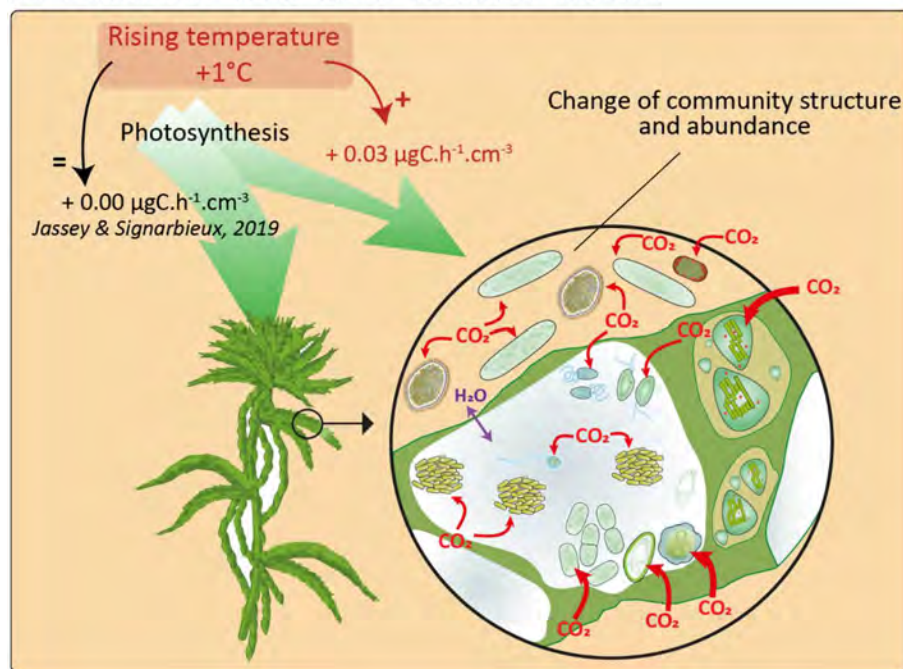


Figure VI.8: As a conclusion of my work, I propose a new view of primary productivity patterns in northern peatlands, in which phototrophic microbes have a significant contribution (A). Under climate change, rising temperature might strengthen the contribution of phototrophic microbes to peatland primary productivity (B).

Effects of climate change on microbial primary productivity

Climate change altered microbial primary production, and I found that rising temperature increased phototrophic microbial photosynthesis by up to 17% per degree gained. As *Sphagnum* communities seem to maintain unchanging levels of productivity in warmed conditions (Jassey & Signarbieux, 2019), microbial photosynthesis could contribute more strenuously to peatland primary productivity and exceed the 9% previously estimated (Fig. VI.8B). Such stimulation could increase microbial C fixation from 75 MT C per year to 94 MT C per year in 2050, with an expected 1.5°C rise. This rough estimation suggests a massive impact of climate change on microbial photosynthesis in northern peatlands. This estimation remains speculative, but it shows the potential importance of microbial photosynthesis in peatlands under future climate change. Moreover, seasonal variability has to be taken into account as well. Indeed, I found that warming effects on microbial photosynthesis fluctuated from positive effect to none according to water availability. The estimation will thus depend on precipitation patterns for which uncertainties are high (Shepherd, 2014), but will certainly be lowered by increased droughts. Furthermore, and at the opposite, rising temperatures are expected to increase more in high latitudes (Masson-Delmotte et al., 2021) and to lengthen growing seasons, removing temperature constraints on photosynthesis in early spring or late autumn. By 2050, growing seasons could be more than 10 days longer than nowadays (Christiansen et al., 2011; Piao et al., 2007). Then a global increase of 1.5°C by 2050 could have a strenuous effect on microbial photosynthesis. Further, shifting precipitation patterns along with temperature in the future, with more drought or less frequent but heavier rainfall (Dai et al., 2018; Fischer & Knutti, 2016; Woodward et al., 2016) could bring cycles during which microbial contribution to peatland C uptake could switch between high and low values. The effects of such a possible versatility on peatland C dynamic need to be evaluated. Yet, it is necessary to understand the fate of microbial photosynthates in peatlands in order to explore these issues and to plainly evaluate the importance of phototrophic microbial productivity in ecosystem functioning.

3. Possible consequences of microbial productivity for peatland C dynamic

Phototrophic microbes use the C they fix for their metabolism. A large part is respired, being released rapidly toward the atmosphere. The amount of C respired has been estimated for several phototrophic microbes, and has been showed to vary according to species and environmental conditions such as pH, drought or light (Humphrey, 1975; Karsten & Holzinger, 2012). On average the photosynthesis to respiration ratio oscillates between 2.5 and up to more than 30 (Hashimoto et al., 2005; Humphrey, 1975; Karsten & Holzinger, 2012) meaning that the respiration of phototrophic microbes ranges between a few percent to 40% of the gross primary production. The remaining amount of C stays for a longer time in the ecosystem. A direct effect is a C fixation, which reduces atmospheric CO₂ levels and can partially offset the release of C due to heterotrophic activities (Wyatt et al., 2021). However, other effects can also happen, depending on the fate of phototrophic microbial organic matter in peatlands. Phototrophic microbial organic matter contributes to phototrophic microbial biomass or can be released in the ecosystem through active or passive exudation (Mühlenbruch et al., 2018). Phototrophic microbial biomass constitute a food source for microbial herbivores, consumers and predators (Ferguson et al., 2021; Gilbert & Mitchell, 2006; Jassey et al., 2011b) (Fig. VI.9). Exudates, which can represent between 5 and 35% of the total C fixation (Myklestad, 1995; Wyatt et al., 2012), contributes to the pool of dissolved organic C. Both exudates and necromass provide a source of organic matter to decomposers such as bacteria and fungi (Fig. VI.9). Therefore, phototrophic microbes in peatlands could shape *Sphagnum* microbial food web. In particular, it could determine heterotrophic microbial communities, controlling their abundance, diversity and physiology through bottom up mechanisms, as it is the case in other terrestrial ecosystems (Davies et al., 2013; Maier et al., 2018; Sauze et al., 2017). Long term experiment in marine ecosystems showed that around 30% of algal exudates is recalcitrant to microbial decomposition and remineralisation (Fry et al., 1996; Meon & Kirchman, 2001; Mühlenbruch et al., 2018; Osterholz et al., 2015). A small fraction of microbial

photosynthates could thus be stored in peatlands (Fig. VI.9). However, and as discussed in chapter five, phototrophic microbes in peatlands release extremely labile exudates stimulating heterotrophic bacteria (Wyatt et al., 2012). These labile compounds cause priming effects, i.e. provide additional energy to invest in the decomposition of more recalcitrant organic matter (Wyatt & Rober, 2020; Wyatt & Turetsky, 2015) such as the one produced by *Sphagnum*. Therefore, phototrophic microbes are thought to indirectly stimulate C release through an increased decomposition of peat matter (Fig. VI.9).

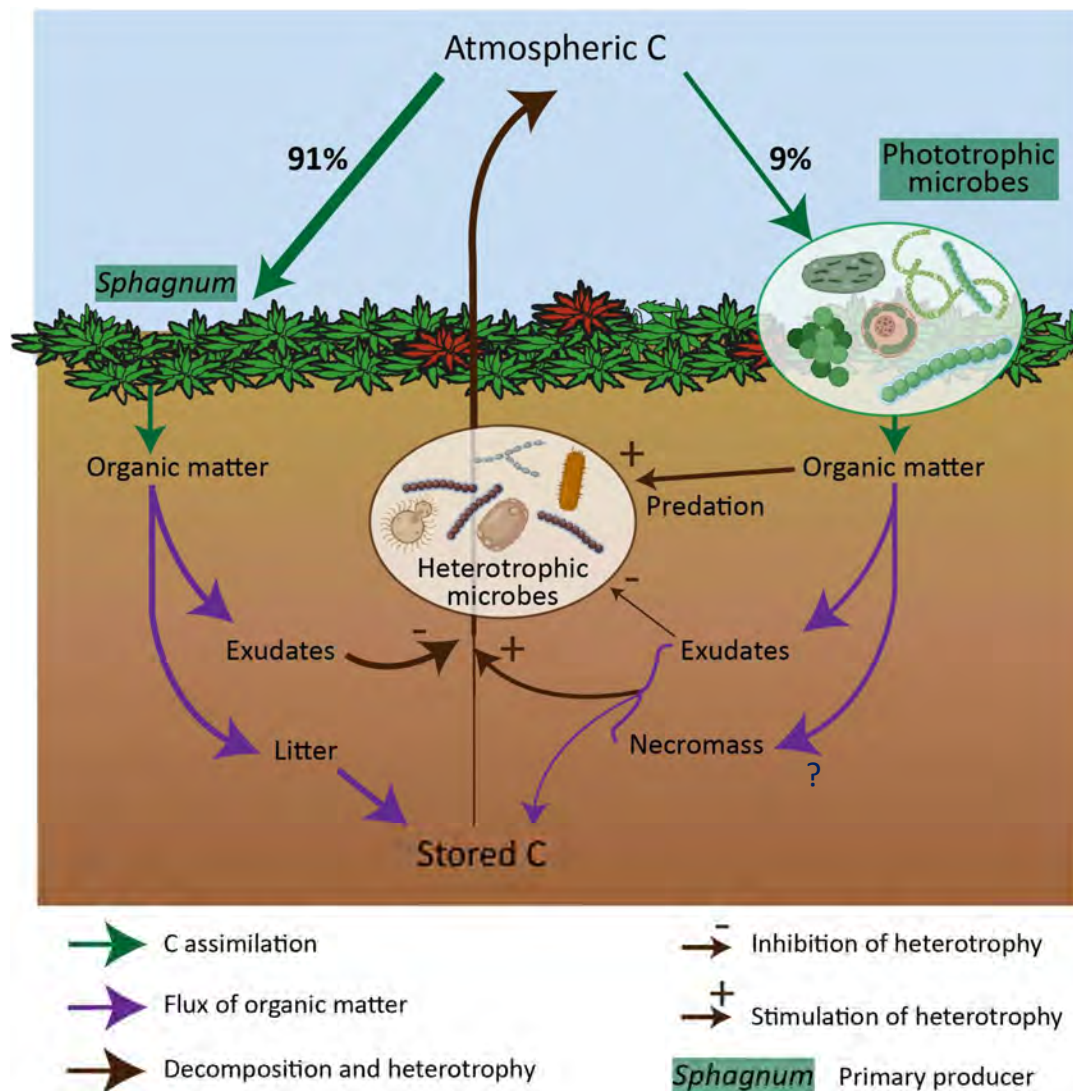


Figure VI.9: Roles of microbial primary productivity in the peatland C dynamic regarding the fate of phototrophic microbial organic matter in the ecosystem.

These effects can nevertheless be modulated by the community structure of phototrophic microbes, as different species usually produce different photosynthates and release different exudates (Kremer & Kirst, 1982; Mühlenbruch et al., 2018; Sorrell et al., 2001). For instance, cyanobacteria usually sequesters excess C in the form of glycogen (Ball & Morell, 2003), while diatoms use the form of chrysolaminarin (Beattie et al., 1961). In terms of exudates, diatoms can release polyphenols (Shannon & Abu-Ghannam, 2016), while cyanobacteria are known to release alkaloids and cyclic peptides (van Apeldoorn et al., 2007) that can have antibacterial or antialgal properties (Berry et al., 2008; Konarzewska et al., 2020; Shannon & Abu-Ghannam, 2016; van Apeldoorn et al., 2007). Therefore, the stimulation of C release by microbial photosynthates might be partially regulated by the composition and structure of phototrophic microbial communities. Yet, the overall stimulation of heterotrophic activities suggests that any shift in the inputs of phototrophic microbial organic matter could dramatically affect the peatland C dynamic. In particular, the role of climate change is particularly concerning because it globally increases microbial photosynthesis, which could induce unexpected positive feedbacks on atmospheric C levels and global Earth temperatures.

From the data of the transplantation experiment (chapter V), I explored the effects that climate change could have on *Sphagnum* microbiome. I found that all trophic groups were affected by the transplantation-induced temperature changes. In particular, my findings show that rising temperature stimulated the abundance of phototrophic microbes and decomposers (bacteria, fungi), but had an opposite effect on predator abundance (heterotrophic protists) (Table VI.1).

Table VI.1: Qualitative effects of rising temperature on the abundance of the different groups constituting the *Sphagnum* microbiome.

	Phototrophic microbes	Bacteria	Fungi	Heterotrophic protists
Temperature effect	+	+	+	-

These results are interesting because they suggest that climate change inhibits predators and therefore limit top-down controls on phototrophic microbes. Such results have already been found in previous research (Jassey et al., 2013, 2015; Reczuga et al., 2018). They suggest that changes in trophic links could explain the increase of phototrophic microbial abundance, which is in line with recent research (Wyatt et al., 2021). Further, the fact that decomposer abundance increased along with phototrophic microbial abundance underlined the possible stimulation of decomposers by algal necromass and exudates. In link with this hypothesis, I found a significant correlation between the abundance of phototrophic microbes and the biomass of fungi (Fig. VI.10A), and even a stronger correlation between phototrophic microbes and bacterial abundance (Fig. VI.10B). This illustrates that phototrophic microbes are key components of a microbial loop, feeding other trophic levels whose functioning allows for C and nutrients recycling in peatlands, and more generally conditions ecosystem functioning (Ferguson et al., 2021; Gilbert et al., 1998a; Mieczan & Tarkowska-Kukuryk, 2013, 2021). Therefore, my results suggest that increased microbial photosynthesis under rising temperature could stimulate microbial decomposition, weakening the peatland C sink and ultimately releasing stored C toward the atmosphere.

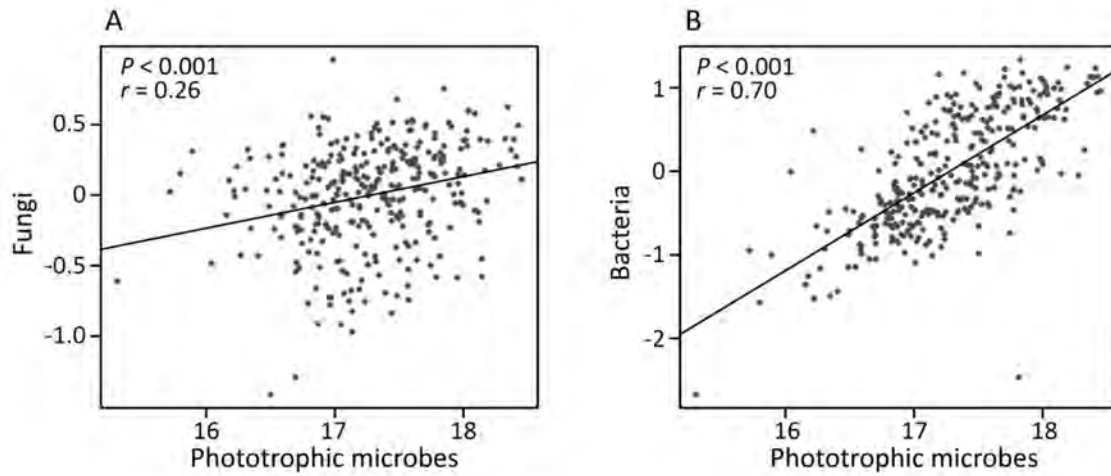


Figure VI.10: Positive correlation found between (A) phototrophic microbial abundance and fungal biomass, and (B) between phototrophic microbial and bacterial abundance in my studies. Phototrophic microbial abundance is expressed as the logarithm of the abundance. I estimated fungal biomass from ergosterol analyses (Montgomery et al., 2000), and the axis in this graph is the residuals of a model taking into account the origin of the sites. Similarly, the axis for bacterial abundance is the residuals of a model taking into account the origin of the sites.

CONCLUSION & PERSPECTIVES in English

Overall, this work contributes to better understand phototrophic microbial communities and their role of primary producers in northern peatlands. Studies conducted in different sites, along microhabitat or continental gradients, revealed a high abundance and a high taxonomic diversity of phototrophic microbes in peatlands. Microbial assemblages and phototrophic community structures also showed high diversities, with for instance communities dominated by phototrophic prokaryotes in wooded hummocks, or at the opposite by phototrophic eukaryotes in lawns. Overall, phototrophic microbial communities were nevertheless dominated by Chlorophyta, Proteobacteria and Cyanobacteria. I found that changes in community structure were driven by environmental factors including amongst other plant community and water availability. In particular, I found that *Sphagnum* and their leachates had a strong determining effect on food web structure, and on the place of specific phototrophic and mixotrophic species.

Despite important structural variations, the functioning and the primary productivity of phototrophic microbial communities remained similar along the continental gradient, and was only affected along microhabitats. This result questioned a decoupling between structure and function and showed a functional similarity between different communities. I estimated that phototrophic microbes contributed around 9% to peatland primary productivity, fixing on average $0.20 \mu\text{gC}\cdot\text{h}^{-1}\cdot\text{cm}^{-3}$. My studies nevertheless suggest that this contribution varies according to seasonal or environmental conditions. In particular this contribution could be much higher when microbial photosynthetic rates

increase (for instance in autumn) and/or when *Sphagnum* productivity decreases (for instance in hummocks microhabitats).

Further, my studies emphasize the sensibility of phototrophic microbial communities to climate change. Rising temperature could radically increase microbial primary productivity when moisture conditions are favourable. The consequences for peatland C dynamic would depend on the fate of microbial photosynthates in the ecosystem. Nevertheless, current literature would suggest a destabilisation of peat C, and a stimulation of heterotrophic activities favouring a release of C from peatlands to the atmosphere. If verified, this phenomenon could bring a dramatic positive feedback to climate change.

My studies bring a new view for the primary productivity in peatlands, yet this view remains incomplete and generates new interrogations. In order to obtain a more complete understanding of microbial photosynthesis in peatlands, I would like to broaden the studies I did. In my studies, I performed a large and exhausting sampling, but that still remained limited regarding the diversity of peatlands on Earth. In particular, I studied the first three centimetres of the *Sphagnum* mat, and focused on five European sites. I would now like to sample at different depth in the *Sphagnum* mat in order to include anaerobic phototrophic microbes in my studies, such as Chlorobi that locate deeper in the peatlands. With this in mind, I would try to use different technics to grasp more precisely anoxygenic photosynthesis that might be underestimated in my studies. I would also like to collect many more data at different local, global and temporal scales. The extended data set would allow studying the relations between environment, community structure and function of phototrophic microbes. It would also allow exploring the intraspecific trait plasticity of phototrophic microbes in peatlands. Finally yet importantly, these studies take their sense in the peatland functioning when we know the effects of microbial photosynthates for the peatland C dynamic. Therefore, it is important to me to study the repercussion of phototrophic microbial exudates, necromass and biomass on peatland heterotrophic activities, and to explore this for different phototrophic species and assemblages. In particular, I would design a microcosm experiment in controlled conditions to estimates the short and

mid-term effects of increased microbial abundance, algal exudates and necromass on microbial food web and its activity, using different species of phototrophic microbes including for instance Cyanobacteria, Chlorophyta and Ochrophyta. I would further design a long-term in-situ experiment, using isotope-labelled phototrophic exudates and necromass to estimate their effects on peatland C sink, and to see if a potential sequestration of some microbial photosynthates occurs.

Beyond these potential perspectives, my work reveals the importance of phototrophic microbes in peatlands, and emphasizes the urgent need to consider their role of primary producers. Only by considering them in peatland models, will it be possible to tend toward a more complete view of the peatland C cycle and to predict its evolution under climate change.

CONCLUSION & PERSPECTIVES en français

Dans l'ensemble, ces travaux contribuent à mieux comprendre les communautés de microbes phototrophiques et leur rôle dans la production primaire des tourbières nordiques. Les études que j'ai réalisées dans différents sites, le long de gradients latitudinaux ou de microhabitats révèlent l'importante abondance et diversité taxinomique des microbes phototrophiques. Les structures des communautés phototrophiques révélaient aussi une grande diversité, avec par exemple certaines communautés dominées par des procaryotes phototrophiques, tandis que d'autres étaient dominées par des micro-eucaryotes phototrophiques. Dans l'ensemble les communautés étaient tout de même dominées par des Chlorophyta, des Proteobacteria et des Cyanobacteria. J'ai trouvé que les changements dans la structure des communautés étaient régis par des facteurs environnementaux incluant entre autres la composition des communautés de plantes, ou la disponibilité en eau. En particulier, j'ai trouvé que les espèces de sphaigne et leurs lixiviats avaient un fort effet déterminant sur la structure des réseaux trophiques microbiens et la place de certaines espèces phototrophiques et mixotrophiques.

Malgré d'importantes variations structurelles, j'ai trouvé que la production primaire des communautés de microbes phototrophiques restait similaire le long du gradient latitudinal, et n'était altérée que par les différents microhabitats. Ce résultat questionne les relations structure-fonction des communautés et montre qu'une similarité fonctionnelle existe entre différentes communautés. J'ai estimé que les microbes phototrophiques contribuaient à près de 9% de la production primaire des tourbières nordiques, fixant en moyenne $0.20 \mu\text{C}\cdot\text{h}^{-1}\cdot\text{cm}^{-3}$. Mes études suggèrent néanmoins que

cette contribution varie selon la saison ou les conditions environnementales. En particulier, cette contribution pourrait être plus élevée quand la photosynthèse microbienne est plus importante (par exemple en automne) et/ou quand la productivité des sphaignes est moindre (par exemple dans certains microhabitats comme les buttes).

Par ailleurs, mes études soulignent la sensibilité des communautés de microbes phototrophiques au changement climatique. J'ai trouvé qu'une augmentation des températures pouvait augmenter drastiquement la productivité microbienne lorsque les conditions d'humidité étaient favorables. Les conséquences sur la dynamique du C des tourbières dépendent du devenir de la matière organique des microbes phototrophiques dans l'écosystème. Néanmoins, la littérature actuelle suggère qu'une déstabilisation du C des tourbières et qu'une stimulation des activités hétérotrophiques sont possibles, ce qui favoriserait le relargage de C vers l'atmosphère. Si cela est vérifié, ce phénomène pourrait entraîner de dramatiques rétroactions positives au changement climatique.

Mes études apportent une nouvelle vision pour la production primaire des tourbières nordiques, mais cette vision demeure incomplète et génère de nouvelles interrogations. Afin d'obtenir une compréhension plus complète de la photosynthèse microbienne dans les tourbières, j'aimerais élargir les études que j'ai réalisées. Dans mon travail, j'ai effectué un important échantillonnage mais qui reste limité au regard de la diversité des tourbières sur Terre. En particulier, j'ai étudié les trois premiers centimètres du tapis de sphaigne, et je me suis focalisé sur cinq sites européens. J'aimerais échantillonner à d'autres profondeurs pour inclure les microbes phototrophiques anaérobiques comme par exemple les Chlorobi, qui se situent plus en profondeur dans le tapis de sphaigne. Dans cette optique, j'aimerais aussi utiliser d'autres techniques pour inclure davantage la photosynthèse anoxygénique qui est probablement sous-évaluée dans mes études. J'aimerais aussi collecter des données à différentes échelles locales, globales et temporelles. Un important jeu de données permettrait d'étudier les relations entre environnement, structure des communautés et fonction des microbes phototrophiques. Cela permettrait aussi d'explorer la variabilité intraspécifique des traits des

microbes phototrophiques dans les tourbières. Enfin, ces études prennent leur sens dans le fonctionnement des tourbières lorsque l'on connaît le devenir de la matière organique des microbes phototrophiques dans la dynamique du C. Par conséquent, je trouve important d'étudier la répercussion des exsudats, de la nécromasse et de la biomasse des microbes phototrophiques sur les activités hétérotrophiques. J'aimerais aussi pouvoir étudier cela au regard de différentes espèces phototrophiques et de différents assemblages microbiens. En particulier, j'aimerais faire une expérience en microcosme pour estimer les effets à court et moyen terme d'une abondance accrue de microbes photosynthétiques, de l'ajout d'exsudats et de nécromasse, sur le réseau trophique microbien et son activité. J'utiliserais pour cela différentes espèces de microbes photosynthétiques incluant par exemple des cyanobactéries, des chlophytes et des ochrophytes. Par ailleurs, j'aimerais faire une expérience in-situ sur le long terme, pour étudier l'effet d'un ajout d'exsudats et de nécromasse marqués (isotopes) sur le puit de C des tourbières, et pour voir si une séquestration de certains photosynthétats microbiens existe.

Au-delà de ces perspectives, mon travail révèle l'importance des microbes phototrophiques dans les tourbières nordiques et souligne le besoin urgent de considérer leur rôle en tant que producteurs primaires. C'est seulement en les incluant dans les modèles de tourbière qu'il sera possible d'obtenir une vision plus complète du cycle du C des tourbières et de prédire son évolution au changement climatique.

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TITLE: Contribution of phototrophic microbes to peatland carbon uptake in a changing climate

ABSTRACT in English:

All ecosystems on Earth depend on primary production, which converts inorganic carbon (C) into organic compounds and living biomass. In terrestrial systems, phototrophic microbes are widespread, and recent global estimates show that they contribute on average to approximately 6% of ecosystem C uptake, in addition to plants. These estimates are however rough, and microbial contribution remains underexplored in many terrestrial systems, including C-accreting systems such as northern peatlands. Considering the functional role of phototrophic microbes could alter our current view of peatland C dynamic and deeply question our prediction of peatland C sink under climate change. This challenge is worthy because northern peatlands play a major role in the global C cycle, and their response to climate change could release the majority of warming-induced soil C loss over the next century, with dramatic consequences for the global climate. To bring a new piece in the understanding of peatland C dynamic, we explored phototrophic microbial communities, their activity and their response to climate change. We found that phototrophic microbes are extremely abundant and diverse in northern peatlands and that environmental drivers such as microtopography, water availability, or plant composition shape their community structure. In particular we found a key role of peat mosses, *Sphagnum*, and of their metabolites in determining and structuring the microbial food web and the place of specific phototrophic microbes. Overall, we showed that phototrophic microbes fix significant amounts of C, on average $0.11 \mu\text{gC}\cdot\text{h}^{-1}\cdot\text{cm}^{-3}$, which represents 9% of peatland primary production. Despite structural differences, we further found that different phototrophic microbial communities respond similarly to climate change, emphasizing the strong functional similarity and redundancy among phototrophic microbes. Rising temperatures stimulate microbial photosynthesis of up to nearly 20% per degree gained, but we found a seasonality in these effects, according to soil moisture content. Benefits of warmer temperatures can flip to neutral when *Sphagnum* moisture is either too dry or too moist. These results reveal the vulnerability of peatland C dynamics to changes in temperature and precipitation patterns. Altogether, our result show the importance of phototrophic microbes as primary producers in northern peatlands. Combined with recent studies showing that phototrophic microbial organic matter can stimulate heterotrophic activities and peat decomposition, our results bring a new and worrying piece in the understanding of peatland C dynamic and its evolution under future climates. Our results highlight the urgent need to focus more intensely on the unseen phototrophic microbes in northern peatlands.

KEYWORDS: Climate change, Carbon cycle, Community structure, Microbial photosynthesis, Peatland, Phototrophic microbe, Primary production,

AUTEUR : Samuel HAMARD

TITRE : Contribution des microbes phototrophiques à la fixation de carbone des tourbières dans un contexte de changement climatique

DIRECTEURS DE THESE : Regis CEREGHINO et Vincent JASSEY

LIEU ET DATE DE SOUTENANCE :

RESUME en français :

Tous les écosystèmes sur Terre dépendent de la production primaire qui converti du carbone (C) inorganique en matière organique et en biomasse. Les microbes phototrophiques sont omniprésents dans les écosystèmes terrestres, et des estimations globales montrent qu'ils contribuent en moyenne à 6% de la fixation de C des écosystèmes. Ces estimations restent cependant grossières, et cette contribution microbienne est sous-étudiée dans de nombreux systèmes, incluant ceux qui stockent du C comme les tourbières nordiques. La prise en comptes des microbes phototrophiques pourrait compléter notre vision actuelle des dynamiques du C dans les tourbières et pourrait aussi remettre en question nos prédictions de leurs réponses aux changements climatiques. L'enjeu est grand car les tourbières nordiques jouent un rôle majeur dans le cycle global du C. Elles pourraient relâcher d'énormes quantité de carbone à cause du changement climatique, avec des conséquences dramatiques sur le réchauffement. Dans ces travaux, nous avons voulu apporter une nouvelle pièce dans la compréhension de la dynamique du C des tourbières en explorant les communautés de microbes phototrophiques, leurs activités photosynthétiques et leurs réponses au changement climatique. Nous avons trouvé que les microbes phototrophiques sont extrêmement abondants et diversifiés dans les tourbières nordiques, et que la structure de leurs communautés est régie par des facteurs environnementaux comme la microtopographie, la disponibilité en eau ou la composition des plantes. En particulier, nous avons trouvé un rôle clé des sphaignes – mousses des tourbières – et de leurs métabolites dans la détermination et la structure des réseaux trophiques microbiens incluant des microbes phototrophiques spécifiques. Dans l'ensemble, nous avons montré que les microbes phototrophiques fixent des quantités importantes de C, $11 \mu\text{gC}\cdot\text{h}^{-1}\cdot\text{cm}^{-3}$ en moyenne, ce qui représente 9% de la production primaire des tourbières. Malgré des différences structurelles, nous avons trouvé que différentes communautés phototrophiques répondent de manière similaire au changement climatique, ce qui souligne une forte similarité et redondance fonctionnelle parmi les microbes phototrophiques. Une augmentation des températures stimule la photosynthèse microbienne de presque 20% par degré. Une saisonnalité existe cependant dans cet effet, dépendant de l'humidité du sol. Les gains dus à des températures plus élevées peuvent s'estomper quand les sphaignes sont trop sèches ou trop humides. Ces résultats révèlent la vulnérabilité de la dynamique du C des tourbières à des changements de température et de régime des précipitations. Dans l'ensemble, nos résultats montrent l'importance des microbes phototrophiques comme producteurs primaires dans les tourbières nordiques. En combinaison avec des études récentes, montrant que les microbes phototrophiques peuvent stimuler les activités hétérotrophiques et la décomposition de la tourbe, nos résultats apportent des informations nouvelles et inquiétantes dans la compréhension de la dynamique du C des tourbières et sa réponse aux changements climatiques. Notre travail souligne le besoin urgent d'étudier plus en détail les microbes phototrophiques dans les tourbières nordiques.

MOTS-CLES : Changement climatique, Cycle du carbone, Microbe photosynthétique, Photosynthèse microbienne, Production primaire, Tourbière, Structure des communautés

DISCIPLINE ADMINISTRATIVE : Ecologie fonctionnelle

INTITULE ET ADRESSE DU LABORATOIRE :

UMR5245 : Laboratoire écologie fonctionnelle et environnement

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