Evaluating the role of metabolites in Sphagnum ecology under climate change : from Sphagnum functional trait space to carbon-related processes

Anna Sytiuk

Université Fédérale
Toulouse Midi-Pyrénées

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

Anna SYTIUK

Le 17 juin 2022

Évaluation du rôle des métabolites dans l'écologie des sphaignes dans un contexte de changements climatiques: de l'espace des traits fonctionnels des sphaignes à la dynamique du carbone

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

Thèse dirigée par
Régis CEREGHINO et Vincent JASSEY

Jury

Mme Elena KAZAKOU, Rapporteure
Mme Geneviève CHIAPUSIO, Rapporteure
Mme Virginie BALDY, Examinatrice
M. Bjorn ROBROEK, Examinateur
M. Régis CEREGHINO, Directeur de thèse
M. Vincent JASSEY, Co-directeur de thèse
M. Christophe ROUX, Président

PhD THESIS OF PAUL SABATIER UNIVERSITY

submitted for the degree of

DOCTOR OF THE UNIVERSITY OF TOULOUSE

Specialty: Functional ecology

Doctoral School ED173 "Geosciences, Astrophysics, Space and Environmental Sciences"

EVALUATING THE ROLE OF METABOLITES IN *SPHAGNUM* ECOLOGY UNDER CLIMATE CHANGE: FROM *SPHAGNUM* FUNCTIONAL TRAIT SPACE TO CARBON-RELATED PROCESSES

defended by

Anna SYTIUK

performed at l'UMR 5245 CNRS–UT3–INPT Functional Ecology and Environment laboratory

supervised by

Régis CEREGHINO and Vincent JASSEY

Defended on 17th of June 2022
before the jury composed of:

Elena KAZAKOU,
Professor, Institut Agro/Montpellier SupAgro- Rapporteur

Geneviève CHIAPUSIO,
Assistant professor, Université Savoie Mont Blanc- Rapporteur

Virginie BALDY,
Professor, IMBE- Aix-Marseille Université- Examiner

Bjorn ROBROEK,
Assistant professor, Radboud University Nijmegen- Examiner

Régis CEREGHINO,
Professor, Université Toulouse III - Paul Sabatier- Thesis director

Vincent JASSEY,
Chargé de recherche CNRS- Thesis Codirector

Christophe ROUX,
Professor, Université Toulouse 3 – Paul Sabatier- President

To Ukraine, to defenders and supporters of Ukraine

To my family, to my friends

"…I'm a scientist. Because I invent, transform, create and destroy for a living and when I don't like something about the world I change it…"

Pickle Rick, "Rick and Morty, s3e3"

"Bird Is The Word!"

Peter Griffin "Family Guy, s7e2"

Résumé

Les changements climatiques sont une menace pour la plupart des écosystèmes. Cependant, leurs effets seront plus prononcés aux hautes latitudes nord, impactant grandement la dynamique du carbone mondiale. En effet, les écosystèmes nordiques, comme les tourbières, jouent un rôle clé dans la dynamique du carbone mondiale en tant que puits de carbone. Les mousses, comme les sphaignes, contribuent de manière significative au piégeage du carbone dans les tourbières, où un tiers du carbone organique du sol est stocké. En effet, leurs caractéristiques morphologiques et biochimiques (métabolites) uniques font qu'elles façonnent activement leur habitat en produisant une litière récalcitrante à la décomposition. De ce fait, elles peuvent influencer la structure et l'activité microbienne et ainsi contrôler le cycle du carbone et des nutriments. Malgré ces connaissances, le rôle des métabolites de la sphaigne, en tant que traits fonctionnels importants pour l'écologie des tourbières, reste peu étudié et, notamment leur réponse aux changements climatiques.

Le but de ce travail de thèse était d'explorer le potentiel des métabolites de la sphaigne pour améliorer notre compréhension mécanistique de l'espace fonctionnel des sphaignes en termes d'intéractions avec les microorganismes du sol mais également en termes de dynamique du carbone dans un contexte de changements climatiques. J'ai également examiné comment les modèles saisonniers des métabolites de la sphaigne répondaient aux changements climatiques et les conséquences que cela pouvait avoir sur l'absorption du carbone par les tourbières. Pour atteindre ces objectifs, j'ai mené plusieurs observations et expériences sur le terrain où des informations sur les traits anatomiques, morphologiques et les métabolites de la sphaigne ont été recueillies, mais également sur les flux de CO_2 des tourbières et sur la structure et l'activité des communautés microbiennes.

Mes résultats montrent que les espèces de sphaigne qui poussent dans des conditions environnementales locales (composition de la végétation, teneur en nutriments) et régionales (température, précipitations) différentes possèdent une série de traits biochimiques divers qui définissent la forme et la fonction de la sphaigne, ainsi que sa résistance aux changements environnementaux. De plus, j'ai constaté que le volume de l'espace des traits de la sphaigne était quatre fois plus grand lorsque les traits biochimiques étaient ajoutés à la suite habituelle de traits morphologiques et anatomiques, que lorsqu'ils étaient exclus. J'ai également démontré que les variations des traits interspécifiques de la sphaigne jouaient un rôle clé dans la composition des communautés microbiennes et de leur traits fonctionnels, en plus des conditions environnementales locales et régionales. En effet, l'ajout des traits fonctionnels de la sphaigne aux variables environnementales locales et régionales dans un modèle d'équation

structurelle (SEM) a permis d'augmenter notre capacité à prédire les variations taxonomique et fonctionnelles des microorganismes des tourbières. De plus, les metabolites de la sphaigne se sont avérés être de meilleurs prédicteurs de la structure et des caractéristiques de la communauté microbienne, par rapport aux caractéristiques anatomiques et morphologiques. Enfin, en utilisant une transplantation réciproque le long d'un gradient latitudinal, j'ai montré que les sphaignes transplantées sur de nouveaux sites avaient des réponses similaires aux changements de climat en termes de concentrations de métabolites et de productivité primaire brute sur toutes les saisons, avec des valeurs maximales dans les sites les plus chauds. Mes résultats ont également montré que les métabolites des sphaignes étaient très plastiques face aux variations de température et de précipitations. La variation du phénotype des sphaignes (représentée graphiquement comme des normes de réaction) avait des pentes et des courbures similaires entre toutes les espèces. Plus intéressant encore, mesdonnées ont montré des liens importants entre les métabolites des sphaignes et les processus liés au carbone, qui étaient les plus importants au printemps et en automne.

En bref, l'approche basée sur les traits biochimiques utilisés dans cette thèse améliore notre capacité à mieux comprendre et prédire l'espace fonctionnel de la sphaigne, la structure de la communauté microbienne associée et les traits microbiens, ainsi que les processus de l'écosystème liés au carbone dans un contexte de changements climatiques.

Abstract

Climate change is a threat to most ecosystems. However, these effects will be most pronounced at high northern latitudes, significantly affecting global carbon dynamics. Indeed, northern ecosystems, such as peatlands, play a key role in global carbon dynamics as carbon sinks, where one third of soil organic carbon is stored. Mosses, such as *Sphagnum* mosses, contribute significantly to carbon sequestration in peatlands, due to their unique morphological and biochemical (metabolites) traits. *Sphagnum* metabolites actively shape peatland habitat by producing recalcitrant litter and driving microbial structure and activities, and possibly controlling carbon and nutrients cycling. Despite this knowledge, the role of *Sphagnum* metabolites as important functional traits in peatland ecology remains poorly studied, particularly their response to climate change.

The aim of my PhD work was to explore the potential of *Sphagnum* metabolites in providing deeper mechanistic understanding of the *Sphagnum* functional trait space, and to predict microbial community composition and functioning across environmental gradients. I further examined how seasonal patterns of *Sphagnum* metabolites respond to climate changes and the consequence for peatland C uptake. To meet these goals, several field observations and experiments were conducted along a latitudinal gradient in Europe. I collected information about *Sphagnum* anatomical, morphological traits, and metabolites, as well as on peatland CO_2 fluxes and on microbial structure and activities. The reciprocal transplantation along a latitudinal gradient spanning five countries allowed to emulate shifts in climate conditions and evaluate *Sphagnum* metabolites plasticity.

My findings showed that *Sphagnum* species growing in different local environmental (vegetation composition, nutrients content) and regional (temperature, precipitation) conditions possess a suite of diverse biochemical traits (metabolites and enzymes) that support *Sphagnum* form and function, as well as *Sphagnum* resistance to environmental changes. Additionally, I found that the volume of the *Sphagnum* trait space was four times larger when biochemical traits were added to the usual suite of morphological-anatomical traits, than when they were excluded. *Sphagnum* interspecific trait variations were shown to play a key role in driving microbial community composition and microbial traits in addition to local and regional environmental conditions. The addition of *Sphagnum* traits to local and regional environmental variables in structural equation models (SEM) increased our capacity to predict and explain the variance of microbial communities and functions in peatlands. Additionally, the metabolites were shown to be better predictors of microbial community

structure and traits compared to anatomical and morphological traits. Finally, using a reciprocal transplantation experiment, I showed that *Sphagnum* species, transplanted to new sites, had similar responses of metabolites concentrations and gross ecosystem productivity over all seasons, with the maximum values in warmer sites. *Sphagnum* metabolites were very plastic in response to temperature and precipitation and the variation in phenotype (graphically represented as reaction norms) had similar slopes and curvatures. More interestingly, my data showed important linkages between *Sphagnum* metabolites and C-related processes, which were the most prominent in spring and autumn. In a nutshell, trait-based approach used in this thesis has a potential for understanding and predicting *Sphagnum* functional space, associated microbial community structure and microbial traits, carbon-related ecosystem processes in the context of climate change.

Acknowledgements

I would like to thank the jury for agreeing to read and evaluate this thesis. Also, I thank every reader for the interest in my research.

Vincent "el patrono" JASSEY, even though you were often a pain in the arse with your "good job; but; yes, but", but I thank you a lot to help me growing and finish this complicated scientific journey. Only you remember me outrage with R, my reactions to the goddamn comments and corrections. Our field trips are one of the best and the most remarkable moments of my PhD. I will not tell anyone about your gross tales, cause you never know who will transmit them to your HR. Well, I think I could write a book about how cool my PhD supervisor was/is, but I afraid I have more than enough of writing done. From all my heart, I thank you for all good and less pleasant times.

I want to thank Regis CEREGHINO, a godfather of my thesis. Thank you for always helping in hard times, for sharing your knowledges and experience. You are the master of text polishing, a boring phrase became so vivid after your touches!

Samuel HAMARD, my PhD buddy, PhD brother, PhD husband, PhD partner in crime, also known as Samybog and "dry as a bog". Thank you for this good time. It was so amazing to grow with you and to see you growing. You are so kind, so funny fella! Luckily, we shared more ups than downs together. Our trips were one of the best times together!!! I am deeply grateful to you, Samy! I wish you all the best with farm opening and I hope one day I can buy (or to get as a present) the products from your farm, cause your farm will be big, big very very big! Ah yes, Bird is the word!

Janna BAREL, my dear colleague, my dear friend, my neighbor. I owe my deepest gratitude to you. Your support meant a world to me. We shared a lot of good moments, lunches, trips and of course, working time. Thank you for all the help, motivation and encouragement! I hope you see you soon somewhere in Finland!

Special thanks to Honorine GEISSEL, a person who helped a lot not only with the labwork, but also with the support in hard times. Thank you for your kindness, your positive energy! I am so happy that now I have a friend to visit in Montpellier!

I would like to express my gratitude to my dear Mixopeat colleagues, Frédéric DELARUE, Ellen DORREPAAL, Martin KÜTTIM, Mariusz LAMENTOWICZ, Bjorn J.M. ROBROEK, Eeva-Stiina TUITTILA. Thank you for your participation in the articles writing, thank you for all your tips and recommendations. I was glad to meet you!

I owe a very important debt to Camille LARUE, the kindest internship supervisor! Thank you for all your experience, your support and just for being so cool!

Bertrand "Mr. Zero or Mr. Putain" POURRUT and Julien "Mr. Dr. Teacher or just Castelino" CASTELIN, thank you for picking me 27th of June 2016 (the day of our the very first skype)! Meeting you was a pivotal moment in my life! I am so grateful for everything what I have now, is because of you! You created a monster!

I would like to thank CIRCE team, especially Josephine, Stephanie, Anne-Marie, Fred, Arthur "Steplerman", Romain, Eric. It was so nice to share good moments with you! Nice talks, all the fun!

Dear Regine and Annick, I cannot imagine how the lab would have been without you! The kindest people in the world. I thank you for all the help and nice talks!

I would like to thank Cyril and Catherine for not only making orders of the lab supplies, but also for nice chats and helping with all that scary sites!

My deepest appreciation goes to Yann. Thank you for always finding a solution with a goddamn computer! I don't know if I can write my thesis without your technical support!

I want to thank Fred, Didier, Jessica, Virginie, Corine, Marie-Jo for all your help at the lab, for your support and for good talks! You are the coolest people, who never say no, when asked for help!

I would like to thank to Jerome, Annie and Thierry! Thank you for always finding a solution to all the issues! Thank you for allowing me to occupy as much lab space as I needed! And, of course, I got a lesson for all my life that butanol is better to boil under a hood!

Special thanks to Franck Gilbert and Arnaud ELGER, for helping with a preparation for the SDU2E competition! Thanks to you that I can write this thesis!

Many thanks to Clarisse, who taught me about biomarkers and who warned about not easy life with them! You were right!!!

I am deeply grateful to Camille, with who I had good talks and breaks! Thank you for all the support and help! Many thanks to Adriana for all good conversations we had. Marie, thank you for bringing a lot of positive energy, hope in 3 years to be invited for your defense. Also, I thank a squad of ensat: Theo, Jeremy, Benjamin with Margeux, Oscar, Columba, Roxaoane — it was nice to hung out with you guys!

My dear ex-neighbor Tim, my friend of hour-outside-is-allowed during the first confinement, thank you for all philosophical conversations and just for having fun together!

I want to thank Tetiana Stefanovska and Natalia Bilera, for recommending and pre-selecting me for SMaP! Also, I thank Valeria Bondr' and the faculty of ecology in NULES.

Thanks should also go to Vika Xiaomi, Vika Polovkysia, Tonia, Alina and Mishania (aka Batia) for your support in hard times and your understanding! I am so happy that I have so nice people who don't forget me despite the distance and time! My dear Canadian Andrii, thank you for not forgetting me! I would like to say thank to my podryzhka (friend) Nadia, also known as "never say Nad'ka", who become a good friend and a free phycologist! I hope one day we will create our Youtube blog! I want to thank Ira, for all the support and encouraging me with your astrological predictions!

I would like to thank Francesco, with whom I have shared the whole experience of the thesis, since the begging. I am so grateful for all your support, for your patience and just for being with me. Thank you for helping me to grow and motiving me when my spirit was down.

Також хочу висловити щиру подяку моїй сім'ї СИТЮК, яка завжди була поруч зі мною! Ви завжди приймали мене без будь-яких поправок і без будь-яких додаткових обґрунтувань, не те що ті кляті наукові журнали! Мені дуже пощастило бути дочкою, сестрою, невіскою, тіткою в нашій сім'ї. Дякую вам за мотивацію, підбадьорювання і любов! Я вас люблю і дуже сумую!

Слава Україні, Героям Слава!

Слава Нації, Смерть ворогам!

Scientific valorization

Research papers

Sytiuk, A., Céréghino, R., Hamard, S., Delarue, F., Dorrepaal, E., Küttim, M., Lamentowicz, M., Pourrut, B., Robroek, B.J.M., Tuittila, E.-S., Jassey, V.E.J., 2022. Biochemical traits enhance the trait concept in *Sphagnum* ecology. Oikos e09119, 1–15**.** DOI: 10.1111/oik.09119

Sytiuk, A., Céréghino, R., Hamard, S., Delarue, F., Dorrepaal, E., Küttim, M., Lamentowicz, M., Pourrut, B., Robroek, B.J.M., Tuittila, E.-S., Jassey, V.E.J.,2021. Predicting the structure and functions of peatland microbial communities from *Sphagnum* phylogeny, anatomical and morphological traits and metabolites Journal of Ecology, DOI: 10.1111/1365-2745.13728

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

Hamard, S., Céréghino, R., Barret, M., **Sytiuk, A**., Lara, E., Dorrepaal, E., Kardol, P., Küttim, M., Lamentowicz, M., Leflaive, J., Le Roux, G., Tuittila, E.S., Jassey, V.E.J., 2021. Contribution of microbial photosynthesis to peatland carbon uptake along a latitudinal gradient. J. Ecol. 109, 3424–3441. DOI: 10.1111/1365-2745.13732

Sytiuk, A., Céréghino, R., Hamard, S., Geissel, H., Dorrepaal, E., Küttim, M., Lamentowicz, M., Pourrut, B., Robroek, B.J.M., Tuittila, E.-S., Jassey, V.E.J. Climate change and seasonality effects on *Sphagnum* metabolite plasticity and their linkages with peatland carbon uptake—in preparation for Journal of Ecology, to submit in June 2022.

Poster presentations

Ecology of plant communities (ECOVEG 14) conference in Toulouse (France) — Apr 2019

British ecological society (BES) conference in Belfast (Northern Ireland) — Dec 2019

Contents

List of figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

List of tables

Chapter *1*

Chapter *3*

Chapter 4

Chapter 6

General introduction

(Version française)

La température mondiale a augmenté de plus de 1°C par rapport à l'ère préindustrielle (Allen et al., 2018) en même temps que des averses plus fortes et inégalement réparties sur le globe, ce qui entraîne des événements extrêmes plus fréquents (Fischer et Knutti, 2016; Medvigy et Beaulieu, 2012). Le réchauffement rapide du climat et les changements environnementaux associés vont affecter la plupart des biomes terrestres, notamment aux hautes latitudes nord où les effets seront les plus prononcés (Ljungqvist et al., 2016; Swindles et al., 2019). L'effet des changements climatiques ont été démontrés pour de nombreuses espèces végétales à court (Chen et al., 2011) et à long terme (Lamentowicz et al., 2019), modifiant la physiologie des plantes ainsi que dans la composition des communautés végétales. Ces changements sont susceptibles d'affecter les processus des écosystèmes liés à l'accumulation du carbone (C) (Alexander et al., 2015; Harrison, 2020; Parmesan et Yohe, 2003) et qui sont dirigés en partie par les plantes dans la plupart des écosystèmes du monde (Elmendorf et al., 2012).

Comprendre comment les propriétés fonctionnelles des plantes répondent à leur environnement et comment elles affectent le fonctionnement des écosystèmes est une question importante de l'écologie fonctionnelle (Calow, 1987). Les traits de vie des végétaux sont une suite de propriétés anatomiques, morphologiques, physiologiques ou phénologiques détectables chez chaque individu (Violle et al., 2007) et le produit de processus évolutifs et de modèles d'assemblage de communautés en réponse à des limitations abiotiques et biotiques (Fernando et al., 2007). En déterminant les propriétés essentielles de l'écophysiologie, de la morphologie et des stratégies d'histoire de vie des plantes, les traits fonctionnels aident à comprendre comment les plantes répondent aux facteurs environnementaux, comment elles influencent les autres niveaux trophiques et et comment elles affectent les processus écosystémiques comme l'assimilation de carbone (Díaz et al., 2004; Garnier et Navas, 2012; Grime, 2006; Lavorel et Garnier, 2002). Par exemple, les traits fonctionnels des plantes ont été appliqués pour évaluer la variabilité des cycles biologiques des plantes (Adler et al., 2013; Díaz et al., 2016; Mazziotta et al., 2018), les relations au sein des communautés végétales (Bruelheide et al., 2018) et les processus écosystémiques (Cornwell et al., 2008; De Deyn et al., 2008). Malgré leur pertinence pour généraliser les projections à travers les échelles organisationnelles et spatiales (Adler et al., 2013), les traits fonctionnels des plantes présentent également quelques limites. En effet, les traits des plantes qui sont largement utilisés par les écologistes (par exemple, la taille des graines, la surface foliaire spécifique et la hauteur des plantes (Díaz et al., 2016) ont un faible pouvoir explicatif des processus écologiques (Plas et al., 2020). Ainsi, une grande fraction des processus écosystémiques reste

inexpliquée. Ce faible pouvoir explicatif des traits fonctionnels pourrait être dû à la lenteur des réponses des traits "classiques", et si le stimulus est éphémère, alors la réponse à ce stimulus peut ne pas correspondre au maximum au besoin du stimulus (Metlen et al., 2009). Par exemple, la façon dont les plantes recherchent des nutriments suggère que la plasticité morphologique est moins réactive et moins économe en énergie que la plasticité biochimique (voir les exemples dans Metlen et al., 2009). Il y a donc des limites à la mesure dans laquelle les traits morphologiques classiques des plantes peuvent prédire les processus des écosystèmes. Des facteurs supplémentaires, plus étroitement liés à la physiologie des plantes, comme les métabolites primaires et secondaires, produits et sécrétés dans le milieu par les plantes (composés biochimiques), pourraient aider à repousser ces limites (Walker et al., 2022). Par exemple, des études récentes ont suggéré que l'utilisation des métabolites secondaires des plantes vasculaires pouvait améliorer les prédictions des processus écosystémiques dans un contexte de réchauffement climatique (Walker et al., 2019).

En raison de leur mode de vie sédentaire, les plantes sont limitées dans leur mouvement pour éviter les conditions environnementales stressantes. Ainsi, les plantes ont développé de nombreux mécanismes qui les aident à la fois à s'adapter aux changements environnementaux, permettant une flexibilité fonctionnelle sans compromettre les processus de développement cellulaire et physiologique, et à distribuer de manière optimale les ressources disponibles (Arnold et al., 2019; Yang et al., 2018). L'un des mécanismes les plus simples et les plus rapides est la production de métabolites (McCue et Hanson, 1990). Le règne végétal produit une pléthore de métabolites, avec une fourchette estimée entre 200 000 et 1 000 000 de composés (Wang et al., 2019). Les métabolites sont des substrats ou des produits de réactions enzymatiques, et une seule plante peut produire un ensemble de métabolites différents, communément appelé le métabolome, qui varie de 5 000 à 10 000 composés (Fernie et al., 2004). Le métabolome des plantes peut être considéré comme un trait fonctionnel complexe, car les enzymes métaboliques individuelles isolées sont rarement liées à la physiologie *in vivo*, sauf si elles sont intégrées dans une voie métabolique (Weng, 2014). La production de métabolites est essentielle pour la croissance des plantes, le réapprovisionnement cellulaire, l'allocation des ressources de la plante entière et l'adaptation aux conditions environnementales changeantes (Berini et al., 2018; Weng, 2014). Par exemple, les plantes répondent au stress environnemental (comme la sécheresse, les attaques d'herbivores) en produisant des métabolites spécialisés, comme les alcaloïdes, les terpénoïdes et les composés phénoliques (par exemple, Cipollini et al., 2012; Defossez et al., 2021; Fernandez-Conradi et al., 2021; Fernandez et al., 2016; Peters et al., 2019; van Dam et

Bouwmeester, 2016; Van der Putten et al., 2013; Weckwerth et Kahl, 2013). En outre, les métabolites sont des médiateurs des interactions plantes-sols en influençant les activités microbiennes avec des conséquences possibles sur les processus de l'écosystème (Iason et al., 2012). Les métabolites des plantes peuvent être une clé pour comprendre le fonctionnement des écosystèmes car ils peuvent être liés à des processus tels que la décomposition et/ou l'absorption de carbone (Chomel et al., 2016; Whitham et al., 2006). Ainsi, le métabolome est le lien entre la perception des signaux environnementaux et leur conversion en traits d'histoire de vie, c'est-à-dire un pont mécanistique entre le génotype et le phénotype de la plante (Fiehn, 2002; Sanchez et al., 2008; Sharma et al., 2021). La détermination des métabolites végétaux peut donc fournir des informations sur la façon dont les plantes se comportent et s'adaptent lorsqu'elles sont exposées à des conditions environnementales changeantes (Ahanger et al., 2018).

De nombreuses tentatives ont été faites pour caractériser la diversité et la dynamique des métabolites au sein des plantes vasculaires (Bakhtiari et al., 2021; Defossez et al., 2021; Obata et Fernie, 2012; Skoneczny et al., 2018; Turner et al., 2016), alors que moins d'efforts ont été consacrés aux plantes non vasculaires telles que les mousses. Pourtant, les mousses contribuent de manière significative à la biomasse aérienne et à la séquestration du C du sol, dans les biomes froids comme les forêts boréales et les tourbières (Tan et Pócs, 2000; Turetsky, 2003), où un tiers du C organique du sol mondial est stocké (Hugelius et al., 2020; Xu et al., 2018). Les sphaignes sont des espèces clés dans les écosystèmes tourbières car elles peuvent se développer dans un environnement extrêmement pauvre en nutriments, avec des conditions anoxiques, froides et acides, tout en contribuant à l'accumulation de C à long terme; leur présence module donc le fonctionnement de l'écosystème (Clymo et Hayward, 1982; Hájek et Vicherová, 2014; van Breemen, 1995). Comme les sphaignes n'ont pas de tissus conducteurs d'eau, leur capacité à maintenir l'humidité dans leurs parties apicales actives dépend de l'efficacité du transport de l'eau de la nappe phréatique vers la partie supérieure. Les sphaignes ont donc une capacité d'échange cationique élevée qui, en même temps, acidifie l'environnement et piège les nutriments (Soudzilovskaia et al., 2010). Les sphaignes produisent également d'autres composés organiques (c'est-à-dire des métabolites), qui servent de source primaire de protons acidifiants dans les tourbières. Certains métabolites, comme les composés phénoliques produits par les sphaignes, sont importants pour la suppression des activités microbiennes (Zhao et al., 2021) ou pour la résistance structurelle à la décomposition (Verhoeven et Toth, 1995). En outre, ces composés peuvent modifier de manière significative la structure des communautés microbiennes dans les tourbières à sphaignes (Hamard et al.,

2019; Jassey et al., 2011b, 2011a) ou avoir des propriétés allopathiques (Chiapusio et al., 2013). Cependant, on ne sait toujours pas quels métabolites sont responsables de la résistance à la décomposition des sphaignes, et donc impliqués dans le stockage du carbone (mais voir James et al., 2021).

Malgré l'importance des tourbières dans le stockage global de C, d'importants processus spécifiques aux tourbières qui régulent l'accumulation de C ne sont pas largement utilisés dans les modèles climatiques actuels (Frolking et al., 2013; Limpens et al., 2008). Ainsi la direction de la réponse du cycle de C des tourbières au climat reste incertaine (Frolking et al., 2011). L'effet des changements climatiques sur les métabolites des sphaignes en soi reste largement inconnu, car la plupart des études réalisées à ce jour se sont concentrées sur l'effet du changement climatique sur les communautés végétales et les flux de carbone (par exemple, Binet et al., 2017; Bragazza et al., 2016; Dieleman et al., 2016b; Jassey et al., 2013; Jassey et Signarbieux, 2019; Robroek et al., 2009). Bien que les processus par lesquels les sphaignes contrôlent la décomposition, l'accumulation et la transformation du carbone et les rétroactions ultérieures sur le climat soient en cours d'élaboration (par exemple, Dorrepaal et al., 2006; Jassey et al., 2018; Jassey et Signarbieux, 2019; Robroek et al, 2007), les interactions "métabolite des sphaignes-microbes" (Binet et al., 2017; Jassey et al., 2011a) et "métabolites des sphaignes-processus des tourbières" (Dieleman et al., 2016a; Wang et al., 2015) dans le contexte des changements climatiques restent encore mal compris. Aujourd'hui, aucune information n'est disponible sur la manière dont les changements temporels des métabolites de la sphaigne rétroagissent sur les processus liés au carbone. Par conséquent, des incertitudes demeurent quant à la réponse des tourbières face aux changements climatiques, et nécessitent des études détaillées sur la façon dont les rétroactions dynamiques des métabolites de la sphaigne influent sur le cycle du C des tourbières, notamment sur la productivité primaire nette. Dans cette thèse, l'objectif global est d'aborder ces incertitudes en explorant le potentiel des métabolites primaires et secondaires des sphaignes à 1) mieux expliquer de l'espace fonctionnel occupé par les sphaignes, 2) mieux prédire la variabilité des communautés microbiennes associées aux tourbières, et 3) à mieux comprendre le lien entre les métabolites des sphaignes et la dynamique du C des tourbières dans le cadre du changement climatique.

(English version)

Global temperature has risen by more than 1°C comparing to the pre-industrial era (Allen et al., 2018) along with unevenly distributed and heavier downpours around the globe, resulting in more frequent extreme events (Fischer and Knutti, 2016; Medvigy and Beaulieu, 2012). Rapid climate warming and associated environmental changes are expected to affect most of the biomes in the northern hemisphere, with the most pronounced effects at high northern latitudes (Ljungqvist et al., 2016; Swindles et al., 2019). A suite of shifts associated with climatic changes have been showed for many plant species in the short (Chen et al., 2011) and in the long term (Lamentowicz et al., 2019). Shifts in plant physiology as well as in plant community composition are likely to affect the ecosystem processes related to carbon (C) accumulation (Alexander et al., 2015; Harrison, 2020; Parmesan and Yohe, 2003) and that are driven by plants in most of ecosystems around the globe (Elmendorf et al., 2012).

Understanding how the functional properties of plants respond to and affect their environment is an important issue of functional ecology (Calow, 1987a). Plant traits are a suite of anatomical, morphological, physiological or phenological properties detectable in each individual (Violle et al., 2007) and the product of evolutionary processes and community assembly patterns in response to abiotic and biotic limitations (Fernando et al., 2007). By determining essential properties of plant ecophysiology, morphology and life-history strategies, functional traits help understanding how plants respond to environmental factors, influence other trophic levels and affect ecosystem processes (Díaz et al., 2004; Garnier and Navas, 2012a; Grime, 2006; Lavorel and Garnier, 2002). For example, traits have been applied to evaluate the variability in plant life history trade-offs (Adler et al., 2013; Díaz et al., 2016; Mazziotta et al., 2018), relationships in plant communities (Bruelheide et al., 2018) and ecosystem processes (Cornwell et al., 2008; De Deyn et al., 2008). Despite their relevance for generalizing projections across organizational and spatial scales (Adler et al., 2013), those traits that are widely used by ecologists (*e.g.* seeds size, specific leaf area and plant height (Díaz et al., 2016) have low explanatory power of ecological processes (Plas et al., 2020). Thus, a large fraction of ecosystem processes remains unexplained. This low explanatory power of functional traits could be due to slow responses of 'classical' traits and if the stimulus is ephemeral, then the response to that stimulus may not maximally match the need for the stimulus (Metlen et al., 2009). For instance, the way plants seek for nutrients suggests that morphological plasticity is less responsive and energy efficient comparing to biochemical plasticity (see examples in Metlen et al., 2009). There are, therefore, some limits to the extent to which classical morphological traits can predict ecosystem processes. Additional drivers,

more closely embodied in plant physiology such as plant metabolites (biochemical compounds) can help pushing those limits (Walker et al., 2022). Moreover, recent studies suggested that the use of plant metabolites can improve predictions of ecosystem processes (Walker et al., 2019).

Due to a sessile lifestyle, plants are limited to avoid stressful environmental conditions. Thus, plants have evolved many mechanisms that help them both to adapt to environmental changes enabling functional flexibility without compromising cellular and physiological developmental processes and to optimally distribute available resources (Arnold et al., 2019; Yang et al., 2018). One of the simplest and quickest mechanism is the production of metabolites (McCue and Hanson, 1990). Plant kingdom produces a plethora of metabolites, with an estimated range of 200 000 to 1 000 000 compounds (Wang et al., 2019). Metabolites are substrates or products of enzymatic reactions, and a single plant can produce a set of different metabolites (*i.e.* metabolome) which ranges from 5 000 to 10 000 compounds (Fernie et al., 2004). The plant metabolome can be regarded as complex traits, as isolated individual metabolic enzymes are rarely related to *in vivo* physiology, unless they are integrated into a metabolic pathway (Weng, 2014). Production of metabolites is essential for plant growth, cellular replenishment, whole-plant resource allocation and adaptation to changing environmental conditions (Berini et al., 2018; Weng, 2014). For instance, plants respond to environmental stress (like drought, herbivores attacks) by producing specialized metabolites, such as alkaloids, terpenoids, and phenolic compounds (*e.g.* Cipollini et al., 2012; Defossez et al., 2021; Fernandez-Conradi et al., 2021; Fernandez et al., 2016; Peters et al., 2019; van Dam and Bouwmeester, 2016; Van der Putten et al., 2013; Weckwerth and Kahl, 2013). Besides, metabolites are mediators of plant-soil interactions by influencing microbial activities with possible consequences for ecosystem processes (Iason et al., 2012a). Plant metabolites can be a key for understanding ecosystem functioning as they may be related to processes such as decomposition and/or C uptake (Chomel et al., 2016; Whitham et al., 2006). Thus, the metabolome is the link between perception of the environmental signals and their conversion into life history traits, *i.e.* a mechanistic bridge between plant genotype and phenotype (Fiehn, 2002; Sanchez et al., 2008; Sharma et al., 2021). The determination of plant metabolites can provide information on how plant perform and adapt when exposed to changing environmental conditions (Ahanger et al., 2018).

There have been many attempts to characterize the diversity and dynamics of metabolites within vascular plants (Bakhtiari et al., 2021; Defossez et al., 2021; Obata and Fernie, 2012; Skoneczny et al., 2018; Turner et al., 2016), but less effort has been directed

towards non-vascular plants such as mosses. Yet mosses make a significant contribution to aboveground biomass and soil C sequestration, in cold biomes like boreal forests and peatlands (Tan and Pócs, 2000; Turetsky, 2003), where one third of global soil organic C is stored (Hugelius et al., 2020; Xu et al., 2018). *Sphagnum* mosses are keystone species in peatland ecosystems as they can thrive in extremely nutrient-poor environment with anoxic, cold and acidic condition, while contributing to long-term C accumulation; their presence therefore modulates ecosystem functioning (Clymo and Hayward, 1982; Hájek and Vicherová, 2014; van Breemen, 1995). As *Sphagnum* mosses lack water-conducting tissues, the ability to maintain moist in their active apical parts relies on the water transporting efficiency from water table to the upper part, thus *Sphagnum* has a high cation exchange capacity which at the same time acidifies the environment and traps nutrients (Soudzilovskaia et al., 2010). *Sphagnum* mosses also produce other organic compounds (*i.e.* metabolites), which serve as the primary source of acidifying protons in peatlands. Certain metabolites like spagnan and phenolic compounds produced by *Sphagnum* have been pointed out to be important in suppressing microbial activities (Zhao et al., 2021) or providing structural resistance to decay (Verhoeven and Toth, 1995). Additionally, these compounds can significantly alter the structure of microbial communities in *Sphagnum* peatlands (Hamard et al., 2019; Jassey et al., 2011b, 2011a) or have allopathic properties (Chiapusio et al., 2013). However, it is still debatable which metabolites are responsible for *Sphagnum* decay resistance, and thus involved in C storage (but see James et al., 2021).

Despite the importance of peatlands in global C storage, important peatland-specific processes that regulate C accumulation are not widely used in current climate models (Frolking et al., 2013; Limpens et al., 2008) and the direction of the response of C cycle to climate remains uncertain (Frolking et al., 2011). The effect of climate change on *Sphagnum* metabolites *per se* remains largely unknown, as most of studies to date are concentrated on the effect of the climate change on vegetation communities and C fluxes (*e.g.* Binet et al., 2017; Bragazza et al., 2016; Dieleman et al., 2016b; Jassey et al., 2013; Jassey and Signarbieux, 2019; Robroek et al., 2009). Although the processes by which *Sphagnum* controls C decomposition, accumulation, transformation and subsequent feedback to climate are developing (*e.g.* Dorrepaal et al., 2006; Jassey et al., 2018; Jassey and Signarbieux, 2019; Robroek et al., 2007), the '*Sphagnum* metabolite–microbe' (Binet et al., 2017; Jassey et al., 2011a) and '*Sphagnum* metabolite-peatland processes' (Dieleman et al., 2016a; Wang et al., 2015) interactions in the context of climate changes remain poorly understood. Nowadays, no information is available on how temporal changes in *Sphagnum* metabolites feedback to C-related processes.

Therefore, uncertainties about the response of peatlands in the face of climate changes call for detailed studies on how *Sphagnum* metabolites dynamic feedbacks to net peatland primary productivity. In this thesis, the overall aim is to address these uncertainties by exploring the potential of *Sphagnum* metabolites in explaining functional trait space, predicting the associated microbial communities, and linking with C dynamic under climate change.

Chapter 1. Bibliographical review

Bibliographical review

1.1. Every peatland is a wetland, not every wetland is a peatland

1.1.1. Definition of peatland

Peatlands belong to a larger set of ecosystems known as wetlands. They comprise from 50 to 70% of wetland ecosystems (Joosten and Clarke, 2002). Peatlands are at the border between terrestrial ecosystems and aquatic ecosystems and are characterized by a high-water level, close to or even above the soil surface. This omnipresence of water affects the aeration of the soil and thus modulates the availability of oxygen (Rydin and Jeglum, 2013; Vitt, 2000). Peatlands are unbalanced ecosystems, where the production surpasses decomposition of the organic matter, thus leading to its accumulation as peat (Vitt, 2000).

Peat is defined as the remains of plant and animal constituents accumulated due to incomplete decomposition under waterlogged, anoxic and some specific environmental conditions (*e.g.* cold, rainy). Most of the material arises aboveground as photosynthetic organic material and is stored as litter, which buries by new layers of litter (Rydin and Jeglum, 2013). Peatlands are used to describe peat-covered lands, with usually >30 cm of peat (Joosten and Clarke, 2002) in most of the countries, excluding Canada where the minimum is 40 cm (National Wetlands Working Group, 1997). Mire is a term to describe a wet terrain, which is dominated by peat forming plants. This term has slightly broader concept comparing to a peatland, as peat accumulation can be in areas where the required depth of peat (*i.e.* 30 cm) is not attained to be quantified as a peatland. The other classifications and terms related to peat-accumulated wetlands can be seen in (Rydin and Jeglum, 2013) and Fig. 1-1.

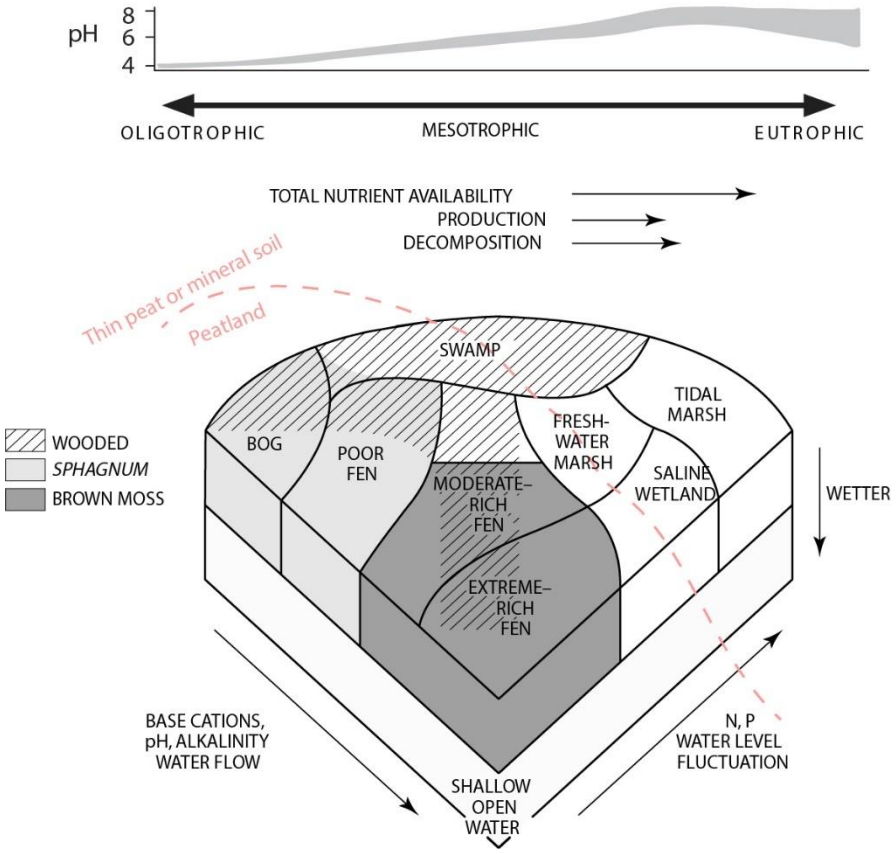


Figure 1-1. Ternary diagram showing the position of broad wetland types in relation to different environmental gradients and ability to accumulate peat (modified from Rydin and Jeglum, (2013) and Vitt, (2000).

1.1.2. Peatlands distribution and productivity

Peatlands cover approximately 3.7±0.5 million km², this occupation corresponds to approximately 3 % of the world's area (Hugelius et al., 2020; Xu et al., 2018). 80% of peatlands are located in the temperate-cold climates in the northern hemisphere (Fig. 1-2, Xu et al. (2018)). Six countries possess more than 50 000km² of peatland and these territories account for 93% of the world's peatlands and five of these countries are mostly in boreal zone. Russia contains 1.42×10^6 km², Canada 1.235×10^6 km², the USA 0.625×10^6 km², Finland 0.096×10^6 km², and Sweden 0.07×10^6 km²; Indonesia has an estimated 0.27×10^6 km² (Vitt, 2008) and Congo has 0.1445×10^6 km² (Fatoyinbo, 2017).

Nichols and Peteet (2019) found that peatland can store up to 1055 Gt of C, although this number is still debated (Ratcliffe et al., 2021; Yu et al., 2021). Indeed, previous estimations were around 415±150 Gt of C (Hugelius et al., 2020; Xu et al., 2018). These stocks of C are equivalent to 5-20% of the global soil C sink, 15–72% of atmospheric C, and 18–89% of global terrestrial C biomass (Minasny et al., 2019). Peatlands are C sinks with very high C density

per unit area (from 50 to >500 kg C m^{-2}) and the rate of accumulation has been 0.5-1 mm per year since the last glacial period (Yu et al., 2010).

Yu et al. (2010) found that northern peatland formation peaked in early Holocene, around 11,000–9000 years ago with the maximum accumulation 25 g C m^{-2} $year^{-1}$ (average accumulation of 18.9 g C m^{-2} $year^{-1}$). Tropical peatland initiation occurred more than 20,000 years ago and peaked about 8000–4000 years ago (with maximum rates of 20– 50 C m^{-2} $year^{-1}$) and with 12.8 g C m^{-2} $year^{-1}$ on average, and southern peatlands (Patagonia) peaked about 17,000–13,500 years ago (with maximum rates of 15– 40 C m^{-2} $year^{-1}$) and with average of 22 C m^{-2} $year^{-1}$. Peatland formation in the northern regions are significantly control by climate and its seasonality. Peatland efficiently cooled the global climate on the millennium scale (Frolking and Roulet, 2007) and undisturbed peatlands continue functioning as net C sinks (Limpens et al., 2008).

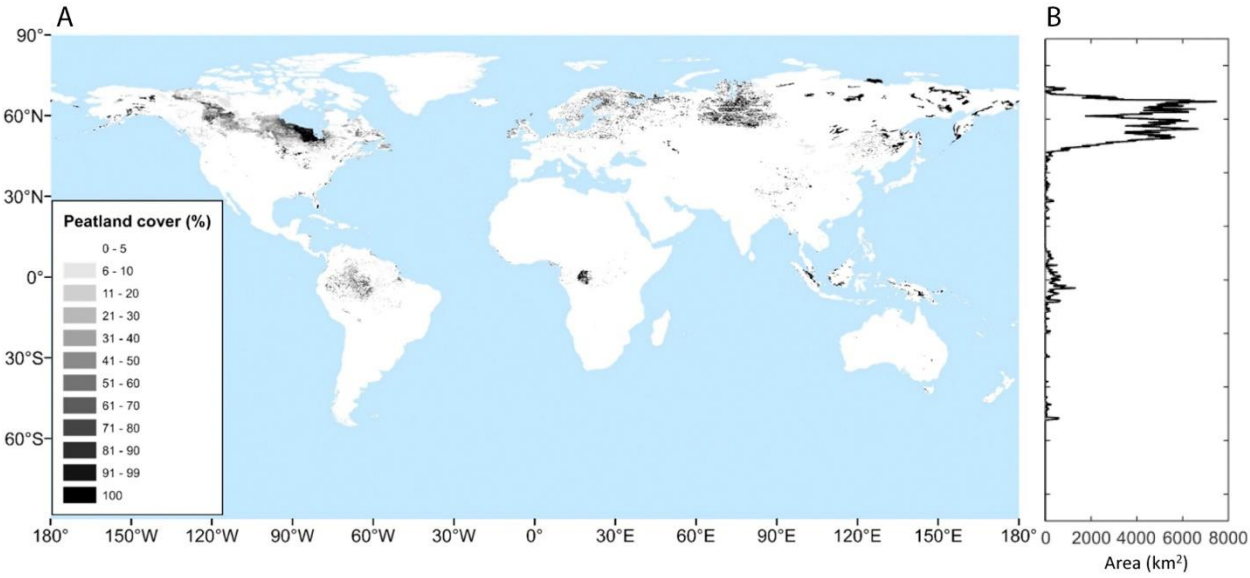


Figure 1-2. (A) Map of global peatland distribution (Xu et al., 2018) and (B) a global estimate of occupied area along the latitude (Minasny et al., 2019)

1.1.3. Peatland formation

The formation of peatland is possible under two main conditions: (1) omnipresent waterlogging and (2) production of plant litter is faster than its decomposition (Vitt, 2008). When these two conditions are synchronized, two main processes of peat are generally distinguished (Fig. 1-3; Heinselman, 1970):

- terrestrialization is the progressive filling of a territory of stagnant water with both exogenous inputs and water-colonizing vegetation by creating impervious iron pan;
- paludification is the formation of peat directly on an anoxic mineral soil (without forming iron pan), due decreased soil porosity (resulting from clogged pores by humic substances) and topographically favorable areas (depressions).

Peatland can be formed by one of those processes or combination of two, depending on the spatial area or the time period (Ruppel et al., 2013).

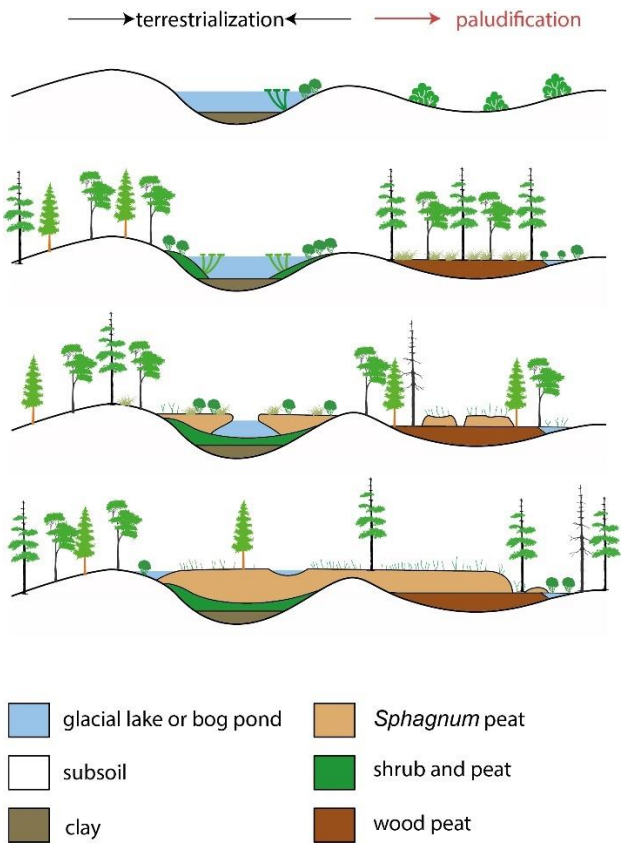


Figure 1-3. The process of peatland formation via terrestrialization (left) and paludification (right) (modified from Anderson et al. (2003) and McLaughlin et al. (2013)

1.1.4. Peatland types

By nature, wetlands can control the water chemistry as they are permanently intact with the mineral soils. Especially of those elements, which are responsible for water acidity/alkalinity like calcium, and plant growth, as nitrogen and phosphorous (Keddy, 2010). In peatlands, due to formation of peat, roots can become isolated from the mineral soils (*i.e.* nutrient source), and thus become considerably depended on deposited nutrients from rainwater or runoff (van Breemen, 1995). Subsequently, acidity/alkalinity and water nutrients status are two critical

factors which differentiate peatland types (Bridgham et al., 2001; Heinselman, 1970; Rydin and Jeglum, 2013; Vitt, 2000; Wheeler and Proctor, 2000 and Fig. 1-4):

- Ombrotrophic peatlands, or bogs, are mainly fed by precipitation and their surface is bulging above the surrounding terrain and subsequently they are isolated from laterally moving mineral-rich soil waters. Their surface can be convex (raised or domed bogs) and they can also be flat or sloping. They are extremely nutrient-poor (oligotrophic) and acidic environments with the pH around 4 or lower. The dominant vegetation consists of *Sphagnum* moss, low sedges (*e.g.* cottongrass), and dwarf shrubs.
- Minerotrophic peatlands, or fens, are fed by belowground waters or by a runoff and the water table is slightly below or just above the surface. Their surface is generally concave or sloping in shape. They are nutrient-rich (especially nitrogen and phosphorus) and the pH of their surface water is generally above 4. The dominant vegetation in these ecosystems is bryophytes (to lesser extent *Sphagnum*), herbs and sedges

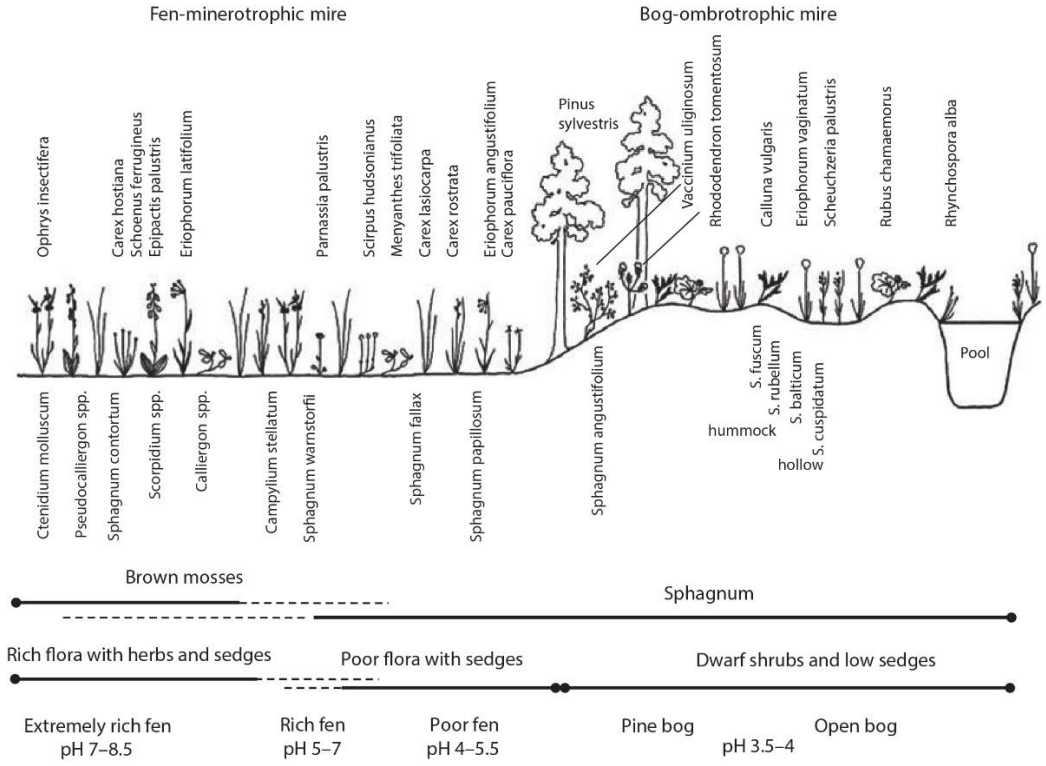


Figure 1-4. Plant species distribution along with the acidity/alkalinity gradient, which differentiate peatland types (modified from Rydin and Jeglum, 2013).

Within these types of peatlands (or even within one peatland) the distinct micro-topography arises regarding the distance to water table (Nungesser, 2003): with hummocks

referred to a topographic over-elevations, hollows as depressions, and lawns as areas in between (Fig. 1-5). These micro-topographic differences result in differences in plant composition, which expressed through different rates of peat accumulation (Johnson and Damman, 1991; Moore, 1991). For example, *Sphagnum fuscum* grows preferentially on hummocks, while *Sphagnum cuspidatum* — in hollows (Fig. 1-5). Interaction between *Sphagnum* species peculiarities (growth, decomposition rates) and moisture content maintain hummock and hollow resilience and control peat accumulation, thus creating a balance with local climate within long period of time (Nungesser, 2003).

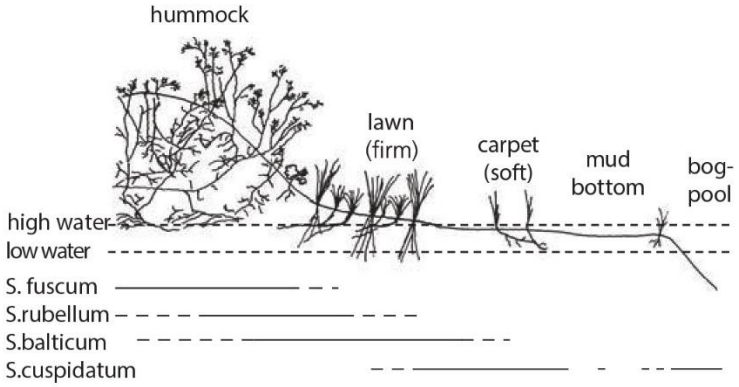


Figure 1-5. Schematic presentation of the microtopographic gradient in a bog (Rydin and Jeglum, 2013).

1.1.5. Vegetation that makes peatlands so awesome

Plant communities are important for peatland carbon dynamic as they directly drive carbon uptake through photosynthesis and indirectly regulate the release of carbon through decomposition (Del Giudice and Lindo, 2017; Dorrepaal, 2007). Different plant species significantly vary in their capacities to uptake or release carbon, with further consequences for carbon cycling. Peatland vegetation is generally divided into five main types of plant communities (Rydin and Jeglum, 2013):

- trees, at low densities in boreal and temperate bogs, are represented mostly by Pinaceae (*Pinus spp, Larix spp., and Picea spp.*) and Betulaceae (*Betula spp.* and *Alnus spp.*);
- shrubs can be found in wooded bogs, hummocky parts of open bog and fen hummocks, more common species are *Andromeda polifolia, Calluna vulgaris, Chamaedaphne*

calyculata, *Erica tetralix*, *Empetrum nigrum*, *Kalmia polifolia*, and *Vaccinium spp.* (both deciduous and wintergreen species), *Betula nana*, *Rhododendron tomentosum*;

- graminoids, which include Poaceae and other plants with similar (a grass like) morphology such as sedges (*Carex*), cotton grasses (*Eriophorum*) and other Cyperaceae, rushes (Juncaceae), *Scheuchzeria palustris* (the only species in its family);
- herbs are in present in low diversity in cirumboreal regions, while more common for (moderately) rich fens, for example *Menyanthes trifoliata*, *Rubus chamaemorus*, *Potentilla palustris* and carnivorous like *Drosera;*
- bryophytes are represented by dominant in many boreal and temperate peatlands, are mostly represented by peat mosses, brown mosses, liverworts, and feathermosses. The genus *Sphagnum* is a peat moss that plays a determining role in the construction of peatlands.

1.1.6. Peatlands provide immense ecosystem services

Peatlands provide a tremendous amount of ecosystem services including four groups of cultural value (recreation and education), resource provision (food and fresh water), regulation of processes (climate and water regulation and C sequestration) and ecosystem support (biodiversity and nutrient cycling) (Fig. 1-6; Davidson et al., 2018).

Peatlands are chronological archives of paleoenvironmental changes. The peat preserves remain of plants (*e.g.* pollen, seeds) and animals which had been living at the peatland allowing to document environmental and climatic information as well as past anthropogenic activities (Lamentowicz et al., 2015). The best-known examples of preservation by peatlands are Lindow (2000 years old) and Tollund (1400 years old) men (Mellegård et al., 2009; Painter, 1991) (Painter, 1991; Stalheim et al., 2009). Societies have been connected to peatlands for the purpose resource collection (plants, hunting, fishing, peat). Nowadays, peatlands provide with cultural, aesthetic, recreational and educational values. Indeed, the particular landscapes of the peatlands due to their unusual vegetation and microtopography, serves as tourist attraction as well as opportunities for education, training and research (Davidson et al., 2018).

Peatlands play an important role in maintaining biodiversity (at ecosystem, interspecies and intraspecies levels) because of the different peatland types and their high spatial heterogeneity (ecosystem diversity), the presence of specialized species including many rare, relict or threatened species (interspecific diversity) and the phenotypic and

genotypic variability within the same species (intraspecific diversity) (Minayeva and Sirin, 2012). In peatlands, microorganism efficiently recycle nutrients and carbon from organic matter to higher trophic levels as well as peatland vegetation, thus supporting nutrients cycling. Peatlands also play an important role in the water cycle. For example, they buffer the effects of a drought by providing some stored water or a flood by retaining part of the excess water, thus regulating the water cycle (Joosten and Clarke, 2002). They also have an effect on water quality, notably by filtering and retaining suspended particle, degrading certain organic micro-pollutants and fixing metals due to their strong cation-exchange capacity (Rydin and Jeglum, 2013).

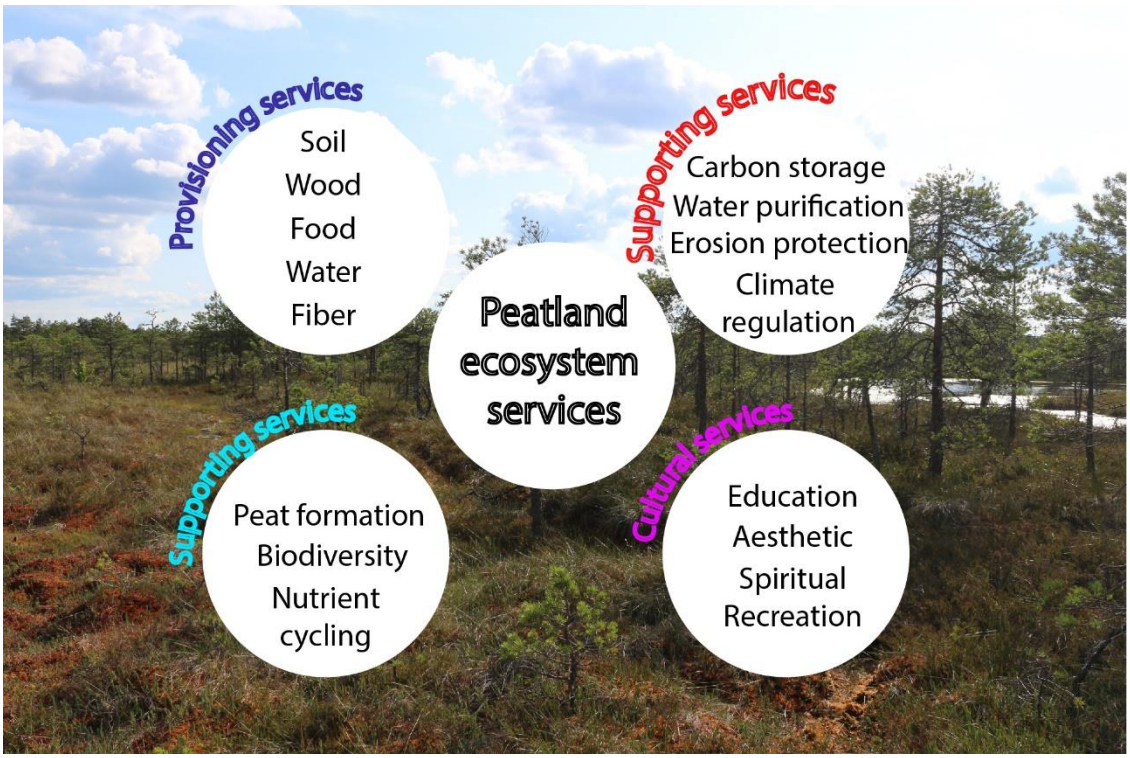


Figure 1-6. Ecosystem, services provided by peatland modified from Davidson et al. (2018). Background photograph was taken in Männikjärve bog, Estonia in July 2019 (personal collection)

The ability of peatlands to store C is highly dependent on the synergy between climate, hydrology and vegetation. However, peatlands and their components will be affected by global change and may have important feedbacks to climate depending on the response of gas exchange between the atmosphere and peatlands (Limpens et al., 2008).

1.1.7. Climate change and peatlands

Despite the services provided, half of the peatland area in Europe has disappeared, which comprises more than 300,000 km² (Joosten and Clarke, 2002). Many peatlands have been degraded by anthropogenic activities and ability to accumulate peat became impossible, *e.g.* agricultural activities. In addition, climate change can affect the peatland functioning and its function for C sequestration.

1.1.7.1. Peatland components under climate change

Northern ecosystems are estimated to store more than 65% of global organic carbon pool (Hengl et al., 2014; Hugelius et al., 2020). Peatlands, as main carbon stocks, are predicted to significantly contribute to warming-induced carbon loss by the end of the next century (Crowther et al., 2016) *via* CO_2 and CH_4 emission to the atmosphere or dissolved carbon leaking to rivers, if peatlands were destabilized by climate change or intensification of land use (Frolking and Roulet, 2007). It is becoming more apparent that warming more likely has a direct effect on carbon cycle feedback by altering the balance between primary productivity and ecosystem respiration (Davidson and Janssens, 2006), however indirect effects though chances in plant community composition can play an important role (De Deyn et al., 2008; Hooper et al., 2012; Ward et al., 2013). A plausible transition from *Sphagnum* moss to vascular plants dominance is generally consistent in the climate and these climate-induced shifts may cascade to the mobility of organic matter in peatland soils (Gavazov et al., 2018; Walker et al., 2016). The intensification of vascular plant growth can be due to increased peat mineralization, and thus decreased light availability for *Sphagnum* capitulum (Malmer et al., 1994). Thus, the climate change leads to increasing competition of *Sphagnum* mosses with vascular plants (Heijmans et al., 2002). The increasing temperatures promoted vascular plant primary productivity (Dorrepaal et al., 2006; Weltzin et al., 2000) and their abundance (Weltzin et al., 2003). The shifts in peatland plant community structure with subsequent effect on ecosystem processes (*e.g.* carbon cycling), can be attributed to significant differences in the degree of degradability of *Sphagnum* and vascular plants litter (Scheffer et al., 2001).

1.1.7.2. Effect on ecosystem primary productivity

The increase of the temperature leads to variability of peatland net primary productivity, when some areas experiencing a decline of net primary productivity due to evaporation (Dorrepaal et al., 2009b), while the other benefits from the extended growing seasons along with warming (Charman et al., 2013). Some studies tried to quantify the effect of rising temperature on peatland plant communities. It was agreed that a temperature increase of 1-3 °C in the short term (a few years) has a positive impact on biomass and size of *Sphagnum* moss

(Breeuwer et al., 2008; Dorrepaal et al., 2003; Sonesson et al., 2002). However, Dorrepaal et al. (2003) cautioned that long-term warming will have negative effect on *Sphagnum* productivity, while Breeuwer et al. (2008) showed that with increasing biomass the density of capitula and stem decreased, leading to a desiccation of the *Sphagnum* mat. Recently, Norby et al. (2019) within the SPRUCE project, showed that warming cause a vast desiccation and loss of *Sphagnum* community with negative effect increasing over time as a cumulative response. Subsequently, desiccation has negative effect on the *Sphagnum* photosynthesis (Titus and Wagner, 1984). Nevertheless, (Jassey and Signarbieux, 2019) showed the existence of functional compensation among *Sphagnum* species, *i.e.* while one species increases the other decreases its photosynthetic activities, which eases or cancels the negative effect of warming on *Sphagnum* community performance.

It has been measured that a climate warming of the surface by 1°C on average in the bog leads to an increase in peat temperature (5 cm depth) that can vary from 0.4 to 2.2°C depending on the season (Dorrepaal et al., 2003). The increase of the temperature by +3°C together with precipitation by 1 mm day^{-1} led to a decrease in the water table from 14 to 22 cm, thus increasing aerobic layer favoring organic matter decomposition (Roulet et al., 1992). Other studies confirmed that primary productivity of *Sphagnum* moss decreases along with decreasing water table due to climate change (*e.g.* Robroek et al., 2007; Weltzin et al., 2001). The decrease of primary productivity along with water level dropdown can be related to the replacement of *Sphagnum* mosses by vascular plants (Jassey et al., 2018; Munir et al., 2015). Under climate change, the *Sphagnum* productivity decrease could then favor even more intense development of vascular plants and thus modify the functioning of *Sphagnum* bogs as suggested by Dorrepaal et al. (2006).

1.1.7.3. Effect on microbial activities and decomposition

The decomposition of organic matter takes place mainly in the actotelm, which is strongly influenced by temperature variation. The microbial activities can be strongly affected by warming, with the optima temperature range from 15 to 25 °C, depending in the type of the microorganism (Dedysh et al., 2000; Dunfield et al., 1993). Atmospheric deposition of nitrogen also affects carbon fluxes in bog. It increases enzymatic activities (β-glucosidase and phosphatase) and lead to increased dissolved organic matter and CO_2 release (Bragazza et al., 2006). Also, it has been shown that with increasing temperatures, total respiration (plants and microorganisms) can increase by 15-53% in minerotrophic and ombrotrophic peatlands (Waddington et al., 2002). (Dorrepaal et al., 2009b)estimated that a climate warming by 1°C over the next few decades could induce a global increase in heterotrophic respiration of 38 to

100 megatonne $C.yr^{-1}$. Thus, the increase in heterotrophic respiration can lead to the increase not only in *Sphagnum* mosses, but also in plants productivity (Heijmans et al., 2002), therefore leading to an increase in labile carbon released by plants, which can eventually become a favorable substrate for methanogenesis (Dedysh et al., 2000; Joabsson et al., 1999). In turn, CH_4 can be methanotrophized by methanotrophs to CO_2, and then used by plants for photosynthesis (Raghoebarsing et al., 2005).

Vascular plants produce litter, which decomposes from three to four times faster comparing to one of bryophytes (Cornwell et al., 2008). Subsequently, *Sphagnum* dominated peatlands have higher rates of carbon accumulation than those dominated by vascular plants (Gorham, 1991).

1.2. The Bryosphere—the rising star of peatland functioning

Bryophytes are ubiquitous and integral parts of many ecosystems, especially those of peatlands and boreal forests. They significantly contribute to aboveground biomass (Bond-Lamberty and Gower, 2007) and are crucial for many ecosystem processes (DeLucia et al., 2003), especially those of global carbon cycling (Gornall et al., 2007; Turetsky, 2003, Fig. 1-7). In peatlands, bryophytes can contribute to over 50% of net ecosystem exchange and control water and nutrients cycling (Moore et al., 2002). Even though brown and feather mosses play important role in peatland functioning, the genus *Sphagnum* (a peat moss) dominates.

According to estimations, *Sphagnum* produces more biomass (both living and dead), than any other genus of plant and it covers 1% of the world's surface (Hallingbäck and Hodgetts, 2000; Rice, 2009). The success of this genus is related to a set of morphological, anatomical, physiological and life history features (*i.e.* functional traits, see below). Besides, *Sphagnum* mosses together with associated cyanobacteria are also important in biological nitrogen fixation (Turetsky, 2003) and contribute considerably to global nitrogen cycling (DeLucia et al., 2003; Matzek and Vitousek, 2003). *Sphagnum* harbor various a tremendous diversity of microbial and mesofauna communities involved in nutrient recycling: primary producers (microalgae, cyanobacteria), decomposers (heterotrophic bacteria, fungi), microbial predators consist of heterotrophic protists (flagellates, ciliates, testate amoebae) and micro-metazoans (rotifers and nematodes) (Bragina et al., 2015, 2014, 2012a; Fisher et al., 1998; Gilbert et al., 1998; Gilbert and Mitchell, 2006; Jassey et al., 2015a; Kostka et al., 2016; Song et al., 2016). Many studies indicated that microbial groups of photosynthetic protists,

cyanobacteria and methanotrophic bacteria provide the host with carbon and/or nitrogen, which in its turn increases *Sphagnum* productivity (Carrell et al., 2019; Jassey et al., 2015a; Kostka et al., 2016). Microorganisms recycle nutrients and carbon from organic matter to higher trophic levels as well as peatland vegetation *via* "microbial loop" — a pathway on which depends the structure and functioning of peatland microbial food web (Gilbert et al., 1998).

This *Sphagnum* mosses and microbial communities association forms a core detrital network that can regulate peatland nutrient fluxes and carbon cycling (Carrell et al., 2019; Gilbert et al., 1998; Gilbert and Mitchell, 2006; Jassey et al., 2015a; Mitchell et al., 2003), which is also called the bryosphere (*sensu* Lindo and Gonzalez (2010), Fig. 1-7). In addition, the bryosphere can have a strong effect on the structure and dynamic of many ecological processes related to above-belowground linkages, notably carbon and nutrient cycling (Lindo and Gonzalez, 2010; Turetsky, 2003; Wardle et al., 2004).

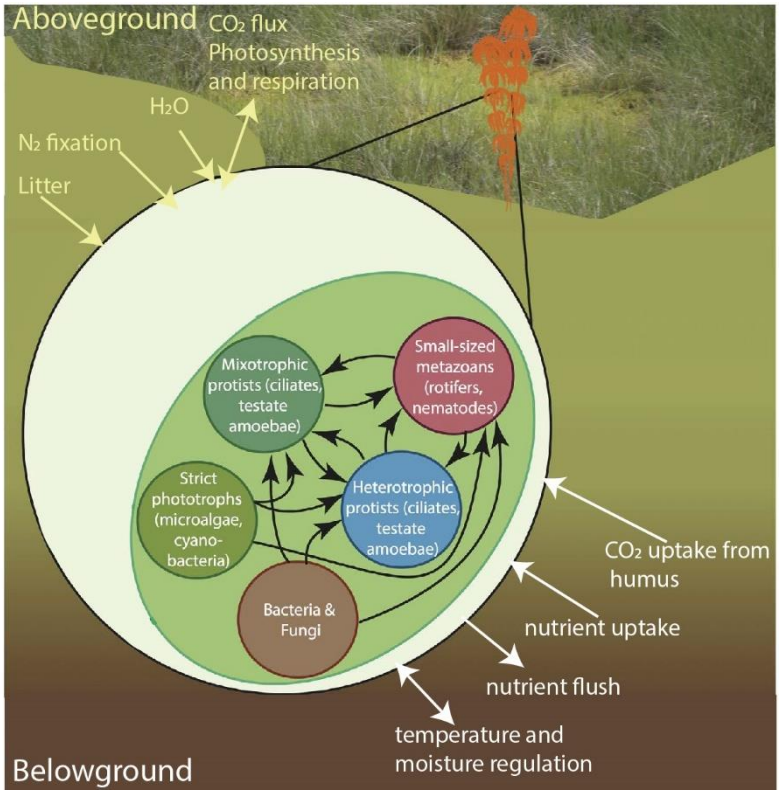


Figure 1-7. Schematic representation of the bryosphere (modified from Jassey et al. (2015); Lindo and Gonzalez (2010).

Sphagnum are poikilohydric and long periods of desiccation and moisture stress have significant effect on the nutrient dynamic in the bryosphere. For example, (Robroek et al.,

2009) showed that deep water table (under summer drought) more likely leads to the decrease of carbon uptake by *Sphagnum*, however quick rainfall events may cancel the negative effect of drought on *Sphagnum* carbon uptake (Nijp et al., 2014). The last can be related to nutrient fluxing from the moss upon rewetting, which can be important source for microorganisms (*e.g.* fungi, (Davey and Currah, 2006).

Turetsky (2003) noted in the review on the C and N dynamic in the bryosphere, that this cycling is likely driven by *Sphagnum* mosses *per se*. *Sphagnum* mosses easily facilitate harsh peatland conditions, while successfully accumulating peat (Chapin et al., 1987), fixing C from the atmosphere (Moore et al., 2002), over competing vascular plants for nutrients and space (Ayres et al., 2006; Malmer et al., 2003), controlling soil moisture and temperature (van Breemen, 1995) and belowground processes (Gornall et al., 2007). *Sphagnum* species constitutes up to 90% of peat (Hájek et al., 2011; Turetsky, 2003) due to the recalcitrant and antibacterial nature of *Sphagnum* litter, which hampers heterogenic decomposition (Fudyma et al., 2019; Hamard et al., 2019; Painter, 1991), and thus this has an extraordinary impact on the global carbon cycle by affecting peatland carbon uptake and storage. Not only litter, but also release of metabolites in the peatland pore water help to control *Sphagnum* growth, defense and competitiveness *via* interaction with the environment and/or other organisms (Erb and Kliebenstein, 2020; Fudyma et al., 2019; Massalha et al., 2017; Verhoeven and Liefveld, 1997).

1.2.1. *Sphagnum* morphology is a key for bryosphere functioning

Unique traits enable *Sphagnum* to act as an ecosystem engineer. These traits drive *Sphagnum* fitness and performance that allow them to over compete other species and thrive under unfavorable environmental conditions and tolerate tissue desiccation (Johnson et al., 2015; Jones et al., 1994).

Due to lack of stomata, *Sphagnum* cannot directly control evapotranspiration and water flux from the leaves, but specific traits indirectly drive the water in the system (D. J. Weston et al., 2015). For instance, the exchange of matter and energy with the environment is controlled by the structure of the canopy, which results from the morphological adaptations including hyaline cells, branching architecture and organization and leaf size (Rydin and Jeglum (2013); Fig. 1-8). *Sphagnum* species growing on hummocks, possess a lot of small close-set leaves and form numerous interconnected small capillary spaces that decreases thickness of boundary layer (*i.e.* enhanced exchange with the environment). This allows a

lateral movement of water through the capillary spaces, whereas close-set pendant branches pressed against the stem form an effective system of vertical water transport (Mccarter and Price, 2014). Contrary, compact cushions and carpets of *Sphagnum* have thicker boundary layers that restrict exchange rates with environment (Rice and Schneider, 2004). Consequently, *Sphagnum* on hummocks can absorb moisture and maintain metabolic activity even under drought (Rice and Giles, 1996).

At the cellular level, *Sphagnum* has two types of cells: a network of small metabolically active cells that are responsible for photosynthesis (*i.e.* chlorocysts) and large dead cells without any organelles - the hyaline cells - responsible for water and ion exchange (Hayward and Clymo, 1983; van Breemen, 1995). In addition, water-filled hyaline cells shelter diverse microorganisms by creating consistent microenvironments for the microbial communities (Bragina et al., 2012a), *i.e.* serve as less acidic 'oases' for microorganisms in the otherwise acidic peatland pore water (During and van Tooren, 1990; Kostka et al., 2016) (Kostka et al., 2016) suggested that the structure and activities of the *Sphagnum* microbiome define the fitness of *Sphagnum* moss.

In addition to tissue hydration, *Sphagnum* photosynthesis relies on CO_2 availability, leaf nitrogen content (especially in rubisco/chlorophyll) and solar radiation. The dynamic water status of the plant is a crucial factor affecting CO_2 diffusion from the environment to the rubisco catalytic sites. Typically, *Sphagnum* water conductivity is mainly external *via* an interconnecting network of capillary spaces on the outer of the plants. (Goffinet and Shaw, 2008; D. J. Weston et al., 2015). *Sphagnum* mosses have a continuous growth and young leaves are gathered on the apical part of the plant that form so-called capitulum, *i.e.* the living part of these plants, where 99% of the light has been absorbed, while the older leaves senescence and die beneath (Hayward and Clymo, 1983). From underneath of capitula and to water table, the organic matter is permeable to gas and water, and thus decomposition starts in this oxidative layer or acrotelm (Clymo and Hayward, 1982; Ingram, 1978). Then, this partially decomposed litter, which is buried under new layers of organic matter, has lower porosity which complicates water passage and peat becomes permanently waterlogged (thus determining water table depth). In this waterlogged layer, oxygen is consumed by aerobic respiration quicker than it can be renewed by diffusion, thus creating anoxic peat column or catotelm (Clymo, 1983). The process of decomposition is the slowest (methanogenesis and sulfate reduction) in catotelm, and thus this determines the rate of carbon will be stored at the given site (Rydin and Jeglum, 2013; Vitt, 2008).

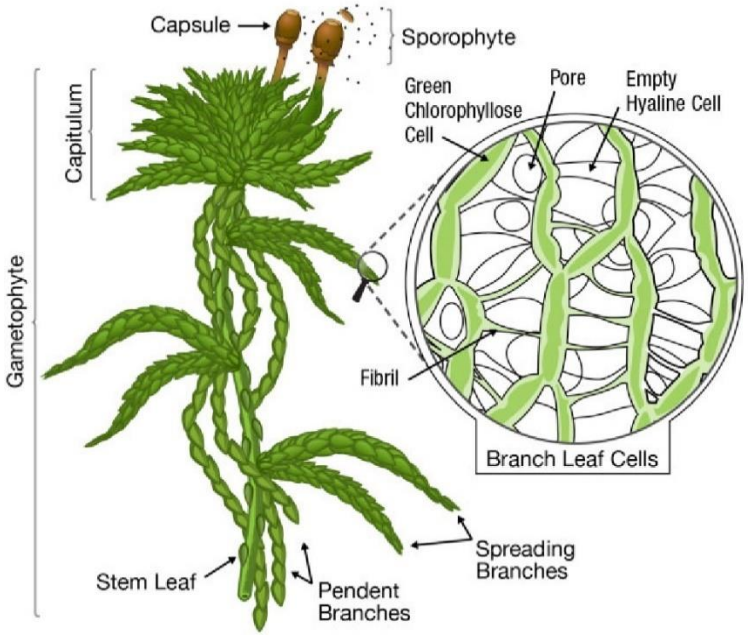


Figure 1-8. Anatomical and morphological structure of *Sphagnum* moss (modified from Weston et al. (2015)

Sphagnum cell walls have high cation-exchange capacities, *i.e.* nutrient cations are taken up from the surroundings in exchange for protons, notably hydrogen ions produced by uronic acid molecules(Clymo, 1963; Soudzilovskaia et al., 2010). These bound polyuronic acids rich in galacturonic residues comprise 10-30% of *Sphagnum* dry weight (Clymo, 1987). The exchange of base cation for organically produced hydrogen ion creates acidity. Due to this exchange mechanism, *Sphagnum* benefits from growing on nutrient poor conditions and acidifications of the surrounding help to inhibit the establishment and grow of many plant competitors, microbial activities and/or herbivores, and affecting the succession in peatlands (van Breemen, 1995). During the succession period in *Sphagnum*-dominated peatlands, pH can drop from over 7 to less than 4, even 3. Nevertheless, this occurs only partially by the cell wall cation exchanger (Vitt, 2000). *Sphagnum* moss also produces other organic compounds (*i.e.* metabolites), which serve as the primary source of acidifying protons in peatlands. For example, *Sphagnum* produces polyphenolic compounds, which have an inhibitory effect on microbial activities promoting decomposition of organic matter, thus favoring peat accumulation (Verhoeven and Toth, 1995). Additionally, these compounds can significantly alter the structure of microbial communities in *Sphagnum* peatlands (Hamard et al., 2019; Jassey et al., 2011b, 2011a)

1.2.2. *Sphagnum* metabolites — a great biochemical invention

In order to perform optimal growth, reproduction and functioning, *Sphagnum* mosses, as every plant, possess two distinct pathways of metabolic machinery (1) primary (also called central metabolism) and (2) secondary (also called specialized metabolism) metabolisms (Taiz et al., 2015).

1.2.2.1. Primary metabolism

Primary metabolism nurses *Sphagnum* growth and development and its basic biochemistry encompasses photosynthesis, respiration, the assimilation of essential nutrients (Kliebenstein and Osbourn, 2012; Sulpice and McKeown, 2015). Primary metabolism begins from the photosynthesis, where the conversion of CO_2 into carbohydrates occurs (Fig. 1-9). *Sphagnum* mosses, as 85% of vascular plants are C_3 plants and photosynthesis undergoes the same pathway (He et al., 2016). However, most vascular plants possess a relatively waterproof cuticle on the cells of the epidermis that force water conduction and gas exchange through the stomata. Due to lack of stomata and cuticle, CO_2 diffusion in *Sphagnum* from the atmosphere to ribulose-1,5-bisphosphate carboxylase (Rubisco) passes through an external water film which differs in thickness depending on environmental conditions (Goffinet and Shaw, 2008; D. J. Weston et al., 2015). In parallel, solar energy is trapped into the chloroplast by light-harvesting complexes and chlorophyll molecules. In the chloroplast, photosystem centers (PSI and PSII) and the electron transport chain (ETC) create chemical bonds with excited electrons. The transferred energy is used by Rubisco to transform the trapped CO_2 into simple sugars *via* Calvin cycle (Fig. 1-9), then it incorporates into mono- or polysaccharides for energy storage (starch). Sugars follow the oxidation with NAD *via* catabolic pathways of glycolysis in the cytoplasm as well as in the mitochondria *via* the tricarboxylic acid (TCA) cycle, coupled to ETC and cellular respiration. During this process, electrons are transferred to oxygen (O_2), reducing it to water (H_2O), and the energy is stored as ATP, which subsequently is used for other metabolic activities (Stephanopoulos et al., 1998; Stitt et al., 2010).

Glycolysis and TCA pathways provide the essential precursors for the primary metabolites biosynthesis like amino acids, lipids and sugars which are universal and indispensable building blocks for cellular macromolecules like DNA, proteins and membranes (Fig. 1-10; Aharoni and Galili, 2011; Erb and Kliebenstein, 2020; Fernie and Pichersky, 2015) as well as for biosynthesis of secondary metabolites (Aharoni and Galili, 2011). The genes

required for production of the primary metabolites are largely conserved across all plants and the production of metabolites follow similar pathways in different species (Kliebenstein and Osbourn, 2012).

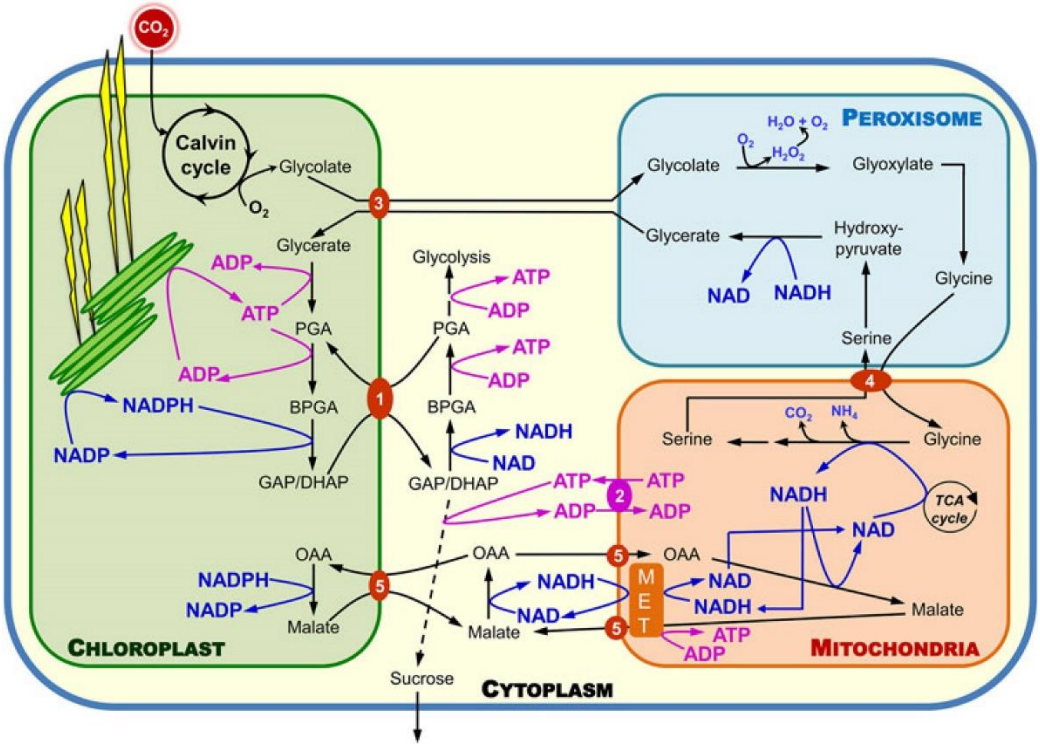


Figure 1-9. Semantical representation of primary metabolism in plant (Sunil et al., 2013). Abbreviations: BPGA bisphosphoglycerate, DTC dicarboxylate/ tricarboxylate transporter, GAP glyceraldehyde-3-phosphate, OAA oxaloacetate, PGA phosphoglycerate

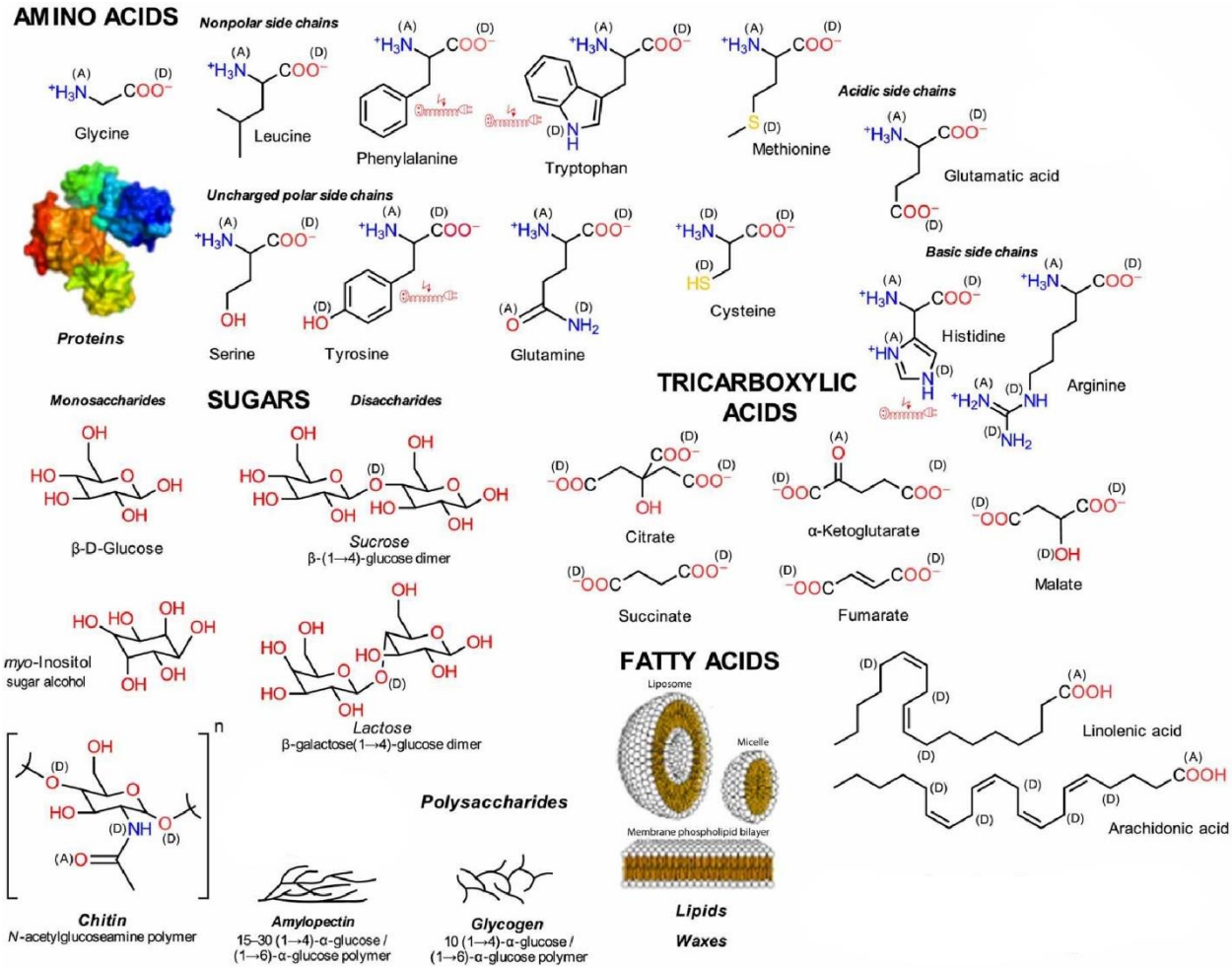


Figure 1-10. Examples of primary metabolites (Hadacek and Bachmann, 2015)

1.2.2.2. Secondary metabolism

Secondary metabolism utilizes the precursors of primary metabolism to produce secondary compounds (*i.e.* secondary metabolites, Fig. 1-11) (Kallam et al., 2019). This can be explained by duplication and neofunctionalization *via* mutation of enzymes which were already used for primary metabolism. If the newly acquired functions efficient invest into plant fitness, thus new gene is stabilized and both genes are conserved (Pichersky and Lewinsohn, 2011). Primary and secondary metabolites are intersected, as primary metabolism provide secondary metabolism with substrate, co-factors as well as energy for metabolic pathways, while secondary metabolism, when needed, can be metabolized and then produced nutrients are transferred to the biosynthetic pathways of primary metabolism (Alnsour and Ludwig-Müller, 2015).

Secondary metabolites are recognized as non-essential compound to the living cell (at least under optimal conditions), but this class shows high structural plasticity compared to primary metabolism (Hartmann, 2007; Wink, 2003). Secondary metabolites are required for plant interactions with abiotic and biotic environments (*e.g.* pathogen defense, osmotic stress) (Hartmann, 2007; Kliebenstein and Osbourn, 2012; Pichersky and Lewinsohn, 2011). Contrary to primary metabolites, they are not present in every species, however they are related to diverse taxonomic groups. It can be due to the fact that the relationship between secondary metabolites and environment created an evolutionary pressure on plants to produce more of new metabolites, thus it led to lineage-specific secondary metabolites (Kliebenstein and Osbourn, 2012). However, many compounds can be found across different species (Tissier et al., 2014).

Secondary metabolism derives from the central processes of photosynthesis, respiration and carbon-nitrogen metabolism as a new group of pathways (Weng, 2014). According to estimations, 10-20 % of the whole plant genes encode enzymes involved into secondary metabolism (Pichersky and Lewinsohn, 2011). For instance, the highly conserved enzyme phenylalanine ammonia lyase (PAL), which connect primary and secondary metabolism, converts the aromatic amino acid (phenylalanine, Phe) at the beginning of the phenylpropanoid pathway into diverse phenolic compounds via Shikimate pathway (Fig. 1-11;Fraser and Chapple, 2011).

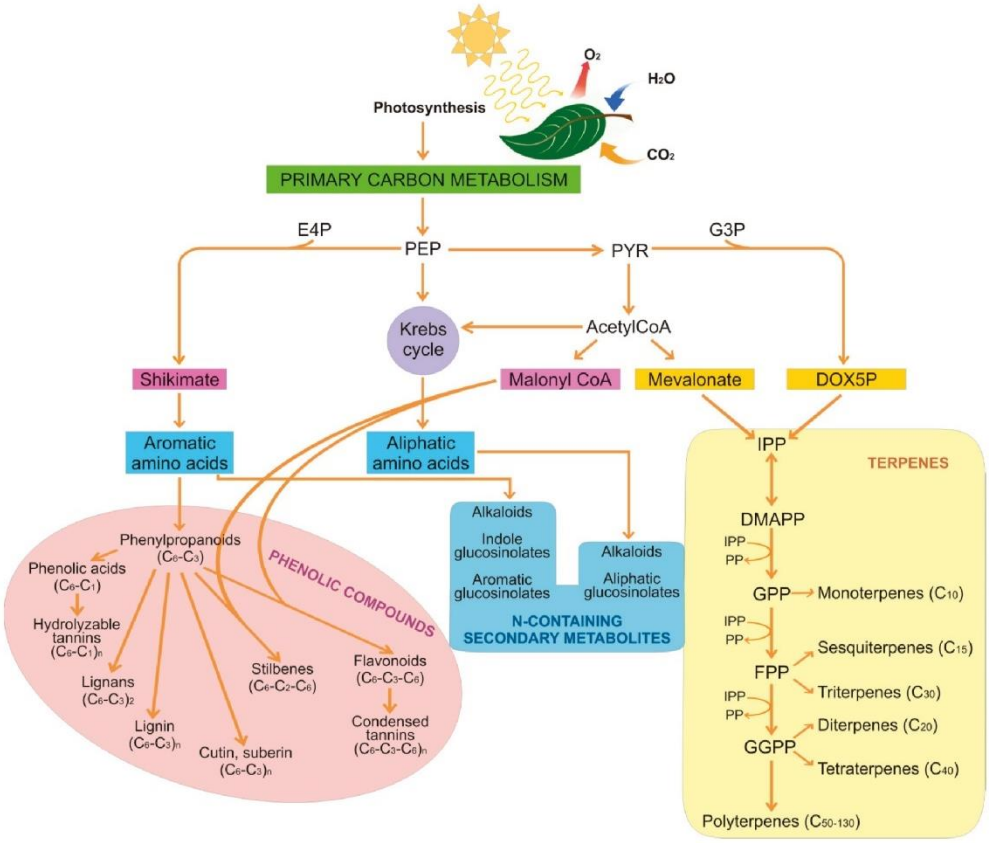


Figure 1- 11. General representation of secondary metabolism in plants (Borrelli and Trono, 2016). Abbreviations: E4P, erythrose 4-phosphate; G3P, glyceraldehyde 3-phosphate; PEP, phosphoenolpyruvate; PYR, pyruvate; DOX5P, deoxyxylulose 5-phosphate; IPP, isopentenyl pyrophosphate; DMAPP, dimethylallyl pyrophosphate; PP, pyrophosphate; GPP, geranyl pyrophosphate; FPP, farnesyl pyrophosphate; GGPP, geranylgeranyl pyrophosphate.

Generally, bryophyte secondary metabolites can be divided into (1) terpenes with ≈1 400 compounds, (2) nitrogen containing compounds (like alkaloids) with ≈20 compounds and (3) phenols with ≈845 compounds and Xie and Lou, 2009).

1.2.2.2.1. Terpenes

Definition

Terpenes are lipophilic compounds that constitute the most abundant and structurally diverse group of the secondary metabolites in plant kingdom, which have been derived from the common five-carbon precursor isopentenyl diphosphate and its isomer dimethylallyl diphosphate, which is synthesized through the mevalonate pathway or the deoxyxylulose-5-phosphate pathway (Fig. 1-10) (Kuzuyama, 2002; Rohmer, 1999). They contain from two (C_{10}, monoterpenes) to more (C130, polyterpenes) isoprene units. Some of the terpenoids, mostly

of mono- and sesquiterpenes are referred as volatile organic compounds (VOCs). Important to mention, that terpenes also play an important role in primary metabolism. Such compound as gibberellinsich, a hormone (diterpene), is indispensable for many growth and developmental processes like stem elongation (Achard and Genschik, 2009).

Ecological role

Terpenes were first known in their volatile form, as they participate to communication between organisms and coping with various stress. They play various roles: inhibitory effect on the growth of plants, pathogen resistance (antimicrobial and antifungal properties) (Klavina, 2018; Xie and Lou, 2009), as well as moss/animal interactions (insect repellents, toxic insecticides, protector from herbivores) (Hadacek and Bachmann, 2015; Xie and Lou, 2009)

1.2.2.2.2. N-containing compounds and fatty acid derivatives

Definition

Alkaloids, one of well-studied groups, contain at least one nitrogen atom, and they usually are synthesized from amino acids (*e.g.* lysine, tryptophan), but the basic skeleton of some alkaloids can be derived from the terpene pathway. The first alkaloids were reported in mosses as simple indole alkaloids with diverse prenyl moieties. Similar compounds may be found in *Sphagnum fallax* and to a lesser extent in *S. magellanicum* as suggested by their UV-spectra (Opelt et al., 2007b).

In mosses, proline (class of nonprotein amino acids), similarly to vascular plants, is synthetized from glutamate or ornithine pathways. The overall process is related to cellular energetics directly *via* the respiratory electron transport chain (Hayat et al., 2012). Proline also participates in the biosynthesis of primary metabolism (as proteogenic amino acid), but also acting as metabolite during plant development (Okumoto et al., 2015). Proline released from *Sphagnum* was found to be fairly abundant in the top-layer, while only traces in deeper layers (Simola, 1975).

Ecological role

Alkaloids have remarkable physiological actions on living organism (*e.g.* analgesic, antimalarial, antiproliferative effects) (Ramawat et al., 2009). Alkaloids, extracted from moss were found to be a muscle relaxant (in mice) and inhibitor of calcium activities (Asakawa and Ludwiczuk, 2018). Due to these properties, alkaloids are mainly studied for pharmaceutical purposes and they are widely used in medical practice (Asakawa and Ludwiczuk, 2018; Ramawat et al., 2009; Trease and Evans, 2009; Ziegler and Facchini, 2008).

Proline play an adaptive role in plant stress tolerance by making osmotic adjustments contributing to the stabilization of subcellular structures (membranes and proteins), scavenging reactive oxygen species and buffering the cellular redox potential (Hayat et al., 2012; Kishor and Sreenivasulu, 2014; Verbruggen and Hermans, 2008). Also proline reported to be toxic to other plants, when was applied at high concentrations exogenously, suggesting its allelopathic properties (Hayat et al., 2012).

1.2.2.2.3. Phenolic compounds

Definition

Phenolic compounds accounts can comprise from 1 to >25 % of total leaf dry mass (Hättenschwiler and Vitousek, 2000; Tissier et al., 2014). Most phenolic compounds are produced *via* the shikimate pathway, which converts simple carbohydrate precursors (L-phenylalanine) derived from glycolysis and the pentose phosphate pathway into aromatic amino acids like phenylalanine. In *Sphagnum*, phenolic acids and flavonoids are synthetize also through shikimate pathway involving PAL enzyme whereas the tyrosine ammonia-lyase (TAL) enzyme is absent (comparing with vascular plants) (Rasmussen et al., 1995a). Polymerization and condensation reactions lead to production of hydrolysable and condensed tannins which form a network associated with the cell wall that contributes to a wall strength (Fig. 1-10, (Verhoeven and Liefveld, 1997). Phenolic compounds are characterized by containing at least hydroxyl functional groups on aromatic ring. They can be classified in different ways, due to the large number and heterogeneity of structures. Based on the basis of their carbon chain, they range from simple phenolic molecule like phenols or phenolic acids to highly polymerized compounds like tannins (Borrelli and Trono, 2016).

Ecological role

Phenolic compounds play an important role in plant growth, defense and competitiveness *via* interaction with the environment and/or with other organisms. Generally, phenols were reported to have allelopathic, antifungal, antimicrobial and antiherbivore properties (Fudyma et al., 2019; Hamard et al., 2019; Opelt et al., 2007; Verhoeven and Liefveld, 1997; see more below)

As mosses do not possess lignified tissues as vascular plants, accumulated soluble phenylpropanoids such as flavonoids may play similar functional role (Weng and Chapple, 2010). Flavonoids protect plants from various abiotic and biotic stresses as well as play an important role in the interaction between the plant and its environment. (Samanta et al., 2011). Flavonoids participate in protection of the cell from UV damages and they possess an

antioxidant capacity due to their ability to donate electrons or hydrogen atoms (Agati et al., 2012; Chobot et al., 2008). Flavonoids play important role in plant-plant and plant-symbiotic bacteria communication (Mierziak et al., 2014). Also, flavonoids can inhibit growth of other plants, show antimicrobial and antifungal properties (Basile et al., 1999a; Xie and Lou, 2009).

Tannins are known not only for their defensive properties against pathogens and herbivores (Chomel et al., 2016; Hättenschwiler and Vitousek, 2000; Verhoeven and Liefveld, 1997), but for their crucial role in ecosystem function and nutrient cycling by slowing down the decomposition (Chomel et al., 2016; Hättenschwiler and Vitousek, 2000; Verhoeven and Liefveld, 1997). Tannins form insoluble complexes with proteins and other biological polymers and metals, which make organic matter inaccessible for decomposition (Verhoeven and Liefveld, 1997; Zak et al., 2019). Tannins can reduce mineralization rates of carbon and nitrogen in soils, due to their toxicity for microorganisms and inhibition of enzyme activities (Bradley et al., 2000; Schimel et al., 1998; Verhoeven and Liefveld, 1997; Zak et al., 2019).

1.3. The most prominent metabolites of *Sphagnum* and their ecological role

Sphagnum mosses possess distinct traits, which help to create hostile environmental conditions for other plant, meta- and microorganisms, as well as affecting ecological processes related to decomposition and nutrient cycling (Rydin and Jeglum, 2013; van Breemen, 1995). The mechanisms by which *Sphagnum* moss retard decomposition are not fully elucidated, but it involves both external environmental conditions created by these species and the internal biochemistry of the *Sphagnum* tissue, especially the low nitrogen to carbon ratio (Bragazza et al., 2006). A passive mechanism of the tissue decomposition resistance is the ratio of structural to metabolic carbohydrates (Turetsky et al., 2008). An active mechanism relies on the metabolites released in the surrounding water, *e.g.* acid hydrolysis of cell-wall polysaccharide 'sphagan' or lignin like phenolics '*Sphagnum* acid' (Hájek et al., 2011; Mellegård et al., 2009; Stalheim et al., 2009; Verhoeven and Liefveld, 1997).

1.3.1. Sphagnan —a pectin like polymer

Carbohydrates play an important role in moss stress tolerance and they differ from the carbohydrates of high plants. Carbohydrates play a double role in moss: (1) building material for cell walls and (2) functional compounds for interaction with the environment. In studies

on *Sphagnum* was found a big portion of polysaccharides (Graham et al., 2010; Maass and Craigie, 1964; Painter, 1983), some of them are acid-insoluble carbohydrates that have polymer-like structure, which mimics properties to vascular plant holocellulose, as well as some primary cell wall material like uronic acids (Hájek et al., 2011; Painter, 1983).

Cell-wall holocellulose of *Sphagnum* comprises of pectin-like rhamnogalacturonan I type polysaccharides (Ballance et al., 2007) with xyloglucomannan (Painter and Shrensen, 1978). Parts of pectin-like polymers, also known as sphagnan, are slowly liberating into the environment under autogenic acid hydrolysis of the cell wall (Painter, 1991). Compounds like uronic acids as galacturonic acid and 5-keto-D- mannuronic acid can be in free form and sphagnan cell-bounded forms. They exchange the protons of the carboxyl group against Ca^{2+} and Mg^{2+} cations, which assign ion-exchange capacity to *Sphagnum*, by acidifying the surrounding water (Soudzilovskaia et al., 2010; Verhoeven and Liefveld, 1997), and was suggested to participate in inhibition of microbial activities (Stalheim et al., 2009). Besides, dissociated carboxyl group of sphagnan when interacts with the free amino groups of extracellular enzymes, disactivates the enzyme by creating a polyelectrolyte complex, *i.e.* process occurs in acid pH ranging from 2.0 to 4.8 and may lead to limitation of carbon and nitrogen mineralization (Ballance et al., 2008). The specific role of sphagnan to have antimicrobial properties was confirmed with the latest analytical techniques (metabolomic analysis by 1H NMR and FTICR-MS; Fudyma et al. (2019). In a nutshell, sphagnan coats cell walls of hyaline cell walls, papillae, fibrils and chlorocystes forming a physical barrier from decomposition and carboxyl groups react with environment via acidification and nutrient exchange (Stalheim et al., 2009; Tsuneda et al., 2001).

1.3.2. Phenolic compounds

Sphagnum phenolics are the most important group of secondary metabolites (Verhoeven and Liefveld, 1997). For example, at the beginning of the last century, (Czapek, 1899) described a molecule responsible for the red color of *S. magellanicum* call walls, which was called sphagnol — without determining its exact composition. Then, several compounds, mostly flavonoids and phenolic acids, were identified including monophenolics p-hydroxybenzaldehyde, p-hydroxybenzoic acid, vanillic and ferulic acids and some unknown compounds namely "C", "D", "E" and "F" (Rudolph and Engmann, 1967). Thus, the term sphagnol was proposed to be eliminated as it was a mixture of several compounds. More interestingly, the substance "D", which was responsible for red coloration of the cell was monophenolic P-(carboxymethyl)-

cinnamic acid or *Sphagnum* acid (von Rudolph, 1972). Rudolph and Samland (1985) observed *Sphagnum* acid in different *Sphagnum* species, despite season and tested moss parts. Later, it was suggested that *Sphagnum* acid has cell-wall nature and can be a manomer derived after sphagnan decomposition (Rasmussen et al., 1995b). (Van der Heijden, 1994) found a biopolymeric polyphenolic network which resembles tannins in vascular plants (recalcitrant compound) as well as the presence of the monomeric phenolics trihydroxy- benzene and gallic acid (trihydroxy-benzoic acid), which are precursors of the biosynthesis of hydrolysable tannins in *Sphagnum*. With the development of analytical technologies, the presence of aforementioned compound was confirmed and a large amount of previously unreported phenolic compounds, specific for *Sphagnum* moss was detected (Chiapusio et al., 2018; Fudyma et al., 2019; Hamard et al., 2019; Klavina, 2018).

The concentration of phenolic compounds was shown to vary between species and within species (Bengtsson et al., 2018; Chen et al., 2021; Opelt et al., 2007b; Rasmussen et al., 1995a; Verhoeven and Liefveld, 1997), along the season (Chiapusio et al., 2018; Jassey et al., 2011a; Klavina, 2018), growing microtopography (Abbott et al., 2013; Opelt et al., 2007b). Additionally, the differences in phenolics content was recorded between capitula and the stem (Jassey et al., 2011b; Rudolph and Samland, 1985).

In brief, *Sphagnum* produces both recalcitrant and water-soluble phenolic compounds. The recalcitrant forms are generally present in the anaerobic zones of the peat following an accumulation over time (Djurdjević et al., 2003), contrary to the soluble forms which are found rather in aerobic conditions.

1.3.3. Ecological role of *Sphagnum* metabolites

The slow litter decomposition and further carbon sequestration in peatlands is related to ability of *Sphagnum* to create unfavorable environment and hamper decomposer growth and activities (Rydin and Jeglum, 2013), thus regulating such ecosystem processes as decomposition (Fenner and Freeman, 2011) and soil respiration (Dieleman et al., 2016a). For example, (Verhoeven and Toth, 1995) compared the degradation of *Sphagnum fallax* a sedge (*Carex diandra*) litter in microcosms. First, they noticed that the *Sphagnum*-dominated litter decayed more slowly than the sedge-dominated litter. Secondly, following the addition of a *Sphagnum* leachate to all microcosms, authors observed that the decomposition of both types of litter was considerably slowed down, whereas the addition of a *Carex diandra* leachate had no effect on the degradation over the microcosms. Therefore, it was assumed that water-

soluble phenolic compounds, more likely *Sphagnum* acid, have a strong inhibitory effect on decomposition.

Sphagnum phenolic compounds can both limit the availability of resources in the environment for decomposers use and their activities (by binding with nitrogen rich proteins and microbial exoenzymes), and coat cell walls, making a physical barrier against decomposition (Freeman et al., 2001b; Hájek et al., 2011; Scheffer et al., 2001; Shetler et al., 2008; Verhoeven and Liefveld, 1997). These phenolic compounds were reported to be toxic to many microbes, also suppressing microbial growth and related carbon release (Fenner and Freeman, 2011; Hamard et al., 2019). For example, p-hydroxyacetophenone and p-hydroxybenzoic acids form a network that is difficult to penetrate for microorganisms in the early stages of organic matter degradation, particularly for fungi (Tsuneda et al., 2001). Moreover, the activities of the hydrolase enzymes like sulphatases, phosphatases or β-glucosidases were suppressed in the presence of cell-bonded phenolics (Freeman et al., 2001a, 1992; Rasmussen et al., 1995a, 1995b). Fudyma et al. (2019) found that two phenols like 2-{Bis[(4-phenyl-1,3-thiazol-2 yl)amino]methyl}phenol and 4-tert- Octylphenol monoethoxylate could be important players in *Sphagnum* antimicrobial properties, while these compounds are not fully responsible for the inhibition of decomposers, which is with line with previous findings (Bengtsson et al., 2018; Mellegård et al., 2009). However, (Bonnett et al., 2006) reported a positive correlation between phenolic compounds increase and carbon release as respired CO_2.

The phenolic compounds extracted from *Sphagnum* have can also have allelopathic effects (Chiapusio et al., 2013; Liu et al., 2020, 2019; Verhoeven and Liefveld, 1997). The growth of vascular plants in *Sphagnum* carpet is slow, which may be related to the production and release of growth-inhibitory compounds (van Breemen, 1995). *Sphagnum* moss can modulate their phenolic production along with vascular plant cover, more likely due to competition with vascular plants (*e.g.* control of the expansion of dwarf shrubs) (Chiapusio et al., 2018; Soudzilovskaia et al., 2010). For example, Chiapusio et al. (2018) found that in hummocks, *Sphagnum* acid from *S. fallax* was negatively correlated with vascular plant richness, while positively with phenols P9 and P11 from S. *magellanicum*, suggesting that the chemical structure of phenolic compounds could define the expansion of vascular plants. Chiapusio et al. (2013) showed that *Sphagnum* extract had drastic negative effect on the germination of the monocot *Lolium* and gymnosperm *Pinus*, while no effect on the dicot *Raphanus* and the radicle growth was suppressed for all species.

Sphagnum can release metabolites to protect against herbivory. Verhoeven and Liefveld, (1997) suggested that *Sphagnum* may accumulate tannins and other phenolic compounds in high quantities to make plant material less tasty for herbivores, or alternatively, it accumulates some specific compounds in small quantities, which can be toxic to herbivores. Chen et al. (2021) found that *Sphagnum* mosses had high phenolic compounds concentrations, when grazing herbivores (mealworms *Tenebro molitor*) were present, but lesser increase when *Sphagnum* was clipped. These findings suggest that *Sphagnum* mosses has evolve the mechanisms, by which they produce more defense compounds, to distinguish between herbivory attack and mechanical damage. Thus, *Sphagnum* mosses produce metabolites to interact with its environment, which in its turn feedbacks to ecosystem processes. Nevertheless, the production of *Sphagnum* metabolites can be affected by ongoing climate changes, which can affect *Sphagnum* interactions with its environment and then cascade to ecosystem processes. While the processes by which *Sphagnum* controls C decomposition, accumulation, transformation and subsequent feedback to climate are developing, the plant–soil– microbe interactions in the context of climate changes remain poorly understood.

More information about other *Sphagnum* metabolites and their ecological roles can be found in Table 1-2.

Table 1-1. Characteristic of the ecological role of *Sphagnum* metabolites used in this study

Class	Role	Reference
Chlorophyll	– Indicator of photosynthetic activity and consequent plant growth – Positively correlated with water availability, nitrogen levels and photosynthetic rates – High levels in shadow with high water availability	(Baxter et al., 1992; Gaberščik and Martinčič, 1987; Gerdol, 1996; Gerdol et al., 1994; Granath et al., 2009a; Harris et al., 2005; Rastogi et al., 2020; Rice et al., 2008; Spatt and Miller, 1981; Zhu et al., 2019)
Carotenoids	– Indicator of photosynthetic activity; high concentration in sun-acclimated mosses to protect chlorophyll from photodamage – Positively correlated with water availability, nitrogen levels and photosynthetic rates. – High levels in shadow with high water availability	(Gerdol, 1996; Gerdol et al., 1994; Granath et al., 2009; Rastogi et al., 2020; Rice et al., 2008; Schmidt-Stohn, 1977; Zhu et al., 2019)
Monosaccharides (glucose)	– Cellular osmoprotection against freezing – Photosyntates can be stored as monosaccharides – Are in big quantities in fast-growing *Sphagnum* – Boost nutrient mineralization by decomposers, which directly and positively feeds back to *Sphagnum* growth	(Hájek, 2014; Skre et al., 1983; Turetsky et al., 2008)
Polysaccharides (*e.g.* sphagnan)	– Directly or indirectly inhibit microbial activity – Participate in cation-exchange capacities – Limitation of C but also N mineralization, thus inhibiting microbial growth – Tanning properties – Structural component of the cell wall, ensuring its resistance to degradation	(Ballance et al., 2007; Hájek et al., 2011; Schellekens et al., 2015; Stalheim et al., 2009; Turetsky et al., 2008; Verhoeven and Liefveld, 1997)
Phenolic compounds	– Regulation of microbial community structure and potentially inhibition of top predators (anti-predator effect) – Toxic to many microbes, also suppressing microbial growth and related carbon release, – Coating cell walls, making a physical barrier against decomposition	(Binet et al., 2017; Chen et al., 2021; Chiapusio et al., 2018; Freeman et al., 2001; Fudyma et al., 2019; Hájek et al., 2011; Hamard et al., 2019; Jassey et al., 2013, 2011b; Mellegård et al., 2009; Opelt et al., 2007b; Rasmussen et al., 1995; Rudolph and Samland, 1985; Verhoeven and Liefveld, 1997; Verhoeven and Toth, 1995)

Table 1-1 continued.

	– Delay litter microbial decomposition by limiting the availability of resources in the environment for decomposers use and their activities – Antifungal properties – Antiherbivore – More likely help *Sphagnum* to compete with vascular plant expansion, negatively affect seedling germination, reduce vascular plant's mycorrhization	
Lignin-like phenolics	– Contribute to structural integrity of the cell-walls – Provide the rigidity to hyaline cells that prevent their collapse during dehydration – Shielding the polysaccharides against decomposers (particularly fungi)	(Hayward and Clymo, 1982; Tsuneda et al., 2001)
Flavonoids	– Signals in plant– microbe interactions – Antimicrobial properties – Inhibition of spore germination – Antifungal properties – UV-absorption, detoxification of ROS and limit oxidative stress (antioxidant properties) – Cell-wall pigment	(Basile et al., 1999a; Fudyma et al., 2019; Opelt et al., 2007c; Xie and Lou, 2009)
Tannins	– Antiherbivore and protection against pathogens – Create complex with proteins and inhibition of enzyme activities – Slows decomposition rate – Reduce mineralization rates of C and N, due to their toxicity for microorganisms and inhibition of enzyme activities – Contributes to the cell wall strength	(Tutschek, 1982; Verhoeven and Liefveld, 1997; Zak et al., 2019)
Proline	– Osmoregulation, contributing to the stabilization of subcellular structures (membranes and proteins) – Scavenging reactive oxygen species and buffering the cellular redox potential – May have allelopathic properties	(Hayat et al., 2012; Kishor and Sreenivasulu, 2014; Verbruggen and Hermans, 2008)

Lipids	– Antimicrobial/antipathogen properties – Can be insoluble component of a cell wall, or a cellular soluble solute which serves as energy source (depending on the composition) – Humification processes and development of peat composition – Can be associated with antibiotic activity – Coating the cell wall surface and more likely contribute to the resistance to decay – Protection against severe environmental stress – Photosyntates can be stored as lipids	(Dembitsky, 1993; Fudyma et al., 2019; Karunen et al., 1982; Klavina, 2018; Lehtonen and Ketola, 1993; Mikami and Hartmann, 2004; Verhoeven and Liefveld, 1997; Xie and Lou, 2009)

1.3.4. Effect of climate change on *Sphagnum* metabolites and other interactions

Phenolic metabolism was significantly impacted by climate warming, suggesting that a decrease of phenolic compounds is related to the decrease in *Sphagnum* moisture and increase of temperature (Jassey et al., 2011a). Some studies pointed that warming has negative effect on phenols content in peatland species (Veteli et al., 2007), including *Sphagnum* (Jassey et al., 2011a). This decrease can be related to a decrease of carbon partioning to phenolic compounds (Herms and Mattson, 1992; Mattson et al., 2005). It can be suggested a trade-off between growth and production of carbon-containing metabolites, with lesser investment into phenols production (Mattson et al., 2005; Veteli et al., 2007), as elevated temperature stimulate better *Sphagnum* growth (Breeuwer et al., 2008). Dorrepaal et al. (2005) suggested that lower concentration of phenolic compounds under warming can be related lower nutrient limitation on growth, comparing to either colder regions. Phenols were suggested to serve as an alternative carbon storage, when other factors but carbon assimilation limit the plant growth (Graglia et al., 2001). In addition, this may imply that with more recurrent drop in *Sphagnum* phenols concentrations, due to more intense and frequent heat waves, will more likely lead to the realizing of the enzymatic latch (Freeman et al., 2001b). Thus, under warming, the decreased content of *Sphagnum* phenols will lead to a decrease of the inhibitory effect on enzymatic activities (notably phenoloxidase activity produced by fungi) and thus causing higher degradation of recalcitrant materials in peatlands (Jassey et al., 2011a). Similarly, Binet et al. (2017) observed a negative correlation between mycorrhizae and litter phenolics recovered under warming.

In some cases, despite the absence of a direct effect of warming on *Sphagnum* phenols quantities, warming could change the qualitative characteristics of phenolic compounds, as it was observed for dwarf shrubs ecosystems (Hansen et al., 2006). For example, Jassey et al. (2013) showed warming significantly affected *Sphagnum* phenolic compounds and microbial communities' interactions, by shifting from negative to positive effect under warming. More precisely, phenolic compounds had strong negative correlation with high-trophic level microorganisms or predators (testate amoebae), suggesting an inhibitory effect on this group of microorganisms. Thus, phenolic compounds can serve as important drivers of testate amoeba community structure and the microbial network stability, which can promote decomposition (Jassey et al., 2011c). The inhibition of top predators will increase bacterial growth and microbial organic matter decomposition leading to increase of carbon and nutrient mineralization and subsequently it can destabilize the plant community productivity

and peatland carbon storage (Dieleman et al., 2016b; Fenner and Freeman, 2011; Jassey et al., 2011a; Wang et al., 2015).

Recent studies documented that phenolic compounds from *Sphagnum* litter were involved in aboveground-belowground interactions (Jassey et al., 2013): control the vertical distribution of microbial communities (Jassey et al., 2011b), enzymatic activities in *Sphagnum* litter (Jassey et al., 2011a), mycorrhizal colonization of *Ericaceous* plants (Binet et al., 2017; Chiapusio et al., 2018) or the germination of *Pinus* on peatlands (Chiapusio et al., 2013). Nevertheless, the strength of these interactions varied between microhabitats (Jassey et al., 2012, 2011b). Most of the aforementioned studies measured the interaction of phenolic compounds with plant and/or microbes (plant/microbes), and only some of them included seasonal and/or response to warming. There is a scarce number of studies on interactions of plant/microbes with other *Sphagnum* metabolites like tannins, flavonoids, carbohydrates. Even though when more detailed profiling of metabolites with including plant/microbes interactions were done, neither seasonal nor warming effects were accounted for biotic interactions (*e.g.* Fudyma et al., 2019; Hamard et al., 2019; Liu et al., 2020; Opelt et al., 2007) as well as *Sphagnum* pigments to warming (Rastogi et al., 2020) and trade-off in resource partitioning into metabolic and structural carbohydrates (Turetsky et al., 2008). Contrary, when other studies considered the seasonal and or warming effect on different compounds, the interactions with plant/microbes were not included (Dieleman et al., 2016b; Klavina et al., 2018). Some efforts were done to evaluate the response of other compounds than phenolics, including the response of *Sphagnum* pigments to warming (Rastogi et al., 2020) and trade-off in resource partitioning into metabolic and structural carbohydrates (Turetsky et al., 2008). Thus, it is crucial to understand how *Sphagnum* metabolites respond to climate and seasonal variations and the possible trade-offs between metabolites (primary vs secondary). Additionally, there is a significant knowledge gap on the dynamic of *Sphagnum* metabolites in aboveground-belowground interactions and how they respond to climate change.

1.4. Objectives of the thesis

The work presented in this thesis aims to explore (i) the potential of *Sphagnum* metabolites and enzyme activities to provide deeper mechanistic understanding of *Sphagnum* trait functional space across environmental gradients, (ii) the extent to which *Sphagnum* metabolites modulate microbial community composition and functioning, and (iii) to examine the seasonal patterns of *Sphagnum* metabolites across space, and (iv) investigate how

Sphagnum metabolites respond to climate changes and what are the consequences of their response for peatland C uptake. Many questions remain unanswered when considering *Sphagnum* metabolites and their role in above-belowground interactions as well as the response to climate change. The main research questions and several auxiliary questions were asked in this thesis to address a knowledge gap in the literature

I) **What is the role of *Sphagnum* biochemicals in *Sphagnum* functional space and ecology?** Are there any linkages among *Sphagnum* traits? If yes, how environment drive those linkages?

II) **How do *Sphagnum* phylogeny and traits drive the spatial variability of microbial community composition and functioning?** Do *Sphagnum* traits, in addition to environmental factors, drive geographical variation in microbial community composition and microbial traits? Do *Sphagnum* metabolites have a stronger effect in shaping microbial properties than anatomical and morphological traits? Is *Sphagnum* phylogeny an important determinant of microbial properties, in addition to environmental factors?

III) **How does climate change affect seasonal patterns of *Sphagnum* metabolites and how does it feedback to peatland carbon uptake?** What are the patterns of *Sphagnum* metabolites from different species in response to climate seasonality? When facing new climate, will *Sphagnum* species plastic response follow the same directions? How climate-induced shifts in *Sphagnum* metabolites will feedback to ecosystem processes of carbon assimilation?

In order to meet the objectives and answer these research questions, I conducted several field observation and experiments where I collected information about *Sphagnum* anatomical, morphological traits, and biochemical traits (metabolites and enzymes), but also on peatland CO_2 fluxes and on microbial structure and activities.

Chapter II presents the approach I developed to quantify several *Sphagnum* metabolite and enzymes using spectrophotometry. I summarized all the tests for protocols adjustment I conducted before any field work. I further describe the reciprocal transplantation experiment in details that have been used in Chapter 5.

Chapter III shows for the first time the potential of *Sphagnum* metabolites and enzyme activities in expanding *Sphagnum* trait space across environmental gradients. We quantified the contribution and the role of each trait group to the functional trait space of *Sphagnum* mosses. The study was conducted in five European *Sphagnum*-dominated peatlands

distributed along a latitudinal gradient in Europe, representing a range of local and regional environmental conditions. Our findings showed that *Sphagnum* growing in different local environmental (vegetation composition, nutrients content) and regional (temperature, precipitation) conditions possess a suite of diverse biochemical traits that supports *Sphagnum* form and function as well as its resistance to environmental changes. We collected one dominant *Sphagnum* species per site, to observe species performance at their site of origin. This chapter was published in Oikos journal (article 1).

Chapter IV presents how and to what extent *Sphagnum* phylogeny, anatomical and morphological traits and metabolites drive the spatial variability of microbial community composition and functioning. This study highlighted the key role of *Sphagnum* interspecific trait variations in driving microbial community composition and microbial traits in addition to local and regional environmental conditions. This chapter was published in the Journal of Ecology (article 2).

Chapter V shows how seasonal patterns of *Sphagnum* metabolites respond to climate changes, and how this influence peatland carbon uptake. To do so, we conducted a reciprocal transplantation experiment in five *Sphagnum*-dominated peatlands and we measured metabolites together with CO_2 fluxes. This work for the first time documents the effect of climate seasonality and changes on previously unreported biochemical traits (metabolites), and relate those shifts to ecosystem process (of gross ecosystem productivity). The results of this chapter will be submitted to Journal of Ecology.

Chapter VI presents the synthesis and the interpretation of the obtained results from aforementioned chapter combined with perspectives of this research.

Chapter 2. Materials and methods

Materials and methods

2.1. Extraction of *Sphagnum* pigments, metabolites, antioxidant enzyme activities and proteins

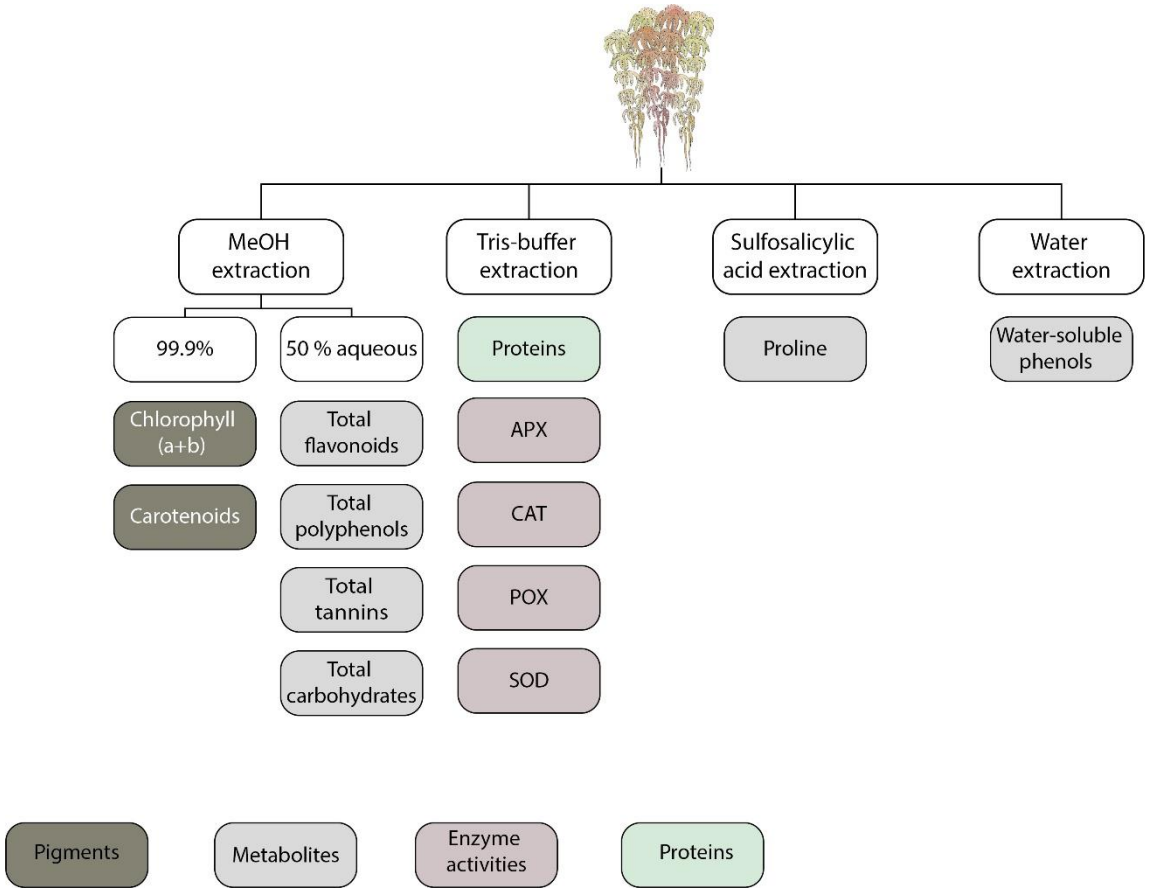


Figure 2-1 A summary of the extraction methods for quantification of *Sphagnum* biochemical traits: pigments, metabolites, antioxidant enzyme activities and proteins. Abbreviations are APX (EC 1.11.1.11) - ascorbate peroxidase activity, CAT (EC 1.11.1.6) – catalase activity, POX (EC 1.11.1.7) – peroxidase activity, SOD activity (EC 1.15.1.1) - superoxide dismutase.

Fig. 2-1 shows the different extractions pathways used to quantify the various *Sphagnum* pigments, metabolites, antioxidant enzyme activities and proteins. Due to anticipated high number of samples (>1000), the goal was to adjust the protocols and, when it was possible, decrease the number of extractions to perform more diverse analyses on all *Sphagnum* samples.

Fig. 2-2 represents the tests, which were performed to improve extractions and identification, including test of mass to liquid ratio, extraction solvent concentration, aided

extraction method, separation method, pre-extraction procedure. This chapter presents only the protocols, which were vigorously tested and significantly adjusted, while some other protocols were previously published, and they are presented in Chapter 3/Sytiuk et al. (2022).

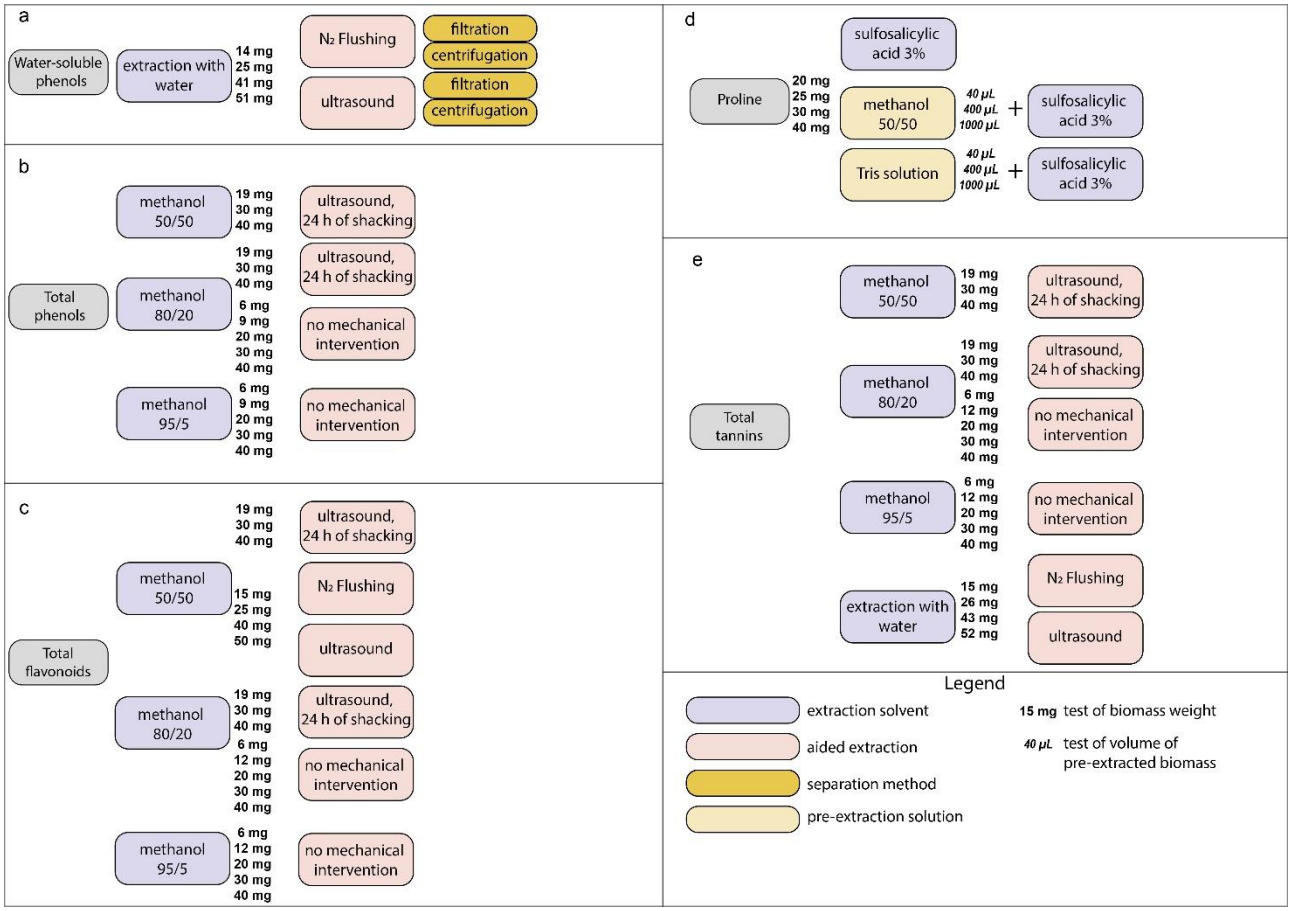


Figure 2-2. Presentation of the performed tests for protocols optimization for (A)water-soluble phenols, (B) total phenols, (C) total flavonoids, (D) proline, (E) total tannins.

2.2. Optimization of the extraction procedure

Sphagnum mosses contain up to 90% of water, but water content can significantly depend on environmental parameters (*i.e.* temperature, precipitation, light level) as well as on *Sphagnum* phylogeny (Silvola and Aaltomen, 1984). To ensure obtaining of comparable results among mosses from different sites and species, prior to extraction of metabolites, *Sphagnum* moss samples were freeze-dried. Then, the samples were homogenized by grinding with glass beads using high-speed benchtop homogenizer at 4.5 m/s. Freeze-drying is more advantageous

method, comparing to air-drying, as it retains higher levels of metabolites, especially those of phenolic compounds (Abascal et al., 2005).

The extraction efficiency of phenolic compounds (*e.g.* flavonoids and tannins) highly depends on the extraction solvent. As phenolic compounds differ in their structure, it gives different solubility properties to those compounds in a particular solvent (Chaves et al., 2020; Do et al., 2020). Methanol was observed to be the most potent solvent for phenolic compounds extraction in vascular plants, which gives high yields of extraction (Do et al., 2020; Iglesias-Carres et al., 2019). As aim of tests was to decrease and unify the number of extractions for total phenols, flavonoids, tannins from *Sphagnum* tissues, a few methanol concentrations were tested (Fig. 2-3).

A combination of alcohol with water was found to be more effective for phenolic compounds extraction than one-component solvents (Naeem et al., 2012; Prasad et al., 2011; Spigno et al., 2007). The addition of water to organic solvent increases polarity of the medium that eases phenols extraction (Prasad et al., 2011). Increasing proportion of the water into the water-methanol solvent release from low- to high-polarity substances. It was found that 50:50 water-methanol ratio was the most acceptable concentration, as it gave high results with the smallest deviation among the replicates for all tested metabolites (Fig. 2-3).

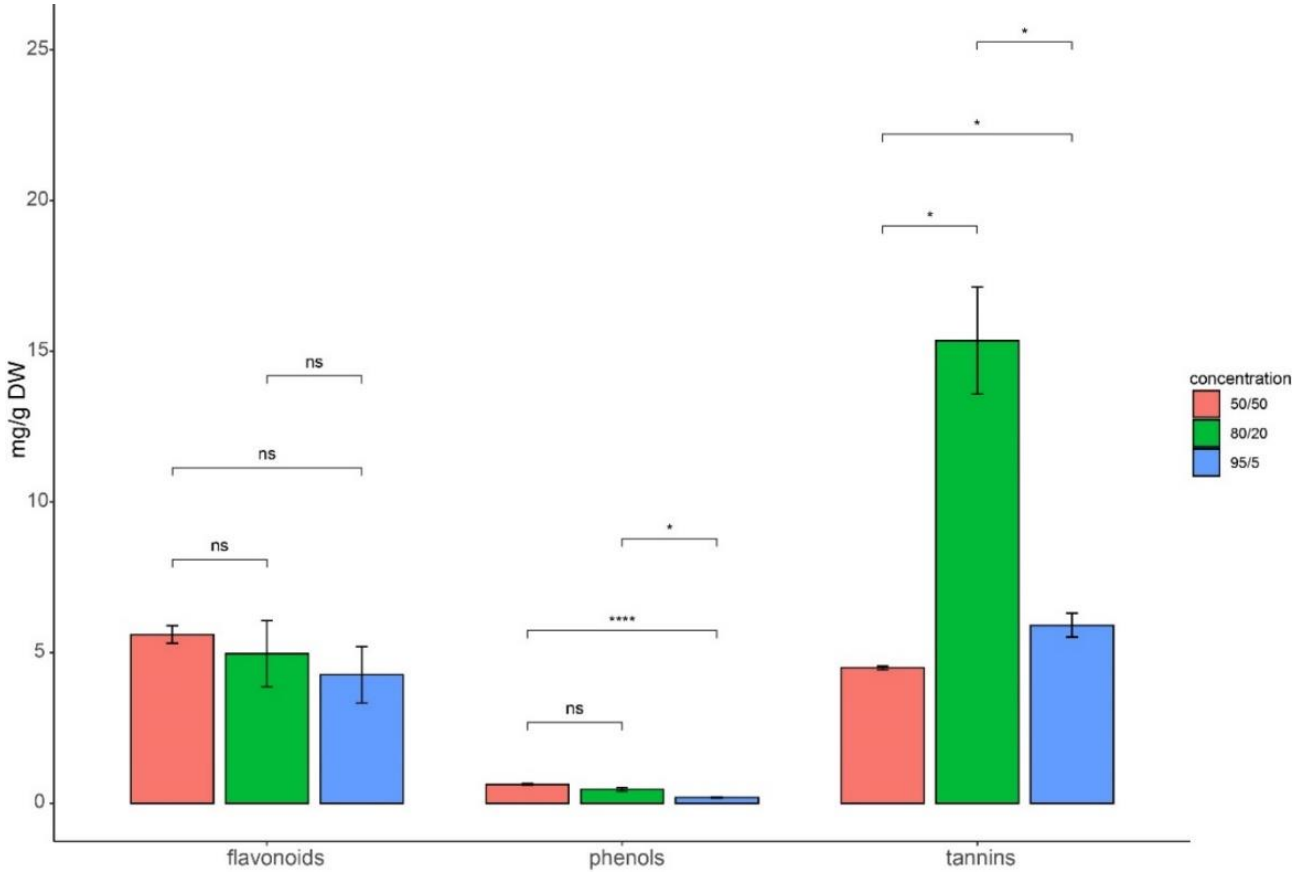


Figure 2-3. Test of the methanol concentration for total flavonoids, phenols and tannins (N=6)

Another important parameter for the extraction efficacy is a ratio of a sample quantity to a solvent (*i.e.* solid-to-liquid ration). We tested three ratios with 20 mg, 30 mg and 40 mg of biomass in 3 mL 50% methanol (Fig. 2-4). A high ratio may fit for the production of the concentrated extract. For quantification of phenolic compounds, a higher solvent volume is needed to ensure that desirable metabolites were completely removed from the plant material into the solvent (Chaves et al., 2020; Fan et al., 2019; Hosseini et al., 2018). More likely, solvent causes the swelling of the plant material, which leads to enchantment of the contact area between solvent and plant, subsequently it reflects the extraction efficiency (de Hoyos-Martínez et al., 2019; Prasad et al., 2011). Nevertheless, it was observed that further increase of the sample:solvent ratio led to decline in the total phenolic compounds concentrations, which might be related to the saturation of the solvent (Benchikh et al., 2019). We selected 30 mg in 3mL 50% methanol as the deviation among replicated was the smallest and the results were relatively high.

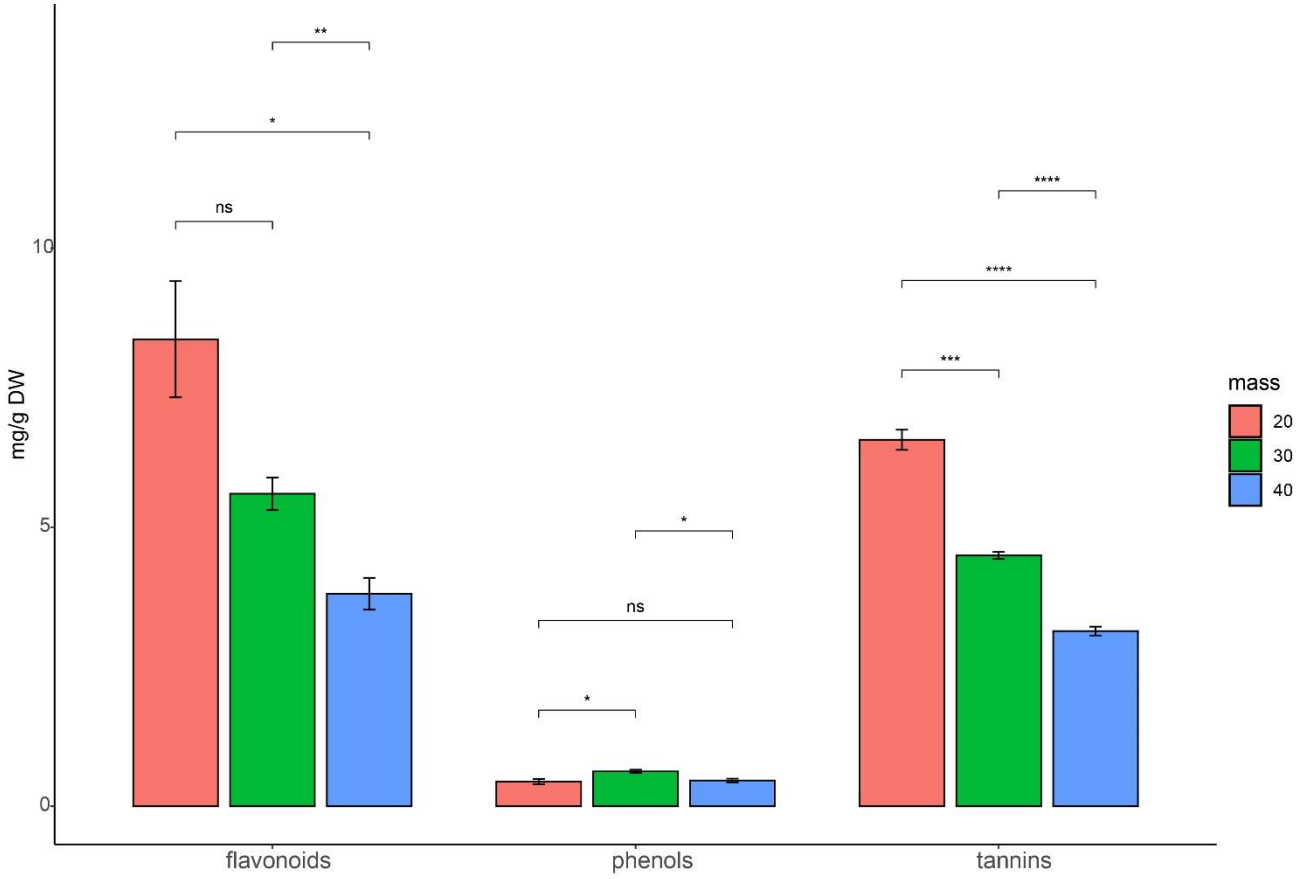


Figure 2-4. Test of the mass-to-volume ration for total flavonoids, phenols and tannins (N=6)

Two aided extraction methods were tested bubbling with nitrogen and ultrasound-assisted extraction. Among those methods, ultrasound-assisted extraction showed higher extraction rates comparing to other methods (Fig. 2-5). This technique is widely used for the extraction of biochemicals from natural resources (Chaves et al., 2020). Ultrasound-assisted extraction mechanism involves the shear force, which creates cavitation bubbles near the sample tissue in acoustic wave propagation in the kHz range (Laborde et al., 1998). Collapse of bubbles can result in the distribution (physical, chemical or mechanical) of cell membranes, and that facilitates the penetration of solvent into cellular compartments, which improve mass transfer and release extractable compounds (de Hoyos-Martínez et al., 2019; Vinatoru, 2001; Vinatoru et al., 1997). This extraction method was shown to cause less degradation of phenolic compounds and increase of extraction yield not only for vascular plant tissues (*e.g.* strawberries, Herrera and Luque De Castro 2005), but also for *Rhytadiadelphus* and *Sphagnum* mosses (Klavina, 2018). Besides, ultrasound-assisted extraction does not require complex equipment and decreases the extraction time.

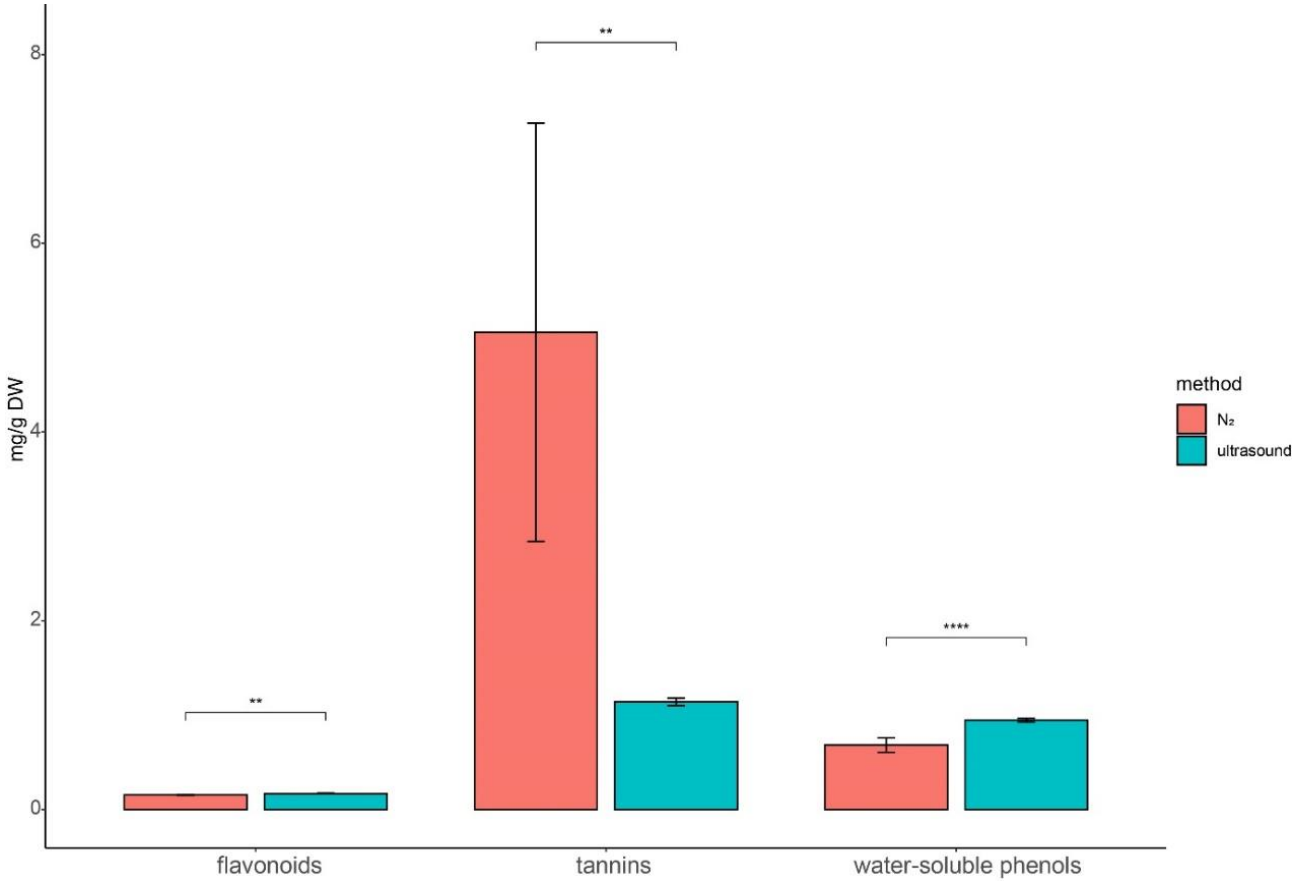


Figure 2-5. Test of the extraction method (N=6)

Thus, after tests of sample to solvent ratios, concentration of methanol and aided extraction techniques, an improved protocol of (Klavina, 2018) was applied for the extraction of *Sphagnum* total phenolic compounds, flavonoids, tannins and carbohydrates: lyophilized moss samples in a high-speed benchtop homogenizer were ground at 4.5 m/s, and then placed 40 mg of moss in a brown glass bottle with 4 mL of cold 50 % aqueous methanol solution (held at 4°C). After that, samples were exposed to an ultrasound bath for 40 min and bottles were shaken in an orbital shaker for 18 hours at 150 rpm, followed by another 40 min of ultrasound. Finally, moss extracts were replaced into 2 mL Eppendorf and centrifuged at 4500 rpm for 5 min at 4 °C. Collected supernatants were then used for further analyses.

2.2.1. Total flavonoids

Total flavonoids content was determined using aluminum trichloride ($AlCl_3$) assay. $AlCl_3$ forms stable acid complexes either with carbonyl (C=O) in C-4 position or with the hydroxyl group (OH) in C-3 or C-5 of flavones and flavonols. In addition, $AlCl_3$ can also form acid

complexes with the with the orthodihydroxyl groups possibly present on the A and/or B ring of flavonoids (Chang et al., 2002). The reaction occurs in basic conditions, where the products of reaction are red aluminum- flavonoid chelates, which capable of absorption under a certain wavelength (Matić et al., 2017).

Trichloroaluminum assay was used to assess the concentration of total flavonoids in *Sphagnum* tissues (Settharaksa et al., 2014). Twenty-five µL of moss methanolic extract was placed into 96-well microplate with 10 µL of 5% $NaNO_2$. Then, the plate was covered with aluminum foil and incubated for 6 min at 20°C. Following incubation, 15 µL of 10% AlCl3 and 200 µL of 1M NaOH were added in each well, the plate was covered and shaken for 1 min. The absorption was measured on the spectrophotometer at 595 nm wavelength. Catechin was used as standard and thus values expressed in mg equivalent catechin per gram of dry moss (mg g^{-1} DW).

2.2.2. Total tannins

Total tannins (*i.e.* flavonols or condensed tannins) are determined by the acid vanillin method (Price et al., 1978). This method is based on the ability of vanillin to react with flavonols units in the presence of acid to produce a colored complex measured at 500 nm. The vanillin reagent (*i.e.* aldehyde) reacts with A-rings of the flavanols in acid solution and the methylene-ols, resulting from aldehyde-flavonol condensation, form a colored (from pink to red) carbonium anion in concentrated acid (Pew, 1948; Sarkar and Howarth, 1976).

The quantification of total tannins followed (Bekir et al., 2013): 50 µL of moss methanolic extract was placed into 96-well microplate and then 100 µL of freshly prepared 1% in 7M H_2SO_4 was added. After 15 min of incubation in the dark at room temperature, the absorbance at 500 nm was measured. Cathehine was used a standard and the results were expressed in mg equivalent catechin per gram of dray moss DW (mg g^{-1} DW).

2.2.3. Total phenols and water-soluble phenols

Folin-Ciocalteu method is widely used methods for phenolic compounds determination (Singleton et al., 1999). Folin-Ciocalteu reagent is a mixture of phosphomolybdic and phosphotungstic acids, that is used for determination of phenolic compound with gallic acid as standard (Singleton and Rossi, 1965). If the reaction undergoes in alkaline medium,

electrons are transferred from phenolic compounds to the mixture of acids, and they form blue complexes which can be spectroscopically determine at 760 nm (Singleton et al., 1999).

2.2.3.1. Total phenols

To identify total phenolic compounds we followed the protocol of Ainsworth and Gillespie (2007) *Sphagnum* methanolic extract was transferred into 96- wells transparent microplate with 40 µL of 10% Folin-Ciocalteu reagent. Then the microplate was covered with aluminum and shaken for 2 min using vortex, 140 µL of 700 mM $NaHCO_3$ was added in each well, and the microplate was covered and incubated at 45oC for 20 min. Finally, the absorption of each well was measured using a spectrophotometer (Biotek Synergy MX) at 760 nm wavelength. Gallic acid was used as standard, so total polyphenolic content was expressed in mg equivalent Gallic acid per gram of dry moss (mg g^{-1} DW).

2.2.3.2. Water-soluble phenols

The quantification of total water-extractable phenols followed Jassey *et al.* (2011b) with some modifications. It was found that the weight of *Sphagnum* biomass can be slightly decreased with conserving the same extraction yield and small deviation between replicates (40 mg instead of 50 mg, Fig. 2-6). Filtration with glass microfiber filter GF/C is an efficient method for separation of residuals, however this method has two significant drawbacks: (1) it is time and material consuming procedure (*i.e.* rinsing the syringe and filter-holder between samples, pricy filters) and (2) potential leakage from filter may interfere the results. Centrifugation at low temperature (4 °C) allows precipitating and attaching derbies to tube walls and then collect the supernatant for further steps (Fig. 2-7). This technique significantly reduces the separation time as up to 30 tubes can be simultaneously proceeded (depending on the centrifuge type).

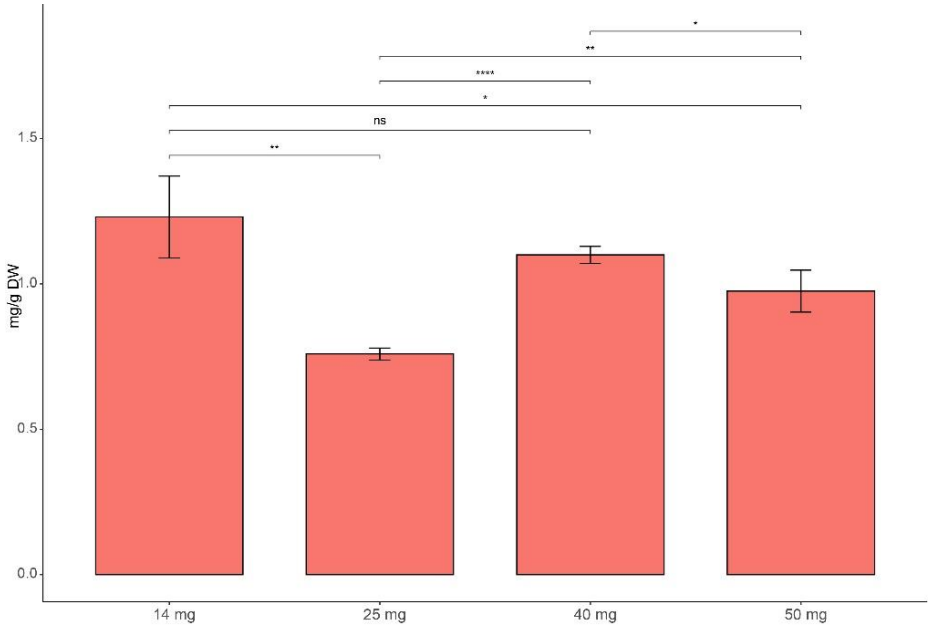


Figure 2-6. Test of the mass-to-volume for water-soluble phenols (N=5)

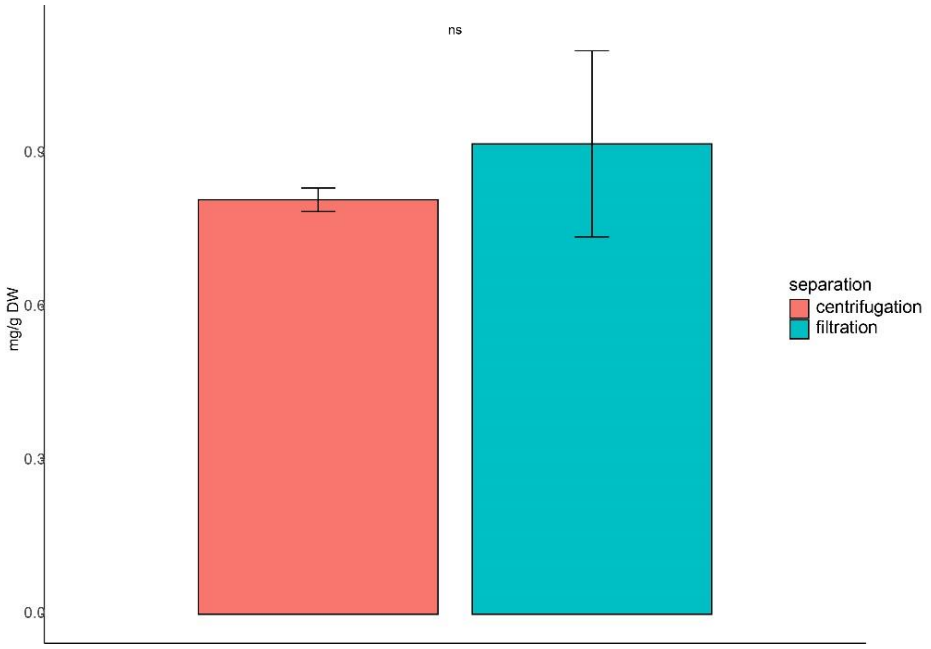


Figure 2-7. Test of the separation method (N=5)

Twenty mg of lyophilized moss together with 5 mL of distilled water were placed into brown glass bottles and exposed to ultrasound in an ultrasound bath for 40 min. After that, test bottles were placed in a shaker for 3 hours at 150 rpm. Once shaking finished, tubes were centrifuged at 4500 rpm for 5 min at 4 °C. Then, 1.75 mL of collected supernatant was transferred in brown glass bottle and 0.25 mL of Folin & Ciocalteu's reagent was added. Test bottles were vigorously mixed with vortex and then 0.5 ml of 20 % Na2CO3 was added and

the vortex was repeated. Finally, we put samples in bain-marie at 40 °C. After 20 min of incubation the absorbance on the spectrophotometer at 760 nm was measured. Gallic acid was used a standard, so total polyphenolic contents were expressed in mg equivalent gallic acid per gram of dry moss (mg g^{-1} DW).

2.2.4. Proline

Sulfosalicylic acid is usually used to extract proline. This acid precipitates proteins, which can be easily removed by centrifugation and leaving the free amino acids in solution. The determination of proline is performed by using acid-ninhydrin method (Bates, 1973). At low pH and at high temperature (100 °C), a proline-ninhydrin interaction forms a red and hydrophobic reaction product, while other proteinogenic amino acids and ninhydrin produce little or no color (Forlani and Funck, 2020).

We used the protocol of Lee et al. (2018) for determination of total proline. We improved the protocol by decreasing the initial biomass from 30 mg to 25 mg, where we had high extraction yield and low deviation among replicates (Fig. 2-8). Briefly, 25 mg of lyophilized moss was ground with high-speed benchtop homogenizer with 1 mL of 3% (w/v) sulfosalicylic acid and centrifuged at 4500 rpm for 5 min at 4oC. Then, 1 mL of collected supernatant was mixed with 2 mL of acid ninhydrin reagent (1.25 g of ninhydrin and 100 mL of acetic acid glacial) and glass tubes were boiled at 100°C. After an hour of boiling, the reaction was stopped by placing tubes on ice. Absorbance was read at 510 nm. A standard curve was prepared with L-proline, thus proline content 245 was expressed as mg of proline per g dry weight (mg g^{-1} DW).

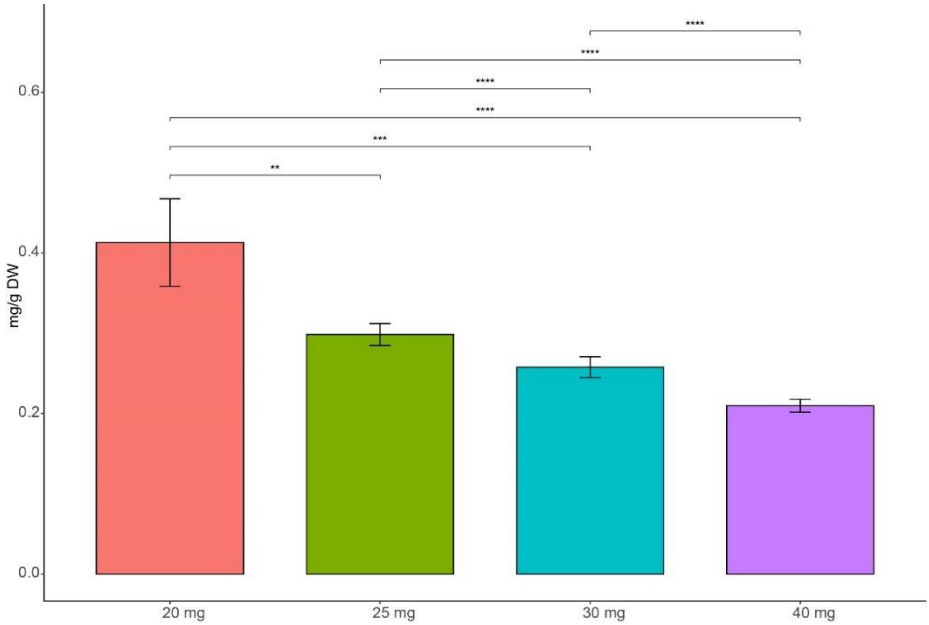


Figure 2-8. Test of the mass-to-volume for proline (N=3)

Chapter 3. Biochemical traits enhance the trait concept in *Sphagnum* ecology

In this chapter, I explored the potential of biochemicals (*i.e.*, metabolites, pigments and antioxidant enzyme activities) to provide deeper mechanistic understanding and predictive power of *Sphagnum* traits space across environmental gradients. Additionally, I question the potential linkages among *Sphagnum* morphological and anatomical traits and biochemical counterparts, as well as their joint response to environment change.

To address these aims, I quantified the contribution and the role of each group of traits to the functional trait space of *Sphagnum* mosses. The study was conducted in five European *Sphagnum*-dominated peatlands distributed along a latitudinal gradient in Europe, representing a range of local and regional environmental conditions. I measured a suite of five anatomical and morphological traits like volume of the capitulum (height × diameter of capitulum), water-holding capacity of the capitulum , number of hyaline cells per leaf area (*i.e.* dead cells storing water), the surface area of hyaline cell (length x width), and width of chlorocystes (photosynthetic cells surrounding hyaline cells) as well as various *Sphagnum* biochemical traits: pigments (chlorophyll, carotenoids), metabolites (total carbohydrates, total phenols, water-soluble phenols, total flavonoids, total tannins, proline, proteins) and enzyme activities (APX, CAT, POX, SOD).

The findings show that *Sphagnum* growing in different local environmental (vegetation composition, nutrients content) and regional (temperature, precipitation) conditions possess a suite of diverse biochemical traits that supports *Sphagnum* form and function as well as its resistance to environmental changes. *Sphagnum* morphological and anatomical traits were intrinsically linked to *Sphagnum* metabolites and enzyme activities, and these relationships were driven by shared responses to local and regional environmental factors. More particularly, *Sphagnum* traits can be grouped into four clusters related to growth, biomass, defense and water stress tolerance. However, *Sphagnum* anatomical/morphological and biochemical traits had relatively poor shared responses to environmental conditions. Regional and local environmental conditions data to further show that biochemicals and their specific linkages with some morphological traits describe dimensions of physiology not captured by anatomical and morphological traits alone. We suggest that these relationships represent previously unreported trade-offs of resource allocation by mosses, whereby *Sphagnum* mosses devote resources to maintain their growth to cope with environmental changes or resist to increasing competition.

This chapter provides strong evidence that measurements of the metabolites and antioxidant enzyme activities, once properly incorporated with classical morphological and anatomical traits, expand our understanding of the coupling between physiology and fitness in *Sphagnum* trait-based studies

Biochemical traits enhance the trait concept in *Sphagnum* ecology

Anna Sytiuk[1]*, Regis Céréghino[1], Samuel Hamard[1], Frédéric Delarue[2], Ellen Dorrepaal[3], Martin Küttim[4], Mariusz Lamentowicz[5], Bertrand Pourrut[1], Bjorn J.M. Robroek[6], Eeva-Stiina Tuittila[7], Vincent E.J. Jassey[1]*

Oikos 2022: e09119

DOI: 10.1111/oik.09119

Accepted 16 January 2022

[1]Laboratoire Ecologie Fonctionnelle et Environnement, Université de Toulouse, UPS, CNRS, Toulouse, France, [2]Sorbonne Université, CNRS, EPHE, PSL, UMR 7619 METIS, 4 place Jussieu, F-75005 Paris, France, [3]Climate Impacts Research Centre, Department of Ecology and Environmental Science, Umeå University, SE-981 07, Abisko, Sweden, [4]Institute of Ecology, School of Natural Sciences and Health, Tallinn University, Uus-Sadama 5, 10120 Tallinn, Estonia, [5]Climate Change Ecology Research Unit, Faculty of Geographical and Geological Sciences, Adam Mickiewicz University in Poznań, Bogumiła Krygowskiego 10, 61-680 Poznań, Poland, [6]Aquatic Ecology & Environmental Biology, Radboud Institute for Biological and Environmental Sciences, Faculty of Science, Radboud University Nijmegen, AJ 6525 Nijmegen, The Netherlands, [7]Biological Sciences, Faculty of Natural and Environmental Sciences, Institute for Life Sciences, University of Southampton, Southampton SO17 1BJ, UK, [8]School of Forest Sciences, Joensuu campus, University of Eastern Finland, Finland.

*corresponding authors: anna.sytiuk@univ-tlse3.fr

Abstract

Sphagnum mosses are key to northern peatland carbon sequestration. They have a range of morphological and anatomical characteristics that allow them to cope with environmental stress. *Sphagnum* also produces a plethora of biochemicals that may prevent stress-induced cell-damage. However, the linkages between *Sphagnum* anatomical, morphological and biochemical traits (*i.e.* metabolites, pigments and antioxidant enzyme activities) are poorly known, neither are their joint responses to environmental change. Here, we quantify and link an array of *Sphagnum* anatomical, morphological and biochemical traits in five *Sphagnum*-dominated peatlands distributed along a latitudinal gradient in Europe, covering a range of regional and local environmental conditions. *Sphagnum* morphological and anatomical traits were intrinsically linked to *Sphagnum* metabolites and enzyme activities, and these relationships were driven by shared responses to local and regional environmental factors. More particularly**,** we found that *Sphagnum* traits can be grouped into four clusters related to growth, biomass, defense and water stress tolerance. We used regional and local environmental conditions data to further show that biochemicals and their specific linkages with some morphological traits describe dimensions of physiology not captured by anatomical and morphological traits alone. These results suggest that *Sphagnum* morphology and function is rooted in the metabolome, and that incorporating biochemicals into the functional trait space concept can enhance our mechanistic understanding and predictive power in *Sphagnum* ecology.

Key words: *Sphagnum*, peatlands, metabolites, antioxidant enzyme activities, bryophytes, climate change.

3.1. Introduction

Recent decades have seen an explosion of research into the use of plant traits to determine how individual plants cope with changing environments (Díaz et al., 2004; Kattge et al., 2011; Reich et al., 2003), and how they can affect ecosystem processes in return (Chelli et al., 2019; Lavorel and Garnier, 2002). Despite their relevance for generalizing predictions across organizational and spatial scales (Adler et al., 2013), the plant traits which are commonly used by ecologists (*e.g.* plant height, seed mass, and specific leaf area; Díaz et al., 2016) only moderately explain ecosystem properties (Plas et al., 2020), thus leaving a large fraction of ecosystem processes unexplained. This indicates that there are some limits to which extent classical morphological traits can predict ecosystem processes, so that additional drivers, more closely embodied in plant physiology such as primary and secondary metabolites, may be required to improve predictions of plant form and function (Walker et al., 2019).

Plants produce thousands of metabolites that collectively determine their fitness *via* their effects on survival, growth and/or reproduction (Weng et al., 2021). For example, plants respond to drought, temperature, herbivore or pathogen stress by producing specialized metabolites, such as alkaloids, terpenoids, and phenolic compounds (Cipollini et al., 2012; Defossez et al., 2021; Fernandez-Conradi et al., 2021; C. W. Fernandez et al., 2016; Peters et al., 2019; van Dam and Bouwmeester, 2016; Van der Putten et al., 2013; Weckwerth and Kahl, 2013). Therefore, plant metabolites can be key for understanding the ecosystem functioning as they may drive ecosystem processes such as decomposition and/or carbon cycling (Chomel et al., 2016; Whitham et al., 2006). As classical morphological traits, plants metabolites are determined by the same suite of evolutionary and ecological processes (Defossez et al., 2021; Sedio et al., 2017). However, they may provide better mechanistic understanding in ecological context as they lie at the interface between genes and environment (Ahuja et al., 2010). The identification and quantification of plant metabolites can therefore provide a snapshot of the overall plant performance and adaptation success when facing changing environmental conditions (Ahanger et al., 2018).

While many attempts have been done to characterize the diversity and the dynamic of metabolites within vascular plants (see examples in Bakhtiari et al., 2021; Defossez et al., 2021; Obata and Fernie, 2012; Skoneczny et al., 2018; Turner et al., 2016), much less has been done for non-vascular plants such as mosses. Yet mosses make a significant contribution to aboveground biomass and soil carbon sequestration, particularly in peatlands (Tan and Pócs, 2000; Turetsky, 2003). *Sphagnum* mosses effectively facilitate wet, anoxic and acidic conditions that inhibit decomposition (Clymo and Hayward, 1982; Rydin and Jeglum, 2006;

Turetsky, 2003). They also produce a recalcitrant litter and release antimicrobial compounds in their surrounding environment that further hampers the decomposition of dead organic matter (Fudyma et al., 2019; Hamard et al., 2019; Turetsky, 2003; van Breemen, 1995). *Sphagnum* mosses have therefore an extraordinary impact on the global C cycle by modulating peatland C uptake and storage. However, despite these general properties we still lack a clear understanding of the species-specific characteristics, or traits, controlling *Sphagnum* growth and/or survival at global and local scale (Bengtsson et al., 2020a). *Sphagnum* species exhibit high interspecific variability in their inherited anatomical, morphological and biochemical traits (Bengtsson et al., 2020b, 2018, 2016; Chiapusio et al., 2018; Dorrepaal et al., 2005; Gong et al., 2020a). While *Sphagnum* anatomical and morphological traits are increasingly used to explain how *Sphagnum* species interact with environmental conditions (Bengtsson et al., 2020b; Jassey and Signarbieux, 2019; Laine et al., 2021), we lack knowledge on interspecific differences in *Sphagnum* biochemical traits, their relationship with anatomical and morphological trait, and how they are affected to local and regional changes.

Sphagnum mosses produce numerous metabolites which can be released in the environment (Fudyma et al., 2019; Hamard et al., 2019; Verhoeven and Liefveld, 1997). These metabolites facilitate *Sphagnum* growth, defense and competitiveness *via* interaction with the environment and/or with other organisms in the environment (Erb and Kliebenstein, 2020; Khare et al., 2020; Massalha et al., 2017; Wink, 2010). These metabolites have been suggested to be involved in specific or multiple functions, but most likely they play a role in moss fitness and stress tolerance (Isah, 2019; Tissier et al., 2014; Yang et al., 2018). More particularly, a wide and important class of primary (carbohydrates, carotenoids) and specialized metabolites (phenols, proline, flavonoids, tannins, proline) could play crucial roles in the growth, photosynthesis, litter-resistance to decomposition and tolerance to abiotic stresses in bryophytes (Cornelissen et al., 2007; Xie and Lou, 2009). For instance, the production of carbohydrates and polyphenols can support the maintenance of the integrity of plant cell-structure and the internal regulation of plant cell physiology (Ferrer et al., 2008; Roberts et al., 2012; Rudolph and Samland, 1985; Tissier et al., 2014). To protect their cells against oxidative damages (Davies, 1986; Dizdaroglu, 1994; Leprince et al., 2000; Sharma et al., 2012), mosses— like vascular plants— further accumulate antioxidants such as flavonoids and/or activate antioxidant enzymes such as catalase (CAT), glutathione reductase (GR), peroxidases (POX)/ascorbate peroxidases (APX) and superoxide dismutase (SOD) (Choudhury et al., 2013; Das and Roychoudhury, 2014; Liu et al., 2016; Minibayeva and Beckett, 2001; Noctor et al., 2018). The regulation of the production of *Sphagnum* metabolites and of the antioxidant

enzyme activities are likely important for *Sphagnum* morphology, growth, physiology and the tolerance to environmental changes (Ahanger et al., 2018). Hitherto, only a limited number of studies have focused on *Sphagnum* metabolites (Chiapusio et al., 2018; Fudyma et al., 2019; Hamard et al., 2019; Klavina et al., 2018; Sytiuk et al., 2021), while antioxidant enzyme activities remains largely unexplored. In addition, the linkages among *Sphagnum* anatomical and morphological traits, metabolites and antioxidant enzyme activities are virtually unknown, while resource allocation trade-offs among these different *Sphagnum* traits could have important ramifications for peatland carbon cycling.

In this work, we aim to explore the potential of biochemicals (*i.e.*, metabolites and enzyme activities) to provide deeper mechanistic and predictive power of *Sphagnum* traits space across environmental gradients. To address this aim, we quantified the contribution and the role of each trait group to the functional trait space of *Sphagnum* mosses. Our study was conducted in five European *Sphagnum*-dominated peatlands distributed along a latitudinal gradient in Europe, representing a range of local and regional environmental conditions. We collected one dominant *Sphagnum* species per site, to observe species performance at their site of origin. With this design we assumed that species were not facing stress conditions. Specifically, our aims were to: (*i*) gather new *Sphagnum* traits information relevant to further ecological and environmental studies, (*ii*) test the strength of the linkages among *Sphagnum* anatomical/morphological traits and metabolites/antioxidant enzyme activities, and (*iii*) assess the extent to which local and regional environmental factors influence these linkages.

3.2. Materials and methods

3.2.1. Study sites

Five sites were selected along a latitudinal gradient spanning different local and regional environmental conditions, from northern Sweden to southern France. Overall, these peatlands covered a range of mean annual temperature from -0.1 °C to 7.9 °C, and a range of precipitation from 419 mm to 1027 mm (Table 3-1, WorldClim v2 (Fick and Hijmans, 2017). Details of these five sites follow.

(1) Counozouls is a moderately rich fen in southwestern France that belongs to the Special Area of Conservation Natura 2000 site "Massif du Madres Coronat" (42°41'19.7"N 2°14'02.4"E) in the Pyrenees mountains. The moss layer was dominated by *Sphagnum*

capillifolium, *S. warnstorfii* and *S. palustre* while vascular plants were dominated by *Molinia caerulea*, *Carex rostrata*, *Ranunculus polyanthemoides*. and *Potentilla anglica*.

(2) Kusowo Bagno is an open bog in northern Poland (53°48'47.9"N 16°35'12.1"E) in a nature reserve and is a part of the Special Area of Conservation Natura 2000 site "Lake Szczecineckie". The peat moss layer was dominated by *S. magellanicum* and *S. fallax*, while *Eriophorum vaginatum*, *Andromeda polifolia*, *Vaccinium oxycoccos*, and *Drosera rotundifolia* were the most common vascular plants at the sampling location.

(3) The Männikjärve bog (58°52'26.4"N 26°15'03.6"E) is in Central Estonia in the Endla mire system. The ground layer was dominated by *S. rubellum*, *S. fuscum* and *S. magellanicum* whereas *Drosera rotundifolia*, *Eriophorum vaginatum*, *Andromeda polifolia*, and *Vaccinium oxycoccos* characterized the vascular plant community.

(4) Siikaneva (61°50'41.6"N 24°17'17.5"E) is an ombrotrophic bog complex located in Orivesi, southern Finland. The *Sphagnum* carpet was dominated by *S. fuscum* in hummocks and *S. papillosum*, *S. majus*, and *S. rubellum* in lawns-hollows. The vascular plant layer was composed of dwarf shrubs (mainly *Vaccinium oxycoccos* and *Andromeda polifolia*), ombrotrophic sedges (*Eriophorum vaginatum* and *Carex limosa*) and herbs (*Scheuchzeria palustris* and *Drosera rotundifolia*).

(5) Abisko (sub-arctic Sweden; 68°20'43.1"N 19°03'58.7"E) is a gently sloping aapa mire surrounded by tundra. *S. balticum* was the numerically dominant peat moss species, whereas vascular plants such as *Carex sp.*, *Andromeda polifolia*, *Rubus chamaemorus and Empetrum nigrum* were scarce.

Table 3-1. Characteristic of regional and local conditions of the five study sites. Mean annual temperature and annual precipitation data are averaged over the period 1960-2018 (WorldClim v2); water table depth and pore water pH were measured directly at the field conditions in July 2018; *Sphagnum* field water content and relative plant/moss cover are presented as mean±SE (n=5). Sites ordered along the south-north latitudinal gradient.

		France	**Poland**	**Estonia**	**Finland**	**Sweden**
Site		FR	PL	EST	FI	SE
Coordinates		42°41'19.7"N 2°14'02.4"E	53°48'47.9"N 16°35'12.1"E	58°52'26.4"N 26°15'03.6"E	61°50'41.6"N 24°17'17.5"E	68°20'43.1"N 19°03'58.7"E
Altitude	(m asl)	1374	145	82	160	281
Microtopography of sampling		lawns	lawns	lawns	lawns	lawns
Mean annual temperature	(°C)	7.9	7.3	4.9	2.9	-0.1
Annual precipitation	(mm)	1027	656	623	611	418
Water table depth	(cm)	-16.5	-60	-20	-8	-10
Pore water pH		4.89	3.56	4.10	3.86	3.83
Sphagnum field water content	(gH_2O/ g DW)	11.4±0.6	4.1±1.1	9.8±1.7	10.6±0.7	13.96±1.8
Relative moss cover	(%)	32.1±4.6	63.3±3.6	77.3±2.6	73.2±3.2	62±3.2
Relative vascular plant cover	(%)	50.2±4.6	19.3±2.2	14.8±1.0	13.1±2.5	18.3±2.9

3.2.2. Sample collection

Sphagnum samples were collected at every site within the same week in early-July 2018. At each site, we selected five homogeneous plots of the same microtopography comprising of lawns (50 x 30 cm each; 5 plots x 5 sites = 25 plots in total, Table 3-1) with a single dominant *Sphagnum* species as based on a vegetation survey (Table S1): *S. warnstorfii* (France), *S. magellanicum* (Poland), *S. rubellum* (Estonia), *S. papillosum* (Finland) and *S. balticum* (Sweden). Dominant *Sphagnum* species were site specific, potentially creating a confounding effect with environmental conditions. However, it has been recently demonstrated that such potential confounding effect between species and site was not an important issue when referring to *Sphagnum* biochemical traits because of the decoupling between *Sphagnum* biochemical traits and phylogeny (see Material and Methods and Figures S1-S3 in Sytiuk et al., 2021). In addition, we provide in Fig. S1 the ranges of variations of the different biochemical traits analyzed in the five *Sphagnum* species based on data from a reciprocal transplant experiment on the same *Sphagnum* species dispatched along our latitudinal gradient. The results show that the variability within the species is higher that between the species and thus that environment has stronger effect on the *Sphagnum* biochemical traits than *Sphagnum* taxonomy. Nevertheless, we acknowledge that anatomical and morphological traits are used to identify *Sphagnum* moss to species level (Isoviita, 1966), and that in our study anatomical and morphological traits cannot be disentangled from *Sphagnum* taxonomy, and hence sites. We therefore used site as fixed effect in all statistical analyses (see numerical analysis section) to avoid any further confusion.

In each plot, we collected 15-20 *Sphagnum* shoots around 10 marked spots. Upon sampling, the living part of *Sphagnum* shoots (top 3 cm from the capitula) were cut immediately, pooled, homogenized and then distributed in plastic bag/tubes for different lab analyses. Samples were kept in a cooler (4 °C) while travelling back to the laboratory. Upon arrival, samples were frozen at -20 °C or kept cold at 4 °C depending on the type of analysis.

3.2.3. Characterizing local environmental conditions

Water-table depth (WTD) and porewater pH were measured directly in the field using a ruler and a portable multimeter Elmetron CX742, respectively. 50 mL of porewater was collected at each plot to analyze water chemistry. Additionally, water-extractable organic matter (WEOM) was extracted from the *Sphagnum* shoots (0-3 cm height) collected in each plot following (Jassey et al., 2018). Briefly, *Sphagnum* shoots were soaked in 30 mL of

demineralized water and then shaken for 90 min at 150 rpm. *Sphagnum* shoots were then dried at 60°C for 48 hours and weighted to obtain dry mass (mg/g DW). Nutrients and ions were measured in porewater and WEOM as follow (Table S2): dissolved organic carbon and nitrogen and phosphorous (measured by combustion on a Shimadzu TOC-L) and ions (SO_4^{2-}, Cl^-, F^-, NO_3^- Ca^{2+}, Mg^{2+}, K^+, Na^+, measured on Dionex Ics-5000+ and Dionex DX-120). Cluster analysis (Ward method) on porewater and WEOM chemistry was used to group the five peatlands according to similarity in their 'nutrient status'. As pore water in Polish site was impossible to collect (too dry), we based our analysis on the four other sites. We found similar clusters between the pore water and WEOM (Fig. S2). This shows that both the pore water and WEOM can be used to define the 'nutrient status' of our sites. Subsequently, we used WEOM chemistry to classify the five sites according to their nutrient richness and pH.

We assessed the dynamic of plant species cover at each date in each of the five sites using pictures taken in each plot (Table S1, Fig. S3). Following Buttler *et al.* (2015), we took two high-resolution images in each plot (25 x 15 cm). On each picture, we had a grid of 336 points laid and quantified species overlaying the grid intersects. This technique did not support an estimation of vertical biomass distribution and possibly underestimated the frequency of certain species (Jassey et al., 2018). However, the potential bias was similar across plots, making species frequencies comparable among sites. We especially distinguished the dwarf-shrubs cover from the non-woody herbaceous cover as these two plant types differ in energy and nutrient allocation and litter production, and as such may have different effects on ecosystem C dynamic (Kruk and Podbielska, 2018).

3.2.4. *Sphagnum* anatomical and morphological traits

We characterized an architectural variability of five *Sphagnum* species using a suite of five anatomical and morphological traits following Jassey and Signarbieux (2019): volume of the capitulum (height x diameter of capitulum), water-holding capacity of the capitulum and shoot, number of hyaline cells per leaf area (*i.e.* dead cells storing water), the surface area of hyaline cell (length x width), and width of chlorocystes (photosynthetic cells surrounding hyaline cells). We randomly selected 125 *Sphagnum* shoots (25 per site) to estimate the volume of the capitula (mm^3) by measuring their height and diameter using a ruler. Then, the same samples were used to quantify the water-holding capacity of the capitula at water saturation. Capitula were submerged in water until saturated, then the plant was suspended horizontally and allowed water to flow naturally after removing capitula from water for two minutes.

Then, every capitula and stems were weighed as water-saturated and dried out after 3 days at 60 °C. The net water content at water saturated of each capitula was expressed in grams of water per gram of dry mass (g H_2O/g DW). For anatomical traits analyses, five *Sphagnum* capitula from every plot (125 capitula in total) were carefully deconstructed to separate *Sphagnum* leaves. Then, all *Sphagnum* leaves were pooled, homogenized, and three leaves (per plot) were taken from that pool to prepare microscope slide from each plot (in total, 375 leaves). We measured the number of hyaline cells per leaf area (number of hyaline cells per mm^2), their surface (μm^2), as well as the width of chlorocystes (μm) using a light microscope connected to a camera (LEICA ICC50 HD) and the size analytic tools (LEICA suite software).

3.2.5. *Sphagnum* biochemical traits: metabolites, pigments, proteins and antioxidant enzyme activities

Fig.3-1 summarizes the different extractions pathways used to quantify the various *Sphagnum* biochemical traits: pigments, metabolites and enzyme activities. *Sphagnum* mosses were previously frozen, lyophilized and stored at -20 °C before performing any biochemical analysis. All details about biochemical extraction and quantification can be found in Supplementary method.

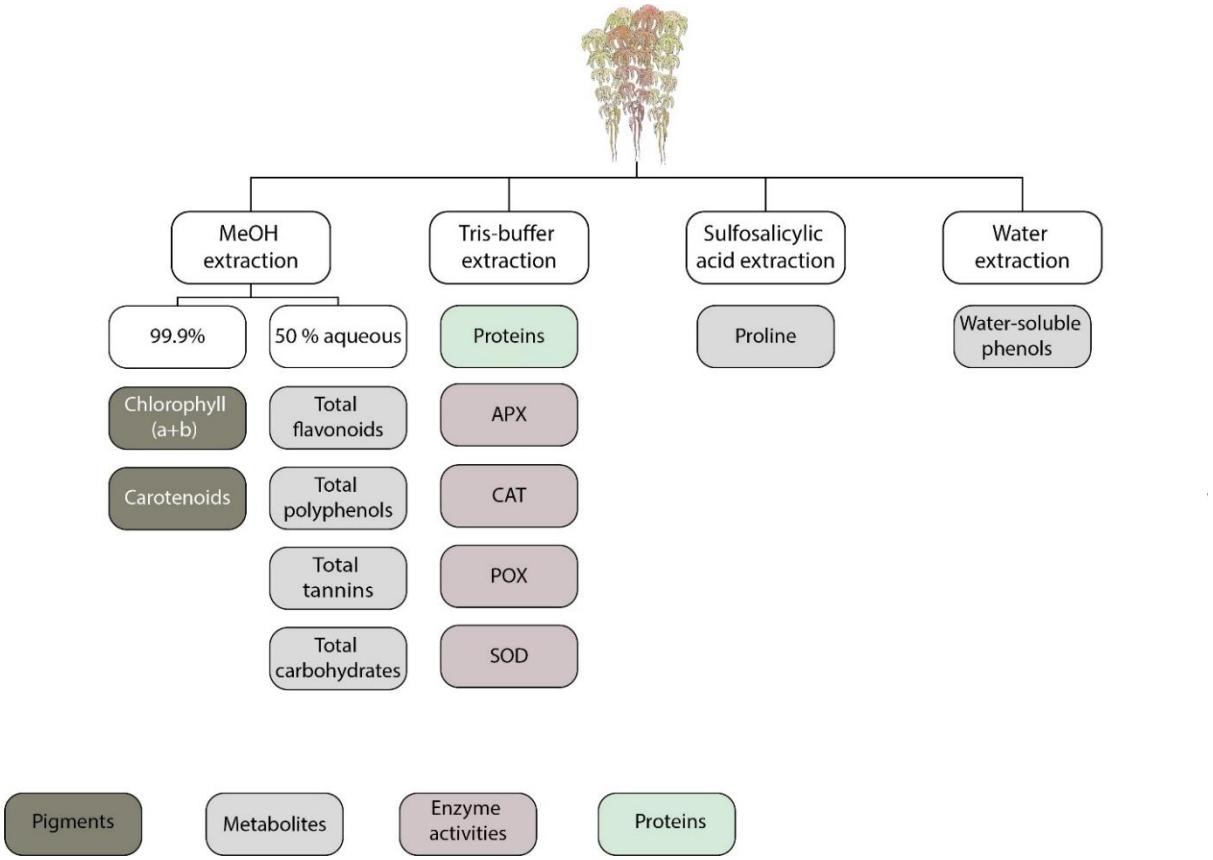


Figure 3-1. A summary of the extraction methods for quantification of *Sphagnum* biochemical traits: pigments, metabolites, antioxidant enzyme activities and proteins. Abbreviations are APX (EC 1.11.1.11) - ascorbate peroxidase activity, CAT (EC 1.11.1.6) – catalase activity, POX (EC 1.11.1.7) – peroxidase activity, SOD activity (EC 1.15.1.1) - superoxide dismutase.

3.2.6. Statistical analyses

All statistical analyses were performed in *R* 3.5.3 (R Core Team, 2019) using specific packages, as specified below. Linear mixed effects models (LMEs) were used to assess the effect of site (fixed effect) on *Sphagnum* traits (anatomical, morphological and biochemical traits), as well as the effect of the site on local and regional environmental conditions and relative plant cover. The models were fitted with plot nested within site as a random effect on the intercept (Pinheiro and Bates, 2000). Tukey's multiple comparison test was used for *post hoc* analyses of differences among the levels of the fixed effects in the final model. Assumptions of normality and homogeneity of the residuals were checked visually using diagnostic plots and a Shapiro test. Log_{10}-transformation was used when necessary in order to meet these assumptions. As the distributions of distribution of water-extractable organic

matter data are not normal, non-parametric Friedman tests were performed to assess the differences between sites.

To represent differences of *Sphagnum* trait space, including anatomical, morphological and biochemical traits, we performed principal coordinate analysis (PCoA) using Gower's distance (Villéger et al., 2008). A standardization of *Sphagnum* anatomical, morphological and biochemical traits was applied on the matrices beforehand (Legendre and Legendre, 2012). To assess which proportion of *Sphagnum* moss functional space was actually occupied by *Sphagnum* anatomical and morphological and biochemical traits among overall traits, we calculated the volume of the observed multidimensional convex hull in the selected ordination space (Barber et al., 1996). The volumes of observed hulls were based on the three first axes of principal component analysis and was quantified using *geometry R* package.

To identify the linkages among *Sphagnum* traits under changing environmental conditions, we used a joint species distribution modelling approach (JSDM, (Pollock et al., 2014). JSDM takes hierarchical approach, which combines abundances and similarities in trait responses to latent parameters such as local and regional environmental variables (*i.e.* traits co-occurrence with environmental parameters). The model begins with a trait joint distribution analysis and builds on inverse prediction that evaluates how environmental parameters affect the distribution of co-occurring traits (Pollock et al., 2014). Then, traits correlations can be divided into two groups: (1) environmental correlations among traits due to similar response of traits to environmental conditions and (2) residual correlations, *i.e.* correlation between traits that are not due to environmental conditions. JSDM was performed with the Bayesian Ordination and Regression AnaLysis as implemented in *boral* R package and using two latent variables to estimate the residual correlations among traits. The trait matrix was spatially detrended beforehand to avoid any confounding effect with regional climate. We used package *igraph* to build networks of either trait's linkages due to shared environmental responses or traits linkages not due to environmental responses. We considered traits co-response to be robust when the correlation between traits due to shared environmental response (or residual correlation) was significant at $P<0.05$. The analysis was performed with *Sphagnum* traits, regional (annual precipitations and the mean temperature of the wettest quarter) and local (pH, WEOM chemistry and plant cover) environmental parameters.

Furthermore, we tested whether combining biochemicals to anatomical and morphological traits improves the characterization of '*Sphagnum* form and function' in the

context of species environmental tolerances. To this end, we built a structural equation model (SEMs; Fig. S4) that tested for associations between the regional and local variables and a latent variable capturing "*Sphagnum* form and function" space– that is, an unmeasured, hypothesized, variable describing the functional space of *Sphagnum* mosses and whose existence may be revealed by the product of measured variables, *i.e.*, the morphological/anatomical and biochemical traits (Fig. S4). Specifically, we constructed our SEM model using the package "lavaan" (Rosseel, 2012), which drew from a hypothesis-driven *a priori* model based on our expectation that biochemicals enhances mechanistic understanding of how environmental change affect *Sphagnum* form and function (Fig. S4; hypotheses: Table S3). The latent variable has been defined by the product of four clusters of *Sphagnum* traits (see Fig. S4 and results). In the model, the four trait-clusters were defined by the site scores of a PCA performed on the traits that belong to each cluster (see Fig. 5A). In other words, cluster 1 was defined by the sites scores of a PCA computed on the variables POX, water-soluble phenols, total phenols, tannins and proline, and so on for the other clusters. The two first PCA axes of each cluster were tested in the SEM model selection process. The variable WEOM is defined by the PCA site scores (first axis) performed on WEOM physicochemical parameters (pH, dissolved organic carbon, nitrogen and phosphorous and ions SO_4^{2-}, Cl^-, F^-, NO_3^- Ca^{2+}, Mg^{2+}, K^+, Na^+). We diagnosed model fits using chi-squared statistics ($P > 0.05$), root-mean squared errors for approximation and residual indices (≤ 0.1) and comparative fit indices (≥ 0.95), and included variables and paths in the final model based on chi-squared statistics ($P < 0.05$) and AIC values.

3.3. Results

In this section we refer to changes in sites (see Table 3-1 for site acronyms), which nevertheless are confounded with *Sphagnum* species identity. We advise to check Fig S1 and Sytiuk et al. (2021), where the potential confounding effect between species and site has been addressed into details, especially for biochemical traits.

3.3.1. Regional and local environmental conditions across the five sites

Climatic conditions varied along the latitudinal gradient. Whilst mean annual temperature and annual precipitation together increased from SE to FR (Table 3-1), we found that *Sphagnum* field water content was the lowest in PL with 4.1 gH_2O/g DW and the highest in SE with 13.96 gH_2O/g DW ($F_{4,16}$=9.1, P < 0.0001; Table 3-1). In addition to climatic and water content availability variability, both *Sphagnum* and vascular plant relative cover differed among the five sites (*Sphagnum*: $F_{4,16}$=25.9, P < 0.001; vascular plants: $F_{4,16}$=31.8, P < 0.001; Table3-1, Table S1). In the warmest site (FR), moss relative cover was the lowest (~32%), and the vascular plant cover the highest (moss: $F_{1,19}$=5.14, P =0.03, vascular plants: $F_{1,19}$=9.02, P =0.007; Table 3-1). The highest moss cover was observed in EST (~78 %) and FI (~73 %), while vascular plant cover was < 6% (moss: $F_{1,19}$=20, P <0.001, vascular plants: $F_{1,19}$=40.8, P <0.0001; Table 3-1). The PCoA analysis showed somewhat contrasting plant community patterns. Three groups emerged from the first and second axes (Fig. S3): one group composed of FR and SE, another group composed of FI and EST and a last one composed of PL only. These patterns strongly related to shrub and herbaceous covers, which were negatively correlated. While shurb cover was the highest in EST, FI and in a lesser extent PL, herbaceous cover peaked in FR and SE sites (Fig. S3). These patterns further accounted for the nutrient status of the different sites. A clustering analysis (Ward method) on the physicochemical properties of the *Sphagnum* WEOM (DOC, DON, DP, pH and ions, see method and Table S2) revealed the exact same three groups than for vegetation composition: FR-SE, EST-FI and PL (Fig. S3). PL differed from other sites because of higher concentrations of dissolved organic carbon, potassium and chlorine (11.8, 0.74 and 1.35 mg/g DW, respectively; Table S2), while SE-FR differed from PL and EST-FI because of higher pH and dissolved phosphorous concentrations (Table 3-1 and Tables S2).

3.3.2. Characteristic of *Sphagnum* anatomical, morphological and biochemical traits

Sphagnum moss from PL had the highest capitulum diameter, capitulum height and capitulum volume with 1 cm^2, 0.424 cm and 0.337 cm^3 respectively, while the lowest values were observed in EST with 0.524 cm^2, 0.25 cm and 0.006 cm^3, respectively (diameter: $F_{4,16}$=27.8, $P < 0.001$; height: $F_{4,16}$=8.53, $P < 0.01$; volume: $F_{4,16}$=23.15, $P < 0.001$; Fig. 3-2). *Sphagnum* from EST had the highest number of hyaline cells (on average 693.2 mm^{-1}) ($F_{4,16}$=21.53, $P < 0.001$), but the highest water holding capacity was found in FI (Fig. 3-2; $F_{4,16}$=17.61, $P < 0.001$). The width of chlorocystes was the highest in FI with 9.86 μm, while the other species had about two-fold lower width (Fig. 3-2; $F_{4,16}$=26.41, $P < 0.001$).

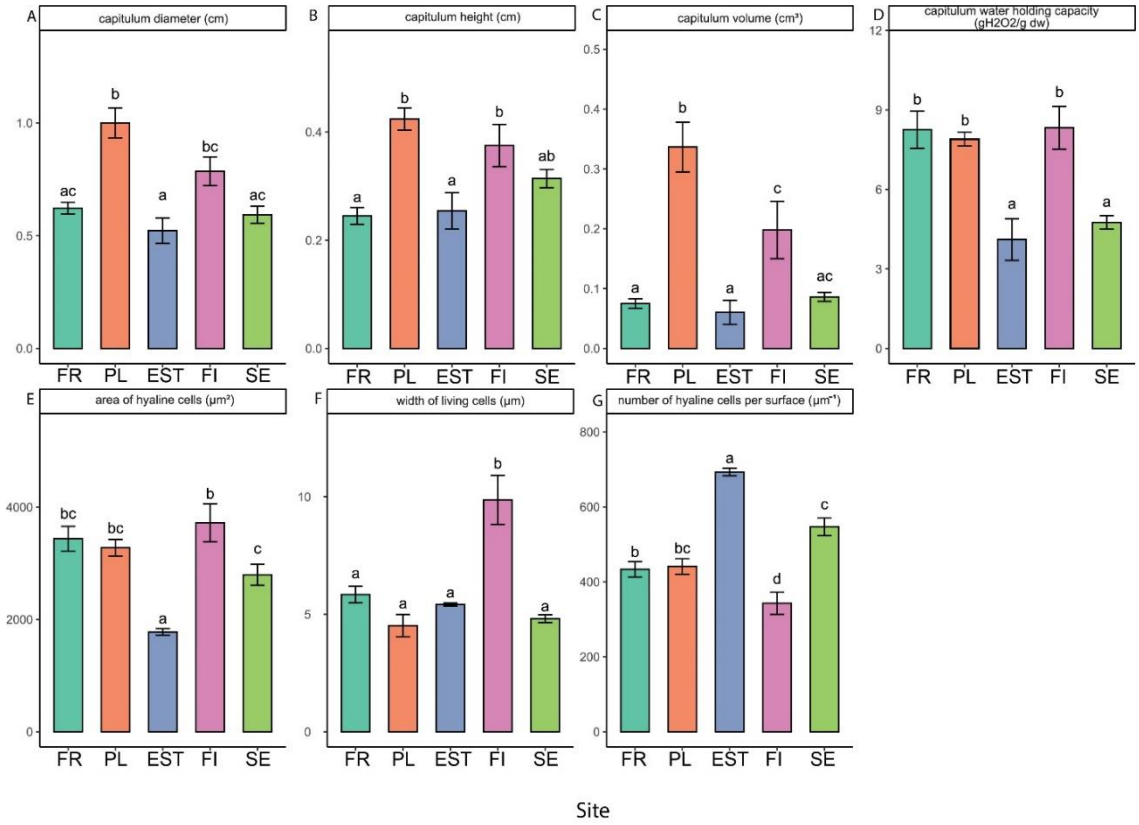


Figure 3-2. Barplot (n=5) of anatomical and morphological traits of dominant *Sphagnum* mosses in five sites. Data represents means and standard errors (SE). Letters indicate significant differences among *Sphagnum* species at P < 0.05 (linear mixed effect models). *Sphagnum* species are indicated by letters FR=France, PL=Poland, EST=Estonia, FI=Finland, SE=Sweden.

For biochemicals, total carbohydrates and proteins concentrations had a maximum concentration in moss from PL (229.08 mg/g DW and 0.17 mg/ml, respectively), and a

minimum in FI (102.07 mg/g and 0.072 mg/ml, respectively; Fig. 3-3; carbohydrates: $F_{4,16}$=18.6, P<0.01 and proteins: $F_{4,16}$=5.33, P=0.0063). Chlorophyll *(a+b)* and carotenoids concentrations followed similar trends with the highest values in PL and the lowest in FI (Fig. 3-3; chl: $F_{4,16}$=3.1, P=0.04; car: $F_{4,16}$=2.9, P=0.052). Water soluble phenolic concentration was the highest in FR (5.61 mg/g DW) and the lowest in FI (0.49 mg/g DW; Fig. 3-4; $F_{4,16}$ = 18.9, P < 0.001). Total phenols peaked in FR, while the lowest concentration was observed in SE (Fig. 3-3; $F_{4,16}$=5.26015, P=0.0067). Total flavonoids also differed among sites (Fig. 3; $F_{4,16}$ = 3.1, P = 0.046), with the lowest values found in *Sphagnum* from SE, PL and EST and the highest in FR. Finally, concentrations of tannins and proline did not reveal any significant variation in their concentrations (Fig. 3-3; P > 0.05).

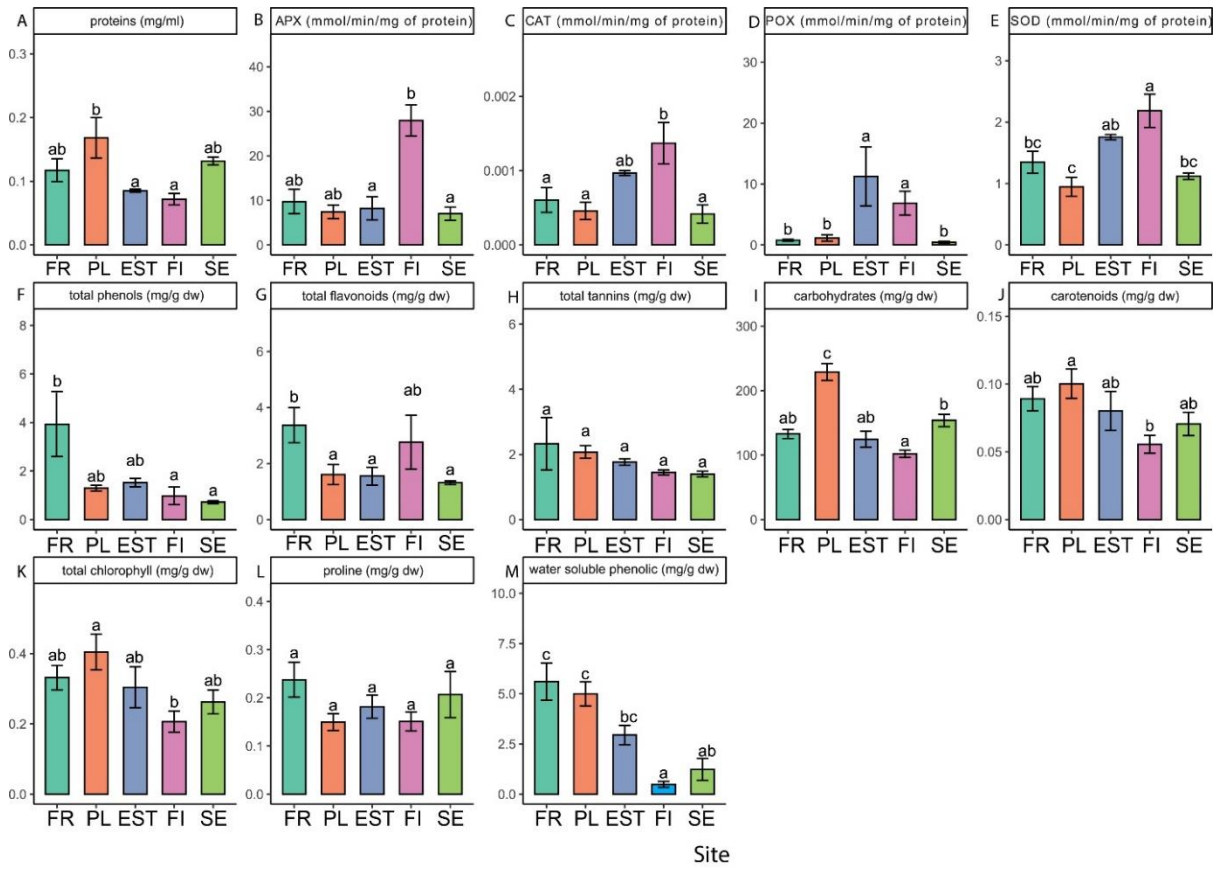


Figure 3- 3. Barplot (n=5) of *Sphagnum* proteins (A), enzymatic activities (B-E), metabolites and pigments (F-M) of dominant *Sphagnum* mosses in five sites. Data represents means and standard errors (SE). Letters indicate significant differences among the sites along a latitudinal gradient at P < 0.05 (linear mixed effect models). *Sphagnum* species are indicated by letters FR=France, PL=Poland, EST=Estonia, FI=Finland, SE=Sweden.

For *Sphagnum* antioxidant enzyme activities, *Sphagnum* from FI showed the highest APX activity with 27.94 mmol min^{-1} mg^{-1}, while mean activity for the four other species was similar and around 12.1 ± 2.37 mmol min^{-1} mg^{-1} (Fig. 3-3; $F_{4,16}$ = 6.9, P = 0.002). CAT and SOD showed similar trends with maximum activities in FI (Fig. 3-3; CAT: $F_{4,16}$ = 5.9, P = 0.0039; SOD: $F_{4,16}$ = 9.52, P < 0.001). The POX activity was the highest in *Sphagnum* from EST with 11.26 mmol min^{-1} mg^{-1}, following by FI with 6.87 mmol min^{-1} mg^{-1}, while almost no activity have been observed in other sites (Fig. 3-3; $F_{4,16}$=14.9, P<0.001).

When all *Sphagnum* traits (*i.e.* the three data sets: (1) metabolites, proteins and pigments (hereafter 'metabolites'), (2) antioxidant enzyme activities, and (3) anatomical and morphological traits) were merged together, the five species formed distinct groups (Fig. 3-4A). However, the separate PCoAs on anatomical and biochemicals parameters showed contrasting patterns (Fig. 3-4B and 3-4C). For *Sphagnum* anatomical and morphological traits, the ordination space showed more or less well separate groups composed of each site/species (Fig. 3-4B), while the PCoA on biochemical parameters showed two distinct groups on the second axis: one with *Sphagnum* from PL and SE and second with FR, EST and FI.

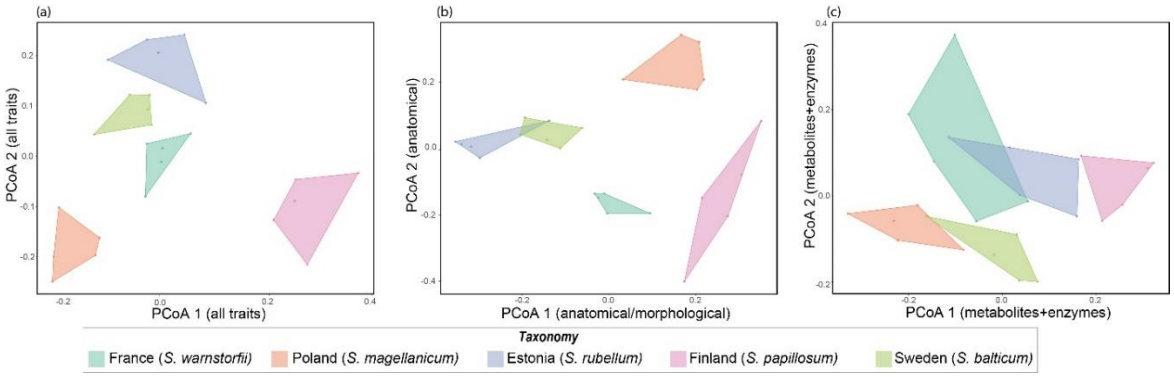


Figure 3- 4. Principle coordinates analysis (PCoA) on the Gower dissimilarity matrix of (A) all *Sphagnum* traits, (B) anatomical and morphological traits, (C) biochemical traits. Groups (hulls) are coloured according to sites spanning from south to north.

3.3.3. Linkages between *Sphagnum* traits, regional and local environmental conditions

Using JSDM approach, we investigated the biochemical features that covary with anatomical and morphological traits across environmental gradients (Fig. 3-5). We found that *Sphagnum*

traits grouped into four distinct clusters of co-occurring metabolites, enzyme activities and anatomical/morphological traits (Fig. 3-5A); each cluster showing shared responses to local and regional environmental conditions (*i.e.*, annual precipitation, the mean temperature of the wettest quarter, nutrient status of the sites and herbaceous plant cover). Cluster 1 was a mix of traits with total tannins, total phenols, POX, water-soluble phenols and proline— some of them being involved in '*Sphagnum* defense'. Cluster 2 was composed of traits involved in antioxidant activities and water-holding capacity (hereafter 'water stress tolerance'): flavonoids, APX, CAT, SOD, capitulum water-holding capacity, area of hyaline cell and the width of cholocyste. Cluster 3 referred to '*Sphagnum* biomass' and was composed of morphological traits only with capitulum diameter, capitulum volume and capitulum height. Cluster 4 referred to '*Sphagnum* growth' with total proteins, total carbohydrates, carotenoids and total chlorophyll. Only the number of hyaline cells did not relate to any of these four main clusters.

Posterior distribution of the trait coefficients (Fig. 3-5B) showed that cluster 1 (defense) and 2 (water stress tolerance) responded negatively to mean temperature of the wettest quarter and herbaceous cover, and positively to annual precipitation. Cluster 2 further responded negatively to WEOM characteristics (the first and second PCA axis Fig. S5). Cluster 1 was mostly positively related to the first PCA axis of WEOM, *i.e.* mostly dissolved C and N, and pH (Fig. S5). Cluster 3 ('capitulum biomass') and 4 ('*Sphagnum* growth') showed somewhat opposite patterns to cluster 1 & 2. They positively correlated with temperature, herbaceous relative cover, and WEOM PC1, but negatively with annual precipitation (Fig. 3-5B). When the effect of local and regional environmental factors on *Sphagnum* traits linkages (residual correlations) was filtered, some co-occurrences among traits remained, the most significant being the one among *Sphagnum* capitulum morphological traits (Fig. 3-5C). Residual correlations among *Sphagnum* traits further showed that non-clustered traits corresponded mostly to traits from cluster 1 & 2.

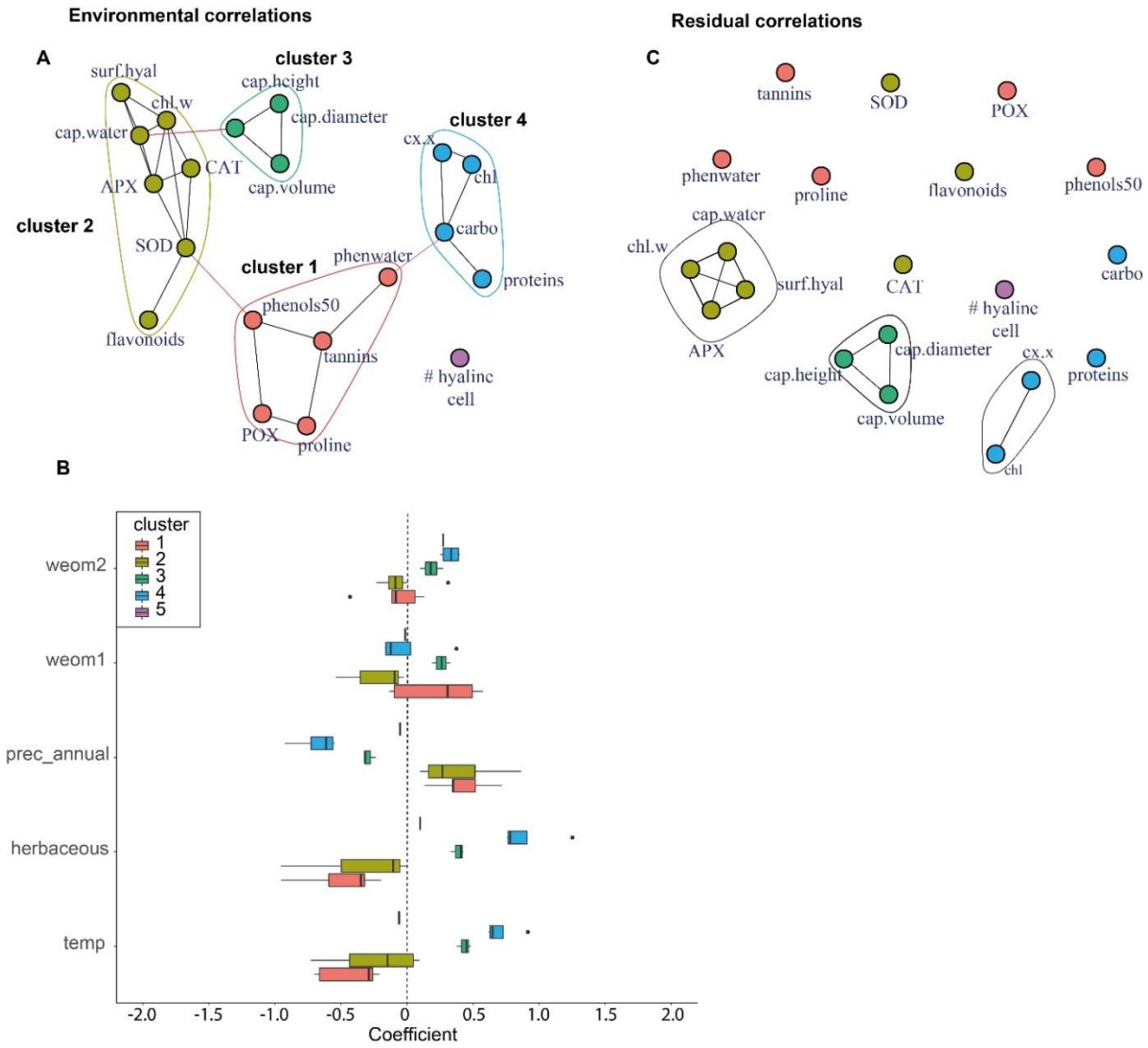


Figure 3-5. Co-response clusters representing species similarity in *Sphagnum* traits-environment relationships: A) shared responses of *Sphagnum* traits to environmental conditions, B) Bayesian coefficient of each trait pooled into their respective clusters to every environmental parameter, C) residual correlations among *Sphagnum* traits. Colors represent four distinct co-response clusters, while non-connected (purple) points represent cluster-unrelated traits. Black lines indicate positive correlations between traits, while red – negative (with $P<0.05$). WEOM is site scores from the two first axes of PCA performed on WEOM physicochemical parameters

3.3.4. *Sphagnum* trait space and contribution of trait-clusters to *Sphagnum* forms and functions

The hypervolume of the *Sphagnum* trait space was four times bigger when biochemical traits were included (trait space = 159.41) than when they were excluded (trait space = 40.34) for every *Sphagnum* species but *Sphagnum papillosum* (FI; Table 3-2). *S. papillosum* showed a

stronger contribution of anatomical and morphological traits to its trait space than other species. Furthermore, we tested which of the different cluster of *Sphagnum* traits (Fig. 3-5A) better define '*Sphagnum* form and function' in the context of environmental variations using a SEM analysis (see method for details on our rationale). Our SEM model revealed that the different clusters of *Sphagnum* traits describe unique aspects of *Sphagnum* form and function (Fig. 3-6). Standardized coefficients from the different clusters to the latent variable '*Sphagnum* form and function' were statistically significant for only cluster 2 ('water stress tolerance', coefficient = 0.50) and cluster 4 ('growth'; coefficient = 0.72; Fig. 3-6). We further found strong relationships between local and regional environmental factors and the latent variable '*Sphagnum* form and function'. More particularly, we found that annual precipitation (coefficient = 0.89, $P < 0.01$), temperature (coefficient = -0.69, $P < 0.01$) and herbaceous cover (coefficient = -0.94, $P < 0.01$) were important determinants of '*Sphagnum* form and function' latent variable, and in a lesser extent nutrient status of the sites (WEOM PC1, coefficient = -0.45, $P = 0.068$).

Table 3- 2. The generalized volume of the hull representing the functional trait space of *Sphagnum* mosses based on three first axes of principal component analysis (PCA) for standardized values of all *Sphagnum* traits (biochemical, anatomical and morphological traits) and only *Sphagnum* traits without biochemical traits.

***Sphagnum* species**	All *Sphagnum* traits	*Sphagnum* traits without biochemical traits
All species together	**159.41**	**40.34**
S. warnstorfii (FR)	2.24	0.11
S. magellanicum (PL)	1.36	0.43
S. rubellum (EST)	0.68	0.29
S. papillosum (FI)	2.56	1.34
S. balticum (SE)	0.23	0.038

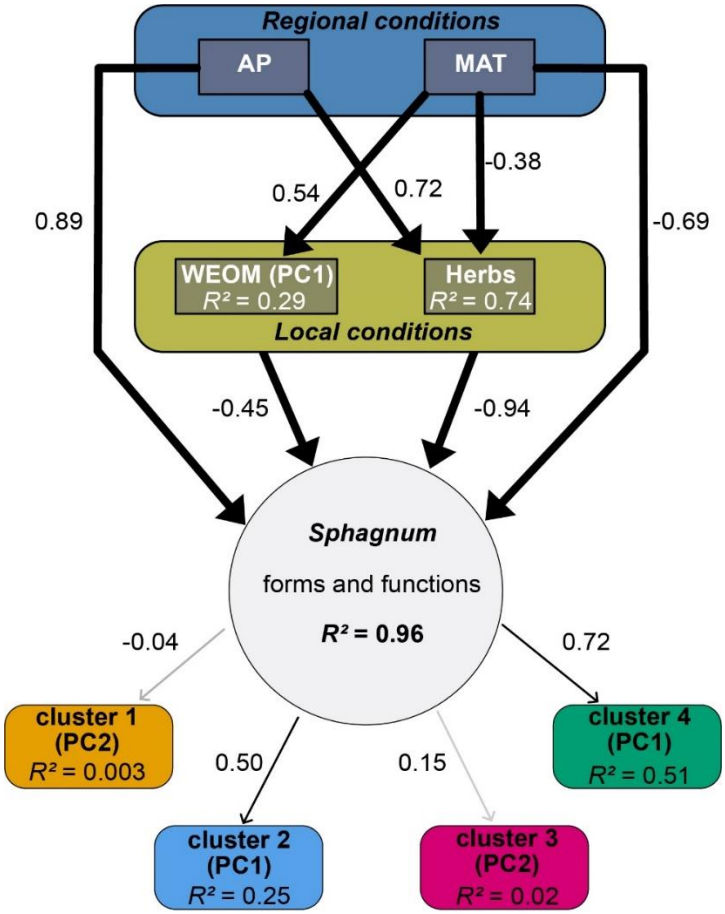


Figure 3-6. Structural equation model (SEM) combining the biochemical and anatomical/morphological traits and environmental factors. SEM showing relationships between global (blue) and local (green) environmental conditions and a hidden, unmeasured variable named "*Sphagnum* form and function", that is a latent variable defined as the product of the four clusters of *Sphagnum* traits identified in Fig. 5A (see method for details). Thin solid arrows show contributions of trait-clusters to the latent variable (latent variable r-squared also displayed), thick solid arrows show effects of local and global parameters on the latent variable and grey arrows illustrate non-significant path coefficients ($P > 0.05$). Numbers indicate the strength and direction of path coefficients. PC1 or PC2 indicate which of the PCA axes has been used in the SEM analysis (see method for details). The global fit of the model was very good: $X2 = 8.95$, $df = 14$, $P = 0.83$; CFI = 1, RMSEA = 0, SRMR = 0.067, AIC = 409.2.

3.4. Discussion

Our results show previously unreported linkages among anatomical, morphological and biochemical traits in *Sphagnum* mosses. We demonstrate that *Sphagnum* traits can be grouped into four clusters which show similar response to local and regional environmental factors. *Sphagnum* traits from the same cluster have very similar responses to environmental factors, while traits from different clusters have the opposite response to those factors. Overall, we found that *Sphagnum* anatomical/morphological and biochemical traits had relatively poor shared responses to environmental conditions. Only *Sphagnum* water holding capacity, chlorocyste width and hyaline cell size were linked with antioxidants like flavonoids and enzyme activities. Our findings also showed that *Sphagnum* biochemicals were regulated by external forces, such as climate, nutrient availability and plant cover, that were not well represented by anatomical and morphological traits. This suggests that these biochemical features (metabolites and enzyme activities) may describe aspects of *Sphagnum* physiology not captured by classical functional traits such as defense and water stress tolerance (*e.g.* antioxidants). Moreover, when local and regional environmental effects were filtered (*i.e.*, residual correlations; Fig. 3-5C), we found that the clusters of traits involving biochemicals (*e.g.* defense and water stress tolerance clusters) were disbanded, whilst the cluster with classical traits (capitulum size related traits) remained. We interpret this result as an evidence that the degree of environmental stability determines the plant performance by regulating the interplay between biochemical (metabolites and enzyme activities) and phenotypical (morphological and anatomical) traits (Falster et al., 2011; Guo et al., 2017; Mazziotta et al., 2018).

The plant metabolome is composed of thousands of biochemicals (or metabolites), which are present in a plant at a given moment, and often referred to as the chemical phenotype of an organism (Fiehn, 2002). Plant metabolites are indeed the ultimate expression agents of genetic changes and the first responders to environmental changes (Handakumbura et al., 2019; Peñuelas and Sardans, 2009). In our study, we found that local and regional environmental factors dispatched traits into four clusters which are involved in *Sphagnum* growth, biomass, defense and water stress tolerance. Our SEM analysis revealed that these different clusters of *Sphagnum* traits describe unique aspects of *Sphagnum* form and function, especially those related to 'water stress tolerance' and 'growth' (Fig. 3-6). Our results further showed that the functional trait space of *Sphagnum* mosses expanded when biochemicals were taken into account. This suggests that *Sphagnum* biochemical traits capture key differences in foliar chemistry and responses to environmental variability which are complementary to the

variation captured by anatomical and morphological traits. We further interpret this result as an evidence that biochemicals offer an effective way to assess variation among *Sphagnum* phenotypes associated to environmental tolerance (Bakhtiari et al., 2020; Callis-Duehl et al., 2017; Chiapusio et al., 2018; Defossez et al., 2021).

We highlighted the importance of vascular plant functional types in driving *Sphagnum* biochemical traits, as showed by the response of traits involved in defense (*i.e.* total tannins, total phenols, water soluble phenols) and growth (*i.e.* carbohydrates, pigments and proteins) along with herbaceous cover. This suggests that *Sphagnum* mosses modulate their whole biochemical machinery in response to increasing vascular plant cover, agreeing with previous findings on phenolic metabolism (Chiapusio et al., 2018). Indeed, *Sphagnum* mosses can compete with vascular plants through the release of specialized metabolites that inhibit vascular plant germination and radicle growth (Chiapusio et al., 2013). In parallel, the increase in carbohydrates, proteins and photosynthetic pigments suggest that *Sphagnum* produce structural and non-structural compounds to maintain its growth and enhance its stress tolerance to cope with vascular plant competition (Liu et al., 2019). In short, we suggest that vascular plant encroachment over *Sphagnum* causes alterations to the moss metabolites production that directly impact its physiology. Our results further revealed higher phenols and tannins concentrations in *Sphagnum* tissues along with increasing precipitation and nutrients (Fig. 3-5B). Such increases could reflect a lesser nutrient limitation on *Sphagnum* growth in warmer and wetter sites (Bragazza and Freeman, 2007; Dorrepaal et al., 2005). This further suggests that *Sphagnum* traits evolved to have specific physiological and defense functions in the adaptation of *Sphagnum* mosses to their growth environment, as showed for vascular plants (Yan et al., 2013). Thus, we could assume that environmental filtering drives not only the taxonomic composition of *Sphagnum* mosses in peatlands (Bjorn J M Robroek et al., 2017), but also selects (or counter selects) on their traits.

Our results showed that *Sphagnum* with high water holding capacity exhibited the highest antioxidant capacity, as evidenced by the high enzymatic activities and flavonoid content in their cells (Nakabayashi et al., 2014). The ability of *Sphagnum* to transport water to the capitula and retain cytoplasmic water is a key for its physiological activity such as photosynthesis (Bengtsson et al., 2020a; Gong et al., 2020a; Hájek, 2020; Jassey and Signarbieux, 2019; Robroek et al., 2009). As *Sphagnum* mosses lack stomata and water-conducting tissues, the ability to maintain moist in their active apical parts (capitula) rely on the water transporting efficiency from water table to the capitula and the desiccation avoidance strategy (Clymo and Hayward, 1982). The desiccation avoidance strategy of

Sphagnum mosses, is mediated by large, dead and empty hyaline cells, which requires strong cell walls to avert the collapse of large capillarity spaces (Hájek and Vicherová, 2014). Bordering chlorocystes (living photosynthetic cells) contain chloroplasts that participate in photosynthesis and thus support *Sphagnum* performance and functioning. We found a positive correlation between the width of chlorocystes and antioxidant enzyme activities (Fig. 3-5A), suggesting that larger photosynthetic cell requires more efficient activities of antioxidant enzymes. The production of antioxidant enzymes, as protection of cell components from oxidative cell damages, is an important feature of desiccation tolerance in plants, and particularly in drought-hardening (Cruz De Carvalho et al., 2012; Minibayeva and Beckett, 2001; Proctor, 1990). Photosynthetic cells are under constant oxidative stress resulting from the accumulation of reactive oxygen species (ROS) during various metabolic processes (Elstner, 1982). To fight against oxidative damages, cells have efficient antioxidative systems (*e.g.* activation of certain enzymes) (Elstner, 1982). Synchronized action of major antioxidant enzymes (APX, CAT, SOD, GR) and specialized metabolites such as flavonoids outcome in detoxification of ROS and limit oxidative stress in plants (Choudhury et al., 2013; Das and Roychoudhury, 2014; Noctor et al., 2018). Our findings demonstrate that the degree of desiccation tolerance of *Sphagnum* mosses is not only limited to its morphological traits (Bengtsson et al., 2020a), but also rely on specific biochemical traits to avoid cell-damages.

To sum up, our findings show that *Sphagnum* growing in different local environmental (vegetation composition, nutrients content) and regional (temperature, precipitation) conditions possess a suite of diverse biochemical traits that supports *Sphagnum* form and function as well as its resistance to environmental changes. Besides, anatomical and morphological traits (*i.e.* width of chlorocyste), in addition to local and regional environmental conditions, could explain some aspects of biochemical traits distribution, and thus potentially revealed unreported linkages among different traits. Shifts in *Sphagnum* metabolites, pigments, proteins and antioxidant enzyme activities indicate that *Sphagnum* biochemical traits underpin *Sphagnum* niche differentiation through their role in specialization towards biotic stressors (*e.g.* plant competitors) and abiotic stressors (*e.g.* temperature and water availability), which both are important factors governing *Sphagnum* growth (D. J. Weston et al., 2015). We suggest that these relationships represent previously unreported trade-offs of resource allocation by mosses, whereby *Sphagnum* mosses devote resources to maintain their growth to cope with environmental changes or resist to increasing competition. Even though our study reports new linkages among anatomical, morphological and biochemical traits, which can be important for further studies on peatland functioning,

some limitations have to be acknowledged and considered for further experiments. The confounding effect between dominant *Sphagnum* species and climate (sampled single per site) and our observations were undertaken at a single date, did not allow us to compare the variation of the responses of *Sphagnum* traits for each species when transferred to different condition (*e.g.* a laditudinal gradient, seasonal variability). However, it didn't prevent us to assess traits interactions with local and regional environmental conditions, as well as linkages among *Sphagnum* traits. Further studies are needed to test the generality of the trade-offs detected here and their importance for peatland carbon cycling. Nevertheless, this study provided evidence that measurements of the metabolites and antioxidant enzyme activities, once properly incorporated with classical morphological and anatomical traits expand our understanding of the coupling between physiology and fitness in *Sphagnum* trait-based studies.

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 thank the Plateforme Analyses Physico-Chimiques from the Laboratoire Ecologie Fonctionnelle et Environnement (Toulouse) for their analyses (water extractable organic matter). ML was supported by the National Science Foundation, Poland under grant no. UMO-2017/27/B/ST10/02228, within the framework of the project 'Carbon dioxide uptake potential of *Sphagnum* peatlands in the context of atmospheric optical parameters and climate changes' (KUSCO2). BJMR was supported by the British Ecological Society research grant (SR17\1427). 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. We also thank the Swedish Polar Research Secretariat and SITES for the support of the work done at the Abisko Scientific Research Station. The authors are grateful to Owen Petchey for his idea on convex hull size calculation.

Author contributions

Anna Sytiuk: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Methodology (lead); Writing– original draft (lead). **Regis Céréghino**: Funding acquisition (supporting); Conceptualization (equal); Formal analysis (supporting); Methodology (supporting); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Samuel Hamard**: Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (equal), Data curation (equal). **Frédéric Delarue**: Funding acquisition (supporting); Formal analysis (supporting); Methodology (supporting);

Writing – original draft (equal); Writing – review and editing (equal). **Ellen Dorrepaal**: Funding acquisition (supporting); Conceptualization (equal); Formal analysis (equal); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Martin Küttim**: Conceptualization (equal); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Mariusz Lamentowicz**: Funding acquisition (supporting); Conceptualization (equal); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Bertrand Pourrut**: Methodology (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Bjorn J. M. Robroek**: Conceptualization (equal); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Eeva-Stiina Tuittila**: Conceptualization (equal); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Vincent E J. Jassey**: Conceptualization (supporting); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Methodology (equal); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting), Project administration (lead).

Data availability statement

Data are available from the Figshare Digital Repository: <https://doi.org/10.6084/m9.figshare.19103279> (Sytiuk et al. 2022).

Supplementary materials

Supplementary method

Sphagnum biochemical traits: pigments and metabolites

Pigments. Chlorophyll a, b and total carotenoids extractions were carried out in subdued light conditions. Twenty mg of lyophilized moss together with 1 mL of 99.9 % cold methanol (held at 4 °C) and 2 glass beads were placed into 2 mL tubes and then ground with high-speed benchtop homogenizer (FastPrep-24™, MP Biomedicals, China) at 4.5 m/s. A small spatula (approximately 0.5 g) of $MgCO_3$ was added to methanol in order to avoid acidification and the associated degradation of chlorophyll (Ritchie, 2006) and then solution was filtered *via* filtration paper to remove suspended particles . Then, the tubes were centrifuged for 2 min at 8000 rpm at 4 °C. The procedure of grinding and centrifugation was repeated two times in total. After that, the supernatant was transferred into 96-wells transparent microplate and the absorbance was measured with a spectrophotometer at 480, 652, and 665 nm. Concentrations of chlorophyll a, chlorophyll b and total carotenoids were calculated according to the extinction coefficients and equations reported by Porra *et al.* (1989). Finally, pigments concentration was expressed as milligram of pigments per g dry weight (mg g^{-1} DW).

Methanol extraction of Sphagnum metabolites. We followed Klavina (2018) (with some modifications) to extract *Sphagnum* metabolites, including total polyphenols, flavonoids, tannins and carbohydrates (Fig. 1). Briefly, we ground moss samples in a high-speed benchtop homogenizer at 4.5 m/s, and then added 40 mg of freeze-dried moss in a brown glass bottle with 4 mL of cold 50 % aqueous methanol solution (held at 4°C). After that, samples were exposed to an ultrasound bath for 40 min and bottles were shaken in an orbital shaker for 18 hours at 150 rpm, followed by another 40 min of ultrasound. Finally, moss extracts were replaced into 2 mL Eppendorf and centrifuged at 4500 rpm for 5 min at 4 °C. Collected supernatants were then used for further analyses.

Total carbohydrates. Total carbohydrates quantification followed Klavina *et al.* (2018) with slight modifications. Moss methanolic extract (20 µL) was diluted with 200 µL of distilled water in 2 mL Eppendorf tube. Then 200 µL of 5 % phenol solution and rapidly 1 mL of 98 % H_2SO_4 were added. After 10 min of incubation at room temperature, test tubes were carefully shaken and then left for 20 min more. Absorbance was read on the spectrophotometer at 490 nm. A standard curve was prepared with glucose and values were expressed in mg equivalent glucose per gram of dry moss (mg g^{-1} DW).

Total polyphenols. The Folin-Ciocalteu method (Ainsworth and Gillespie, 2007) was used to determine total polyphenol content in *Sphagnum* tissues. *Sphagnum* methanolic extract was transferred into 96-wells transparent microplate with 40 µL of 10 % Folin-Ciocalteu reagent. Then the microplate was covered with aluminium foil and shaken for 2 min using vortex, 140 µL of 700 mM $NaHCO_3$ was added in each well, and the microplate was covered and incubated at 45 °C for 20 min. Finally, the absorption of each well was measured using a spectrophotometer (Biotek Synergy MX) at 760 nm wavelength. Gallic acid was used as standard and total polyphenolic content was expressed in mg equivalent Gallic acid per gram of dry moss (mg g^{-1} DW).

Total flavonoids. We used trichloroaluminum assay to assess the concentration of total flavonoids in *Sphagnum* tissues (Settharaksa et al., 2014). Twenty-five µL of moss methanolic extract was placed into 96-well microplate with 10 µL of 5 % $NaNO_2$. Then, the plate was covered with aluminium foil and incubated for 6 min at 20 °C. Following incubation, 15 µL of 10 % $AlCl_3$ and 200 µL of 1M NaOH were added in each well, the plate was covered and shaken (vortex) for 1 min. The absorption was measured on the spectrophotometer at 595 nm wavelength. Catechin was used as standard and thus values expressed in mg equivalent catechin per gram of dry moss (mg g^{-1} DW).

Total tannins. We used acid vanillin assay to quantify total tannins concentrations in *Sphagnum* tissues (Bekir et al., 2013). Into a 96-well microplate we put 50 µL of moss methanolic extract and then 100 µL of freshly prepared 1% solution of vanillin in 7M H_2SO_4 was added. After 15 min of incubation in the dark at room temperature, the absorbance at 500 nm was measured. Catechin was used a standard and the results were expressed in mg equivalent catechin per gram of dray moss DW (mg g^{-1} DW).

Total water-extractable polyphenolic compounds. The quantification of total water-extractable polyphenols followed Jassey *et al.* (2011*a*) with some modifications. Twenty mg of lyophilized moss together with 5 mL of distilled water were placed into brown glass bottles and exposed to ultrasound in an ultrasound bath for 40 min. After that, test bottles were placed in a shaker for 3 hours at 150 rpm. Once shaking finished, tubes were centrifuged at 4500 rpm for 5 min at 4 °C. Then, 1.75 mL of collected supernatant was transferred in brown glass bottle and 0.25 mL of Folin & Ciocalteu's reagent was added. Test bottles were vigorously mixed with vortex and then 0.5 ml of 20 % Na_2CO_3 was added and the vortex was repeated. Finally, we put samples in bain-marie at 40 °C. After 20 min of incubation the absorbance on the spectrophotometer at 760 nm was measured. Gallic acid was used a standard, so total

polyphenolic contents were expressed in mg equivalent gallic acid per gram of dry moss (mg g^{-1} DW).

Proline analysis. We used acid ninhydrin assay to determine total proline (Lee et al., 2018). Briefly, 25 mg of lyophilized moss was ground with high-speed benchtop homogenizer (4.5 m/s) with 1 mL of 3 % (w/v) sulfosalicylic acid and centrifuged at 4500 rpm for 5 min at 4 °C. Then, 1 mL of collected supernatant was mixed with 2 mL of acid ninhydrin reagent (1.25 g of ninhydrin and 100 mL of acetic acid glacial) and glass tubes were boiled at 100 °C. After an hour of boiling, the reaction was stopped by placing tubes on ice. Absorbance was read at 510 nm. A standard curve was prepared with L-proline and proline concentration was expressed as mg of proline per g dry weight (mg g^{-1} DW).

Sphagnum biochemical traits: total proteins and antioxidant enzyme activities

We quantified the activity of four antioxidant enzymes involved in the oxygen-scavenging system: ascorbate peroxidases (APX), catalases (CAT), total peroxidases (POX) and superoxide dismutases (SOD). To evaluate enzyme activities, 50 mg of ground lyophilized moss was shaken with high-speed benchtop homogenizer at 4.5 m/s with 1 mL of extraction buffer containing 100 mM Tris buffer pH 7.0, 0.5M EDTA, PVP 6 g/L, 0.5M ascorbate, β-Mercaptoethanol, industrial protease inhibitor cocktail (Sigma). Then the moss extract was centrifuged at 4500 rpm for 5 min at 4 °C (Pourrut, 2008). Finally, the supernatant (hereafter 'enzyme extract') was collected and stored at -80 °C for APX, CAT, POX, SOD enzyme activities measurements. The activity of a specific enzyme was assessed by the rate of reduction (APX, CAT and SOD) or increase (POX) in absorbance in an aliquot tailored by the addition of reagents specific to that enzyme.

Dosage of total proteins was further determined according to Bradford (1976), using bovine serum albumin (BSA) as a standard. Briefly, 10 µL of enzymatic extract and 190 µL of Bradford reagent were added to 96 wells microplate. Then microplate covered with aluminium foil was shaken in a shaker for 10 min at 150 rpm and finally, the absorbance was read at 595 nm. APX, CAT, POX and SOD were expressed as µmol per min per mg of proteins (µmol min^{-1} mg of proteins).

APX activity was determined by adding 10 µL of enzyme extract to 230 µL of a reaction medium consisting of 0.5 M potassium phosphate buffer (Na_2HPO_4 + KH_2PO_4), pH 7, in a 96-wells UV-microplate. Then 15 µL of 10 mM ascorbate was added and microplates were covered with aluminium foil. At the last moment, 10 µL of 100 mM H_2O_2 was added, and the decrease of absorbance due to ascorbate oxidation was quickly measured during the first 5

minutes of reaction at 25 °C. Enzyme activity was estimated using the molar extinction coefficients 290 nm, ε = 2.6 mM^{-1} cm^{-1} (Nakano and Asada, 1981).

POX activity was measured by mixing 40 µL of enzyme extract and 180 µL of a reaction medium containing 31.25 mM potassium phosphate buffer, pH 6.8, and 10 µL of 250 mM pyrogallol in 96-wells microplate. At the last moment, 10 µL of 500 mM H_2O_2 was added, and the formation of purpurogallin was followed at 420 nm during the first 5 minutes of reaction at 25 °C. Enzyme activity was estimated using the molar extinction coefficients of purpurogallin at 420 nm, ε = 2.47 mM^{-1} cm^{-1} (Maehly and Chance, 1954).

CAT activity was determined by adding 10 µL of enzyme extract to 200 µL of a reaction medium consisting of 10 mM phosphate buffer, pH 7.8, in 96-wells UV-microplate. At the last moment, 10 µL of 100 mM H_2O_2 was added and the consumption of H_2O_2 was measured at 240 nm during the first 5 minutes of reaction at 25 °C. Enzyme activity was estimated using the molar extinction coefficients 240 nm, ε = 39 M^{-1} cm^{-1} (Aebi, 1984).

SOD activity was measured in shadowed conditions by adding 20 µL of enzyme extract to 190 µL of a reaction medium containing 50 mM potassium phosphate buffer, pH 7.8, 20 µL of 250 mM methionine, 1.22 mM nitrobluetetrazolium (NBT), and 10 µL of 50 µM of riboflavin in 96-wells microplate covered with aluminium foil. A first lecture of absorbance was performed on the spectrophotometer at 560 nm and then microplate was exposed to light at 15-W fluorescent lamp at 20 °C in order to launch the reaction of blue formazan formation (Pourrut, 2008). After 10 min of incubation the microplate was covered with aluminium foil to stop the reaction, and a second lecture of absorbance was performed at 560 nm. One unit of SOD activity was defined as the amount of enzyme required to result in a 50% inhibition of the rate of NBT reduction, and thus SOD activity is expressed as unit per mg of protein.

Supplementary figures

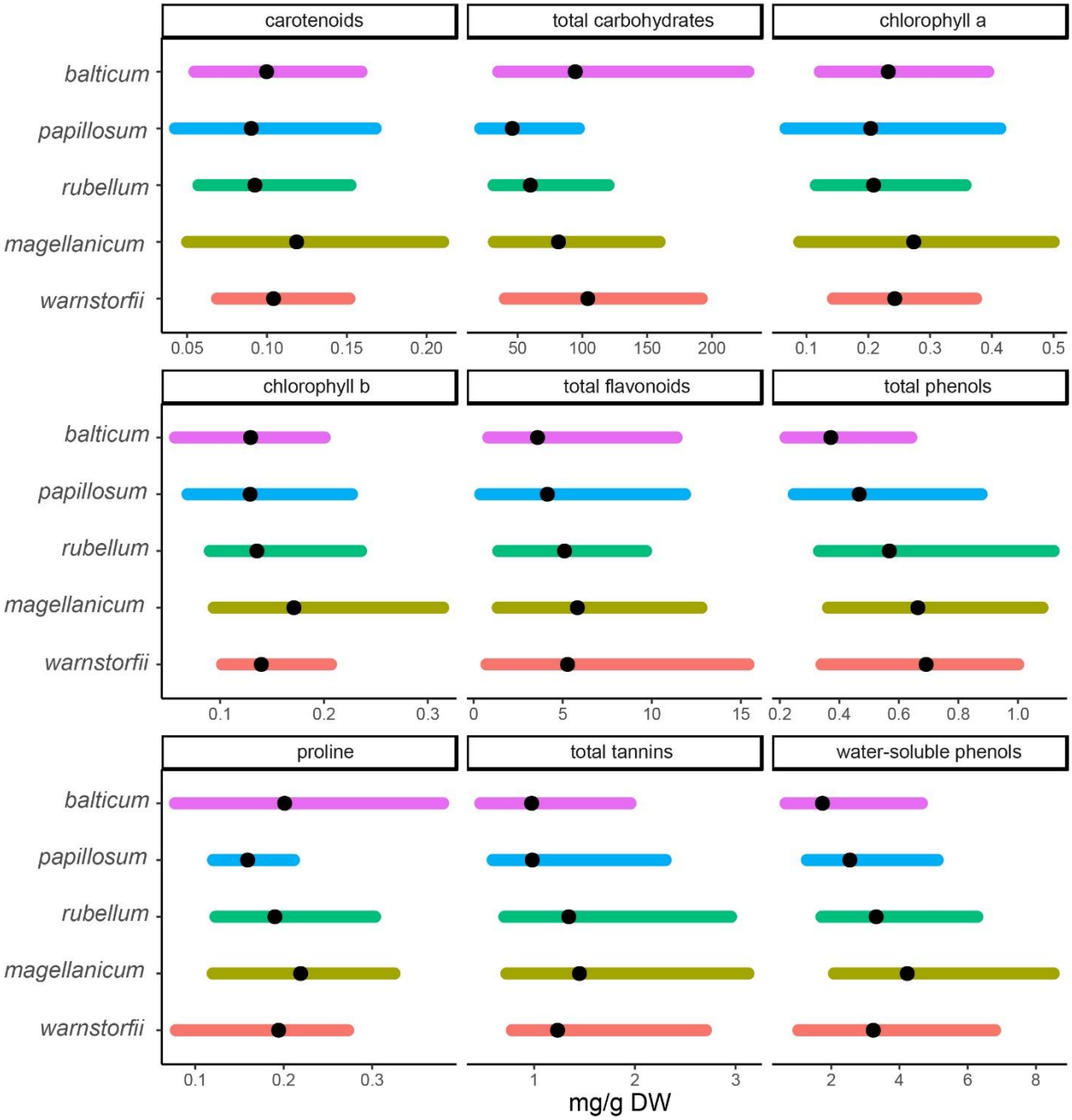


Figure S1. The ranges of variations of the different biochemical traits analysed in the five *Sphagnum* species based on our unpublished data on a reciprocal transplant experiment on the same *Sphagnum* species dispatched along our latitudinal gradient (mean±SE; n=25 per species). The samples were collected in July 2019 (one year after the installation of the experiment).

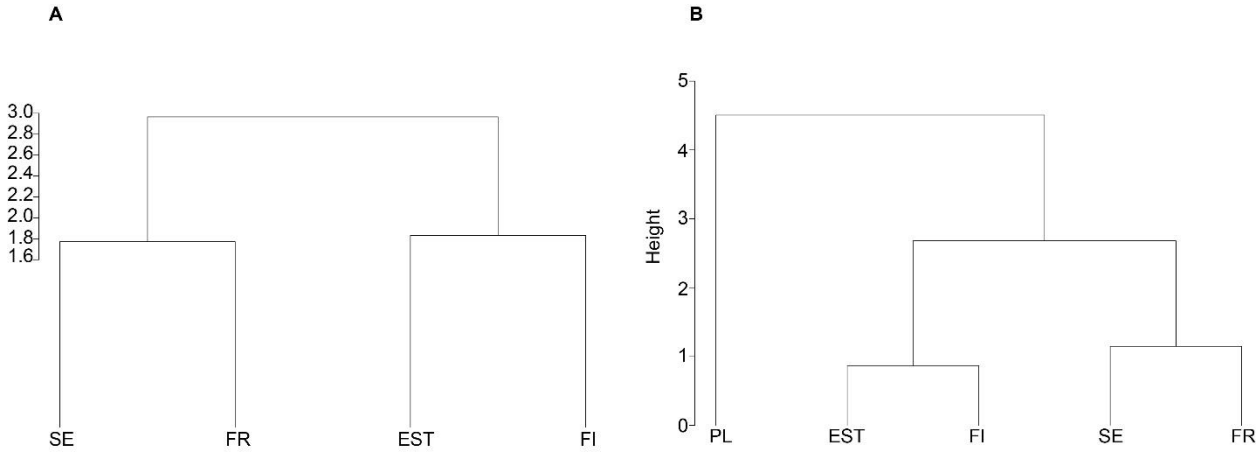


Figure S2. Cluster analysis on pore water (A) and WEOM (B) chemistry. Abbreviations: FR=France, PL=Poland, EST=Estonia, FI=Finland, SE=Sweden.

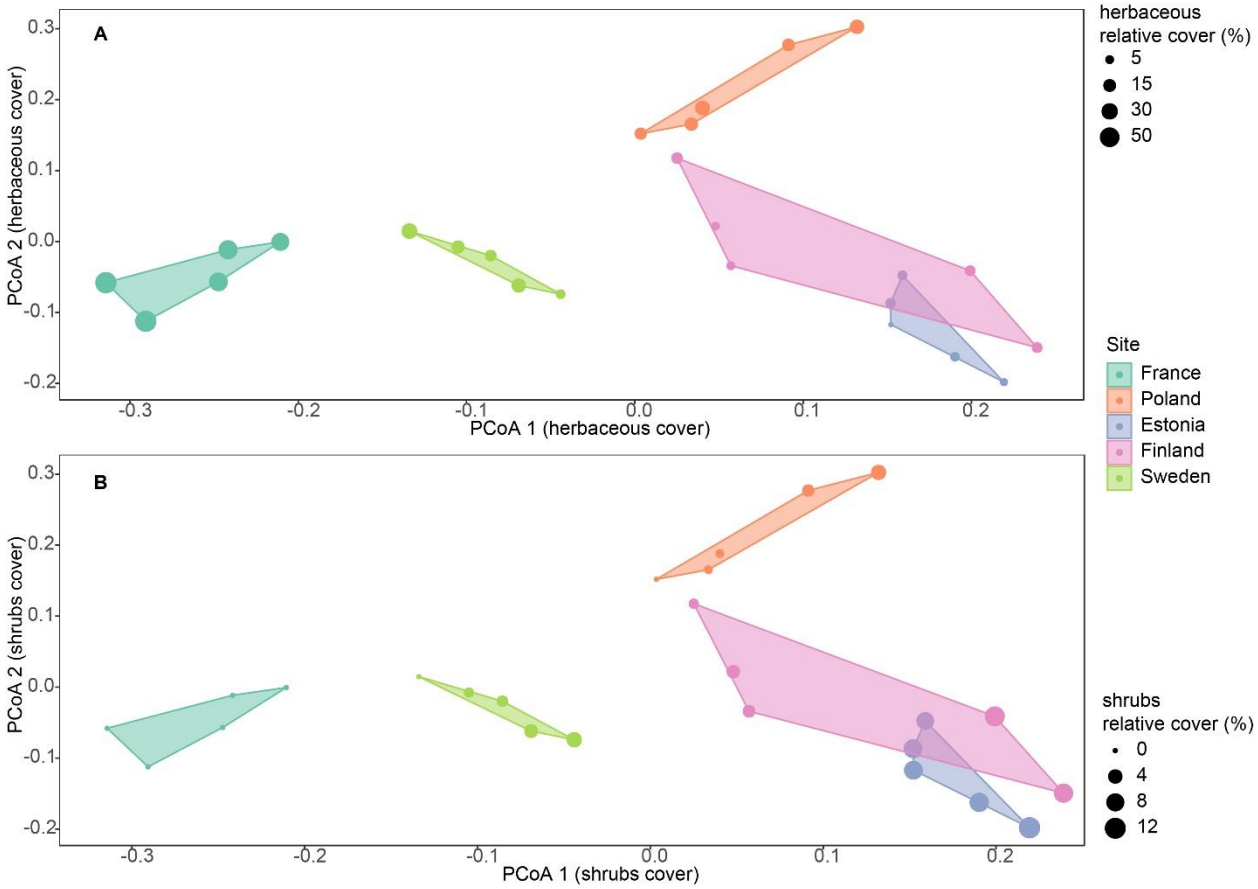


Figure S3. Principal component analysis (PCoA) on vascular plant relative cover in five study sites. The size of dots corresponds to herbaceous (A) and shrubs (B) relative cover and expressed as % of plant group per plot (50 x 30 cm). Sites ordered along the south-north latitudinal gradient.

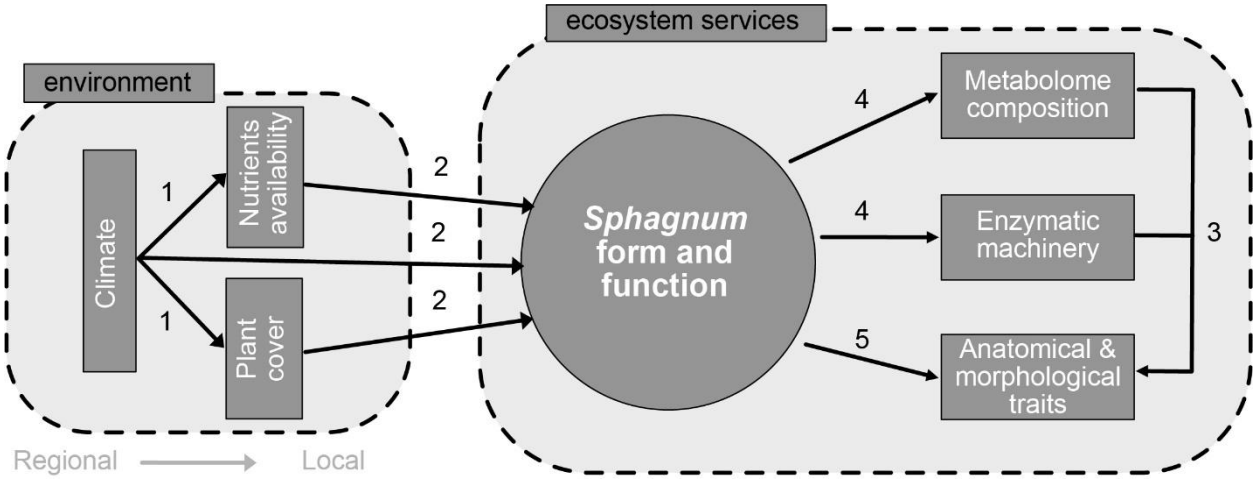


Figure S4. SEM a priori model. Hypotheses behind the different paths are given in Table S3.

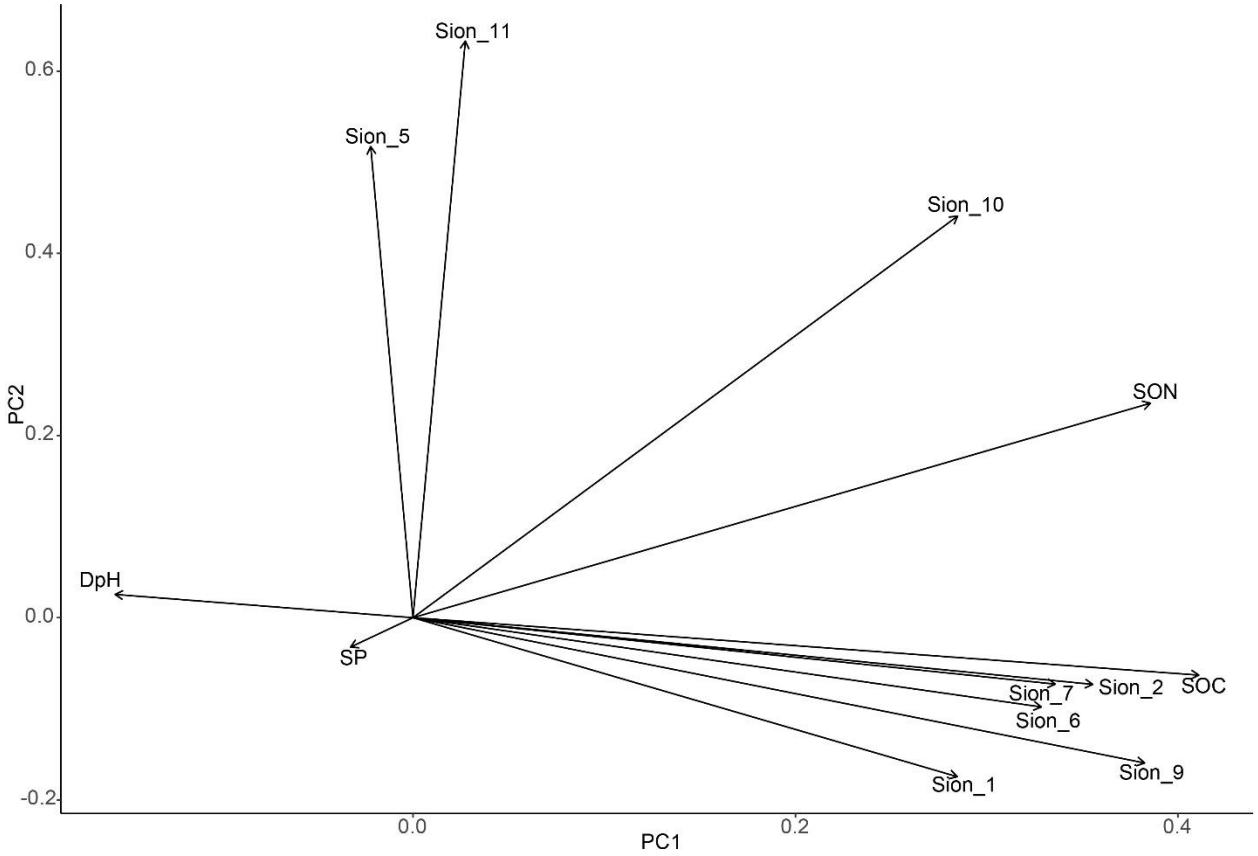


Figure S5. Biplot of principal components analysis for WEOM nutrients concentrations and pore water pH in five sites. First two axes cumulatively represent 62.8 % of the total variance. Loadings upon each axis are indicated by arrows and lines—PC1 (45.8 % of total variance) is a "nutrients concentration," whereas PC2 (17% of total variance) is predominantly a "pH". Abbreviations: DpH=pore water pH, SOC=dissolved organic carbon, SON= dissolved organic nitrogen, SP= dissolved organic phosphorus, Sion_1=Fluorine, Sion_2=Chlorine, Sion_5=Nitrate, Sion_6=Sulphate, Sion_7=Sodium, Sion_9=Potassium, Sion_10=Magnesium, Sion_11=Calcium.

Supplementary tables

Supplementary table S1. Vegetation composition of the five study. Species relative abundance expressed as mean % of plant cover per plot (50 x 30 cm) ± SE (n=5). Sites ordered along the south-north latitudinal gradient.

		France	Poland	Estonia	Finland	Sweden
Mosses	*Polytrichum strictum*	0.36±0.24	0	0	0	0
	Sphagnum balticum	0	0	0	0	61.96±3.21
	Sphagnum rubellum	0	0	34.76±10.19	0	0
	Sphagnum magellanicum	0	37.6±14.2	22.26±4.88	0	0
	Sphagnum fallax	0	25.65±15.82	0	0	0
	Sphagnum fuscum	0	0	20.71±8.71	0	0
	Sphagnum palustre	2.14±1.26	0	0	0	0
	Sphagnum papillosum	0	0	0	73.15±3.15	0
	Sphagnum warnstorfii/Sphagnum capillifolium	30±4.68	0	0	0	0
Vascular plants	*Andromeda polifolia*	0	0.12±0.07	5.65±1.16	3.27±1.05	1.85±0.61
	Empetrum nigrum	0	0	0	0.3±0.13	0.42±0.42
	Vaccinium oxycoccos	0	1.55±0.88	3.81±1.19	1.85±0.8	0
	Carex sp.	0	0	0	0	6.37±2.02
	Carex rostrata	15.89±3.570	0	0	0	0
	Drosera rotundifolia	0.3±0.19	0.12±0.07	1.79±0.46	0.71±0.45	0
	Eriophorum vaginatum	0	17.56±1.77	3.57±1.19	6.96±1.29	0
	Molinia caerulea	24.17±5.19	0	0	0	0
	Oxycoccus palustris	0	0.12±0.07	0	0	0
	Potentilla anglica	3.51±1.22	0	0	0	0
	Rubus chamaemorus	0	0	0	0	0.18±0.19
	Ranunculus polyanthemoides.	15.83±8.46	0	0	0	0
	Litter	15.3±3.14	15.54±7	5±0.96	12.92±1.13	19.11±1.43

Supplementary table S2. Location and climatic data for the five study sites averaged over the period 1960-2018 (WorldClim v2) and water-extractable organic matter (WEOM) chemistry (mean±SE, n=5). Sites ordered along the south-north latitudinal gradient.

		France	**Poland**	**Estonia**	**Finland**	**Sweden**	
Site		FR	PL	EST	FI	SE	
Coordinates		42°41'19.7"N 2°14'02.4"E	53°48'47.9"N 16°35'12.1"E	58°52'26.4"N 26°15'03.6"E	61°50'41.6"N 24°17'17.5"E	68°20'43.1"N 19°03'58.7"E	
Climate data							
Mean Temperature of the wettest quarter (BIO8)[1]	(°C)	9.2	16.9	14.4	12.6	8.9	
WEOM chemistry*							χ^2 (*P-value*)
dissolved organic carbon (DOC)	(mgC/L)	3.43±0.43	11.76±1.74	5.44±1	1.48±0.23	4.04±0.49	16.64(0.00227)
dissolved organic nitrogen (DON)	(mgN/L)	0.09±0.008	0.16±0.02	0.07±0.01	0.03±0.004	0.09±0.02	15.52(0.0037)
dissolved phosphorous (DP)	(mgP/L)	0.024±0.002	0.007±0.0008	0.006±0.001	0.005±0.0005	0.02±0.009	15.84(0.0032)
F^-	(mg/L)	0.052±0.01	0.122±0.04	0.03±0.007	0.021±0.003	0.088±0.05	15.52(0.0037)
Cl^-	(mg/L)	0.368±0.07	1.351±0.12	0.27±0.04	0.097±0.03	0.13±0.04	15.84(0.0032)
NO_3^-	(mg/L)	0.0093±0.009	0.0008±0.0003	0.00028±0.0002	0.00019±0.0001	0.0039±0.003	10.24(0.037)
SO_4^{2-}	(mg/L)	0.0061±0.0006	0.0176±0.01	0.004±0.0009	0.0018±0.0004	0.0024±0.0005	15.68(0.0035)
Na^+	(mg/L)	0.27±0.02	0.497±0.06	0.31±0.05	0.22±0.03	0.32±0.06	8.32(0.08)
K^+	(mg/L)	0.23±0.08	0.74±0.22	0.11±0.02	0.03±0.01	0.1±0.07	13.28(0.0099)
Mg^{2+}	(mg/L)	0.045±0.007	0.086±0.02	0.0078±0.002	0.0007±0.0004	0.041±0.03	13.76(0.008)
Ca^{2+}	(mg/L)	0.16±0.04	0.079±0.015	0.031±0.01	0±0	0.41±0.3	16.16(0.003)

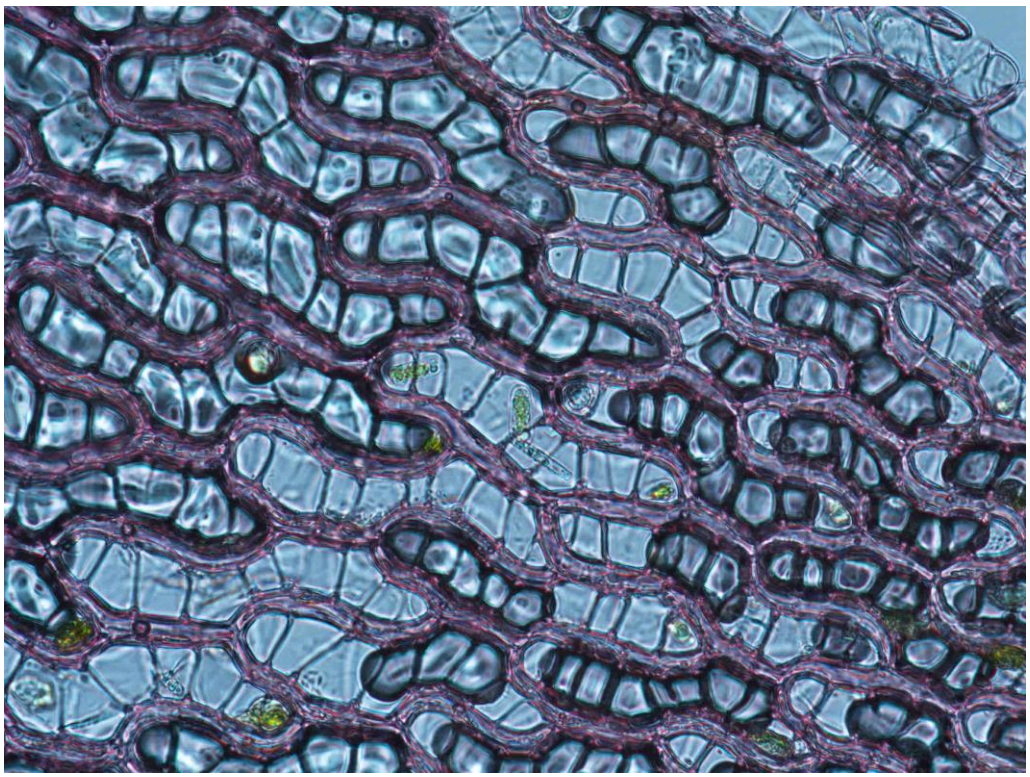
*Measured in early July 2018.

[1]The maximum monthly temperature occurrence over a given year (time-series) or averaged span of years (normal).
(from O'Donnell, M.S., Ignizio, D.A., 2012. Bioclimatic Predictors for Supporting Ecological Applications in the Conterminous United States. U.S Geol. Surv. Data Ser. 691 10.)

Supplementary table S3. Components of hypotheses represented by the *a priori* structural equation model

Path	**Causal hypothesis**	**References**
1	Climatic variation leads to changes in local conditions (*e.g.* nutrients and plant community composition)	(Fort, 2015; Gajewski, 2015; Meng et al., 2011; Ordoñez et al., 2009; Rishmawi et al., 2016)
2	Regional and local environmental variations select for certain morphological traits, metabolites and enzymatic pathways involved in defense, water stress tolerance, temperature, light and oxidative stress tolerances.	(Bjorkman et al., 2018; Defossez et al., 2021; Díaz et al., 2016; Sardans et al., 2020; Walker et al., 2019; Weston et al., 2015)
3	*Sphagnum* metabolites and enzymes are the foundation of *Sphagnum* physiology and so affects morphological and anatomical traits	(Schuman et al., 2016; Wanget al., 2019; Weckwerth, 2011; Weng et al., 2021)
4	*Sphagnum* biochemicals dictates *Sphagnum* form and function independently of anatomical/morphological traits	(Gargallo-Garriga et al., 2020; Sedio, 2017; Yan et al., 2021)
5	Anatomical/morphological traits are key descriptors of *Sphagnum* form and function	(Adler et al., 2014; Kelly et al., 2021)

Chapter 4. Predicting the structure and functions of peatland microbial communities from *Sphagnum* phylogeny, anatomical and morphological traits and metabolites



In this chapter, I explored how and to what extent *Sphagnum* phylogeny, anatomical and morphological traits and metabolites drive the spatial variability of microbial community composition and functions. More particularly, I ask whether *Sphagnum* traits, in addition to environmental factors, are important drivers of geographical variation in microbial community composition and traits. Do *Sphagnum* metabolites have a stronger effect in shaping microbial properties than anatomical and morphological traits? Is *Sphagnum* phylogeny an important determinant of microbial properties, in addition to environmental factors? These are the main questions I wanted to answer in this chapter.

To address these questions, I conducted an observational study across five European *Sphagnum*-dominated peatlands representing a wide range of climatic and edaphic conditions. I measured a suite of *Sphagnum* anatomical and morphological traits and metabolites, as described in the previous chapter. I also measured various microbial properties such as microbial biomass of consumers (testate amoebae, ciliates, rotifers and nematodes), phototrophs (microalgae and cyanobacteria), and decomposers (fungi and bacteria), which was extracted from *Sphagnum*. Collected microbial traits were classified into three main microbial life history strategies: growth yield, resource acquisition and stress tolerance. Using structural equation modeling (SEM) and phylogenetic distance analyses, I investigated the role of *Sphagnum* traits in shaping microbial community composition and functioning along with environmental conditions.

I found that microbial community and trait composition did not vary along with *Sphagnum* phylogenetic distance. The findings indicated that certain microbial taxa and traits were strongly related to particular *Sphagnum* anatomical and morphological traits and metabolites, while other microbial taxa and traits were more generalist and mostly influenced by environmental (climatic and edaphic) conditions. Hence, *Sphagnum* interspecific trait plasticity may drive microbial community composition and functional diversity in addition to climatic and local condition variables. Using the SEM approach and taking into account the response of *Sphagnum* traits to climatic and edaphic conditions, multi-model comparisons revealed that the addition of *Sphagnum* traits generally did increase the predictive power (R^2) of SEMs, especially for the biomass of decomposers (+42%), phototrophs (+19%), and growth yield traits (+10%) while avoiding overfitting the models. This suggests that *Sphagnum* anatomical and morphological traits and metabolites are important regulators of *Sphagnum*-microbial interactions. *Sphagnum* anatomical and morphological traits are rather poor predictors with only few correlations with microbes and their traits, thus they played

auxiliary role. Contrary, *Sphagnum* metabolites are important drivers for microbial community structure and traits, with numerous diverse effects on microbial community and traits.

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

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

Anna Sytiuk[1]*, Regis Céréghino[1], Samuel Hamard[1], Frédéric Delarue[2], Amélie Guittet[2], Janna M. Barel[1], Ellen Dorrepaal[3], Martin Küttim[4], Mariusz Lamentowicz[5], Bertrand Pourrut[1], Bjorn J.M. Robroek[6,7], Eeva-Stiina Tuittila[8], Vincent E.J. Jassey[1]

Journal of Ecology, 110, 80– 96

DOI: 10.1111/1365-2745.13728

Accepted: 1 June 2021

[1]Laboratoire Ecologie Fonctionnelle et Environnement, Université de Toulouse, UPS, CNRS, Toulouse, France,[2]Sorbonne Université, CNRS, EPHE, PSL, UMR 7619 METIS, 4 place Jussieu, F-75005 Paris, France, [3]Climate Impacts Research Centre, Department of Ecology and Environmental Science, Umeå University, SE-981 07, Abisko, Sweden, [4]Institute of Ecology, School of Natural Sciences and Health, Tallinn University, Uus-Sadama 5, 10120 Tallinn, Estonia, [5]Climate Change Ecology Research Unit, Faculty of Geographical and Geological Sciences, Adam Mickiewicz University in Poznań, Bogumiła Krygowskiego 10, 61-680 Poznań, Poland, [6]Aquatic Ecology & Environmental Biology, Institute for Water and Wetland Research, Faculty of Science, Radboud University Nijmegen, AJ 6525 Nijmegen, The Netherlands, [7]Biological Sciences, Faculty of Natural and Environmental Sciences, Institute for Life Sciences, University of Southampton, Southampton SO17 1BJ, UK, [8]School of Forest Sciences, Joensuu campus, University of Eastern Finland, Finland.

*corresponding author: anna.sytiuk@univ-tlse3.fr

Abstract

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

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

4.1. Introduction

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

Biotic and abiotic factors influence the composition of soil microbial communities. Climatic (*e.g.* temperature, precipitation) and edaphic conditions (*e.g.* soil pH, moisture) are often seen as important determinants of microbial communities (Borowik & Wyszkowska, 2016; Singh et al., 2009; Wang et al., 2020) yet they cannot completely explain the full variation observed within microbial communities (De Gruyter et al., 2020). This suggests that biotic interactions also play an important role in shaping microbial communities (Geisen, 2020). Trophic and non-trophic (*e.g.* competition) interactions among microorganisms are important, but often neglected (Gralka et al., 2020). Recently, plant species identity (Burns et al., 2015), plant phylogeny (Barberán et al., 2015) and plant community composition (de Vries et al., 2012; Robroek et al., 2015) have also been identified as important drivers of microbial communities. However, disparity remains once individual plant leaf and root traits are taken into account (Leff et al., 2018), suggesting that plant traits are poor predictors of microbial communities and microbial processes (see Sweeney et al., 2020). Alternatively, the effect of plant species identity and/or community composition on microbial communities may mostly rely on chemical interactions between plant and soil microbes (van Dam and Bouwmeester, 2016). Plants produce a plethora of biochemicals, and can release over a hundred different metabolites in their surroundings that can attract, deter, or even kill belowground microbes (Fernandez et al., 2016; Hamard et al., 2019; Hu et al., 2018; Pinton et al., 2001). Elucidating which plant characteristics (phylogeny, morphological and anatomical traits and/or metabolites) govern microbial communities, particularly in addition to microbial interactions and climatic and edaphic conditions, is thus urgently needed to predict the structure of

microbial communities, their functioning and subsequent ramifications for biogeochemical cycles (Bardgett and Wardle, 2010).

We address this knowledge gap by examining the understudied linkages between peat mosses (*i.e. Sphagnum* moss) and their associated microbiome. *Sphagnum*-dominated peatlands store more carbon (C) than any other terrestrial ecosystem (Nichols and Peteet, 2019). Carbon accumulation in *Sphagnum*-peatlands results from cold, acidic, nutrient-poor and water-saturated conditions that have hindered microbial decomposition of litter over millennia (Rydin and Jeglum, 2006). *Sphagnum* mosses also facilitate their own growth by creating unfavorable conditions for vascular plants, generating recalcitrant litter and changing physical and chemical properties of the soil (Turetsky, 2003; van Breemen, 1995). As *Sphagnum* do not possess roots, the leaf-associated microbiome comprises crucial functions, such as defenses against pathogen and additional nutrient supply for *Sphagnum* growth and development (Opelt, et al., 2007b). The association between *Sphagnum* moss and its microbiome, *i.e.* the bryosphere (*sensu* Lindo & Gonzalez, (2010)), plays a key role in peatland C dynamics. These *Sphagnum*-associated microbial communities include a core detrital network for C and nutrient cycling (Gilbert et al., 1998; Jassey et al., 2015; Lindo & Gonzalez, 2010). Unique anatomical and morphological traits of *Sphagnum*, especially the cell structure of leaves - with one layer of photosynthetically active cells (chlorocystes) and dead, water-filled hyaline cells, create consistent microenvironments for the microbial communities (Bragina et al., 2012a). Large hyaline cells can serve as less acidic 'oases' for microorganisms in the otherwise acidic peatland pore water (Kostka et al., 2016). *Sphagnum* also actively excretes bioactive metabolites (*i.e.* biochemicals) to their surroundings such as polyphenols (Rasmussen et al., 1995a; Rasmussen et al., 1995b; Rudolph & Samland, 1985; Schellekens et al., 2015), flavonoids (Sytiuk et al., 2020), carbohydrates (Hájek et al., 2011; Painter, 1991; Tetemadze et al., 2018; van Breemen, 1995), and tannins (Sytiuk et al., 2020; Verhoeven and Liefveld, 1997), that have been related to the functioning of peatlands (Verhoeven and Liefveld, 1997). Many of these metabolites show antimicrobial properties (Fudyma et al., 2019). For example, *Sphagnum* phenolics have been suggested to reduce vascular plant's mycorrhization (Binet et al. 2017; Chiapusio et al., 2018), and inhibit bacterial growth (Mellegård et al., 2009), decomposition (Freeman et al., 2001; Verhoeven & Liefveld, 1997; Verhoeven & Toth, 1995) and microbial respiration (Hamard et al., 2019). As *Sphagnum* species engineer their environment (van Breemen, 1995; Bengtsson et al., 2016; Bengtsson et al., 2018), both *Sphagnum* anatomical/morphological and biochemical traits may be expected to steer the structure and function of peatland microbial communities. A better identification

and comprehension of these drivers are crucial for predicting the composition of the microbial community and its functioning in peatlands.

Here, we explore how and to what extent *Sphagnum* phylogeny, anatomical and morphological traits and metabolites drive the spatial variability of microbial community composition and functioning. To do so, we conducted an observational study in five European *Sphagnum*-dominated peatlands representing a wide range of climatic and edaphic conditions. Because *Sphagnum* microbial community composition can vary across space (Mitchell et al., 2003; Robroek et al., 2021), and according to the variation of edaphic factors such as pH and nutrient richness (Bragina et al., 2013a; Jassey et al., 2014; Opelt et al., 2007a), we hypothesized that (1) microbial community composition and functional traits will show distinct patterns among the five peatlands. We expected (2) that geographical variation in microbial community composition and microbial traits is driven by climatic/edaphic conditions as well as *Sphagnum* anatomical and morphological traits and metabolites. In particular, we hypothesized that (3) *Sphagnum* traits will explain a fraction of variation in microbial community composition and microbial traits that is not explained by climatic and edaphic conditions. Among *Sphagnum* traits, we predicted that (4) *Sphagnum* metabolites have a stronger effect in shaping microbial properties than anatomical and morphological traits, since metabolites are released into *Sphagnum* surroundings and can directly influence microbial community composition and/or microbial traits. Finally, as *Sphagnum* traits do not exclusively vary with climatic and edaphic conditions (Sytiuk et al., 2020), but also according to phylogeny (Laine et al., 2021), we hypothesized that (5) *Sphagnum* phylogeny is an important determinants of microbial properties, in addition to climatic and edaphic conditions and *Sphagnum* traits.

4.2. Material and methods

4.2.1. Sites, sampling design and sample collection

We selected five *Sphagnum*-dominated peatlands along a latitudinal gradient from northern Sweden to southern France to represent a wide range of edaphic and climate conditions (Table 4-1, Table S1, S3). In each site, a preliminary vegetation survey (see Table S2) allowed us to select five homogeneous plots (50 x 30 cm each; 5 plots x 5 sites = 25 plots in total) dominated by a single *Sphagnum* species: *S. warnstorfii* (France, FR), *S. magellanicum* (Poland, PL), *S. rubellum* (Estonia, EST), *S. papillosum* (Finland, FI) and *S. balticum* (Sweden, SE). Dominant *Sphagnum* species were site specific, potentially creating a confounding effect with climate/edaphic conditions. To overcome this issue, we measured phylogenetic differences among *Sphagnum* species at five sites, and found that *Sphagnum* phylogeny did not covary with climatic variation (*i.e.* mean annual temperature, $F_{1,3} = 0.15$, $P = 0.72$, Fig. S1). Despite the absence of phylogeny-climate covariation, it remains true that species identity and site variation were still potentially confounding. We thus quantified metabolite plasticity (*i.e.*, water-soluble phenols) of the five *Sphagnum* species using a reciprocal transplantation along the latitudinal gradient to determine whether *Sphagnum* metabolite production is more sensitive to environmental variability than to taxonomy. We found that the concentration of water-soluble phenols increased for all *Sphagnum* species along the latitudinal gradient (Fig S2a, b), and more importantly that the variance of water-soluble phenol concentrations within the same species at different temperatures was higher than between the different species at the same temperature (Fig. S2c). Together, these findings show that water-soluble phenol concentrations in *Sphagnum* tissues vary independently of taxonomy. However, other metabolites may depend on taxonomy. To exclude this potential, we used unpublished data (Jassey, Allard and Robroek, unpublished data) on *Sphagnum* metabolomic profiling from 56 European ombrotrophic peatlands (see sites in Robroek et al., 2017). A PCoA analysis revealed that that the metabolomic composition of *Sphagnum* species was strongly determined by local and regional conditions (site effect, $P < 0.05$), rather than by taxonomy (species effect, $P = 0.46$; Fig. S3). Altogether, these additional analyses demonstrate that a potential confounding effect of species and site was not an important issue when referring to *Sphagnum* metabolites. However, we acknowledge that anatomical and morphological traits are used to identify *Sphagnum* moss to species (Isoviita, 1966), and that in our study anatomical and morphological traits cannot be disentangled from *Sphagnum* taxonomy. We therefore advise caution when using these data to predict microbial communities and microbial activities.

Table 4-1. Site conditions and climatic data of the study sites

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

*Measured in early July 2018

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

4.2.2. Characterizing climate and site conditions

For each site, we extracted bioclimatic data from WorldClim v2 (Fick and Hijmans, 2017): mean annual temperature, temperature seasonality, annual precipitation, and precipitation seasonality averaged over the 1960-2018 period (Table S1). Water-table depth (WTD) and pH were measured directly in the field using a ruler and a portable multimeter Elmetron CX742, respectively (Table 4-1). Water-extractable organic matter (WEOM) was extracted from the *Sphagnum* shoots (0-3 cm height) collected at the five sites according to Jassey et al. (2018) (Table S3). Briefly, *Sphagnum* shoots were soaked in 30 mL of demineralized water and then shaken for 90 min at 150 rpm. *Sphagnum* shoots were then dried at 60°C for 48 hours and weighted to obtain dry mass (mg/g DW). The water extract was filtered with Whatman filter (1 µm pore size) and several physical-chemical parameters were analyzed: a TOC analyser (Shimadzu TOC-L) was used to quantify dissolved organic carbon, nitrogen and phosphate (WEOC, WEON and WEOP respectively). To measure dissolved organic matter aromatic content and molecular weight (WEOCq), we used absorbance measurements between 250 and 660 nm (15 wavelengths in total) in 200 µL sample aliquots in 96-well quartz microplate using a BioTek SynergyMX spectrofluorometer (Jaffrain et al., 2007). For a blank, we used demineralized water filtered through Whatman filter to correct our values for the potential C released from the filter. Spectral slopes ($S_{250-660}$, nm^{-1}) were calculated using linear least squares regressions with Ln-transformed absorptions. High $S_{250-660}$ values indicate low molecular weight material (Hansen et al., 2016).

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

4.2.3. *Sphagnum* anatomical and morphological traits

We characterized a suite of four anatomical and morphological *Sphagnum* traits determining the capacity of *Sphagnum* moss to provide shelter for microbial communities following Jassey & Signarbieux (2019): volume of the capitulum (height x diameter of capitulum), water-holding capacity of the capitulum and shoot, number of hyaline cells per leaf area (*i.e.* dead cells storing water), the surface area of hyaline cell (length x width) and width of chlorocystes (photosynthetic cells surrounding hyaline cells). In total, 125 individuals (25 per site) were randomly collected to estimate the volume of the capitula (mm^3) by measuring their height and diameter using a precision ruler. Then, we used the same samples to quantify the net water content of the capitula and stem (first cm) at water saturation. Capitula and stems were submerged in water until their maximum water retention capacity was reached. Excess water was removed by allowing water to drain naturally for two minutes. Then, individual capitula and stems were weighed as water-saturated and subsequently dried for three days at 60°C. The net water content at water saturation of each individual was expressed in grams of water per gram of dry mass (g H_2O/g DW). For anatomical analyses, we carefully deconstructed five *Sphagnum* capitula in each plot (in total, 125 capitula) to isolate *Sphagnum* leaves. Then, we pooled all *Sphagnum* leaves, homogenized, and took three leaves from that pool to prepare microscope slides from each plot (375 leaves analyzed in total). We quantified the number of hyaline cells per leaf area (number of hyaline cells per mm^2), their surface (μm^2), as well as the width of chlorocystes (µm), using a light microscope connected to a camera (LEICA ICC50 HD) and the size analytic tools (LEICA suite software).

4.2.4. *Sphagnum* metabolic fingerprint

We assessed the metabolic fingerprint of *Sphagnum* mosses using two different approaches. First, we quantified a set of nine moss metabolites that can influence microbes. The different extractions pathways used for quantifying the various *Sphagnum* metabolites are detailed in Sytiuk et al. (2020). Briefly, *Sphagnum* mosses were frozen, lyophilized, ground and stored at

-20°C prior to biochemical analysis. Then, we used (i) a 99.9% methanol extraction for quantifying *Sphagnum* pigments (chlorophyll a, b and total carotenoids), (ii) a 50% methanol extraction for quantifying total polyphenols, flavonoids, tannins and carbohydrates, (iii) a water extraction for quantifying water-extractable total polyphenols, (iv) a sulfosalicylic acid extraction for quantifying proline and (v) a dosage of proteins with bovine serum albumin (BSA). All metabolites were quantified using spectroscopy at different wavelengths. Secondly, we characterized the polysaccharides, aromatic and aliphatics content of *Sphagnum* mosses using Fourier Transform Infrared Spectroscopy (FT–IR-ATR; (Hodgkins et al., 2014). 30 mg freeze-dried and ground *Sphagnum* was placed directly on a germanium crystal and pressed down with a flat tip to improve distribution and contact. Spectra were acquired by 64 scans at a 2 cm^{-1} resolution over the range 4000–600 cm^{-1}. All spectra were corrected for water vapor, CO_2 and for differences in depth of beam penetration at different wavelengths (ATR correction; Opus software). All spectra were then normalized. For each spectrum, normalization involved (i) a subtraction of the minimum absorption value applied to the whole spectrum followed by (ii) a multiplication - also applied on the whole spectra - to obtain a spectral maximal absorbance value of 1 for each *Sphagnum* sample. Six main absorption peaks were used as an indicator of *Sphagnum* polysaccharides, aromatics and aliphatics: 1) the 1064 cm^{-1} region (combination of C–O stretching and O-H deformation) is associated to polysaccharides; 2) the 1515 cm^{-1} region (C=C; aromatic compounds) is assigned to lignin/phenolic backbone; 3) the 1610 cm^{-1} region (C=C streching; aromatic compounds and/or asymmetric C-O stretch in COO-) is associated to lignin and other aromatics, or aromatic or aliphatic carboxylates; 4) the 1724 cm^{-1}-1710 cm^{-1} region (C=O stretch of COOH or COOR) corresponds to free organic acids, carboxylic acids, aromatic esters; 5) 2850 cm^{-1} region (symmetric CH_2) is associated to aliphatics; and 6) 2920 cm^{-1} region (antisymmetric CH_2) is associated to aliphatics. We used the ratio between the relative intensities of FT–IR absorption bands, where 1610 cm^{-1} region was used as denominator due to its highly recalcitrant nature, in order to evaluate *Sphagnum* fingerprints and their degree of degradability.

4.2.5. Microbial abundances and biomass

Microbial consumers (testate amoebae, ciliates, rotifers and nematodes), phototrophs (microalgae and cyanobacteria), and decomposers (fungi and bacteria) were extracted from *Sphagnum* following Jassey et al. (2011a). For bacterial counts, a 1-mL sub-sample was stained with SYBR Green (0.1x final concentration) and incubated in the dark for 15 minutes. Then

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

4.2.6. Microbial traits

Following the revised life history theory for microbial traits (Malik et al., 2020), we collected microbial traits classified into three main microbial life history strategies: growth yield, resource acquisition and stress tolerance. We quantified 14 traits in the growth yield strategy: biomass per cell, biovolume per cell, body size (length and width), the quantum yield of photosystem II for phototrophs, photosynthetic pigments content per cell for phototrophs, growth rate, reproduction rate, nutrition type and respiration rate per cell. We classified 15 traits in the resource acquisition strategy: nine microbial enzyme activities, C uptake by phototrophs, predation rates, nitrogen fixation, methanotrophy, metabolism and hunting strategies. Finally, five traits were assigned to the stress tolerance strategy: morphology, locomotion, response to warming and drought, tolerance to desiccation. A total of 34 microbial traits were either directly quantified or acquired from the literature (see Supplementary method on microbial traits for more details).

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

4.2.7. Numerical analyses

All statistical analyses were performed in *R* 3.5.3 (R Core Team, 2019) using packages, as specified below. Linear mixed effects models were used to assess the *Sphagnum* taxonomy effect (fixed effect) on the microbial biomass of each trophic group, CWM of each microbial trait and *Sphagnum* traits. The models were fitted with plot nested within *Sphagnum* taxonomy as a random effect on the intercept (Pinheiro and Bates, 2000). Tukey's multiple comparison test was used for *post hoc* analyses of differences among the levels of the fixed effects in the final model. Normality and homogeneity assumptions of the data, as well as model residuals, were assessed using a Shapiro test and diagnostic plots. Log_{10}-transformations of the data were applied if needed in order to meet these assumptions. To

represent differences in microbial community composition, microbial trait composition and *Sphagnum* traits, we performed principal coordinate analysis (PCoA) using Gower's distance that allowed mixing of different types of data (*i.e.* qualitative and quantitative traits) while giving them equal weights. A standardization (*Sphagnum* anatomical and morphological traits and metabolites) or Hellinger transformation (microbial community composition and microbial traits) was applied on the matrices beforehand (Legendre and Legendre, 2012). We used Spearman correlations to test the potential relationships between microbial community composition, CWM of microbial traits and *Sphagnum* traits and/or climatic and edaphic factors.

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

To assess whether differences in *Sphagnum* anatomical and morphological traits and metabolites predicted variation in microbial community composition and microbial traits beyond the explanatory power of climatic and edaphic conditions (Leff et al., 2018), we built a set of path diagrams subjected to structural equation modelling (Grace et al., 2010, 2014). We compared the explanatory power of the models, assessed through adjusted R^2 values and Akaike Information Criterion (AIC), by framing four types of models (Fig. 4-1). First, we tested the effects of climatic and edaphic conditions on each (hereafter 'single' SEM models) trophic group (*i.e.* the biomass of either decomposers, phototrophs, predators or the total microbial biomass) and microbial trait strategy (*i.e.* either growth yield, resource acquisition and stress tolerance strategies or the overall traits composition; Fig. 4-1a) separately. Second, we tested the effects of climatic and edaphic conditions on the interactions (hereafter 'interactions' SEM model) among/within microbial community composition and microbial trait strategies (Fig. 4-1b). Third, we tested the effect of *Sphagnum* anatomical and morphological traits and metabolites (*i.e. Sphagnum* traits; in addition to climatic and edaphic conditions as in the first model) on each trophic group and microbial trait strategy separately (Fig. 4-1c) and in interaction (Fig. 4-1d). The benefits gained (ΔR^2) by including *Sphagnum*

anatomical and morphological traits and metabolites into the models were calculated as follows:

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

We further compared AIC values between models with and without *Sphagnum* traits to check for potential overfitting (Burnham and Anderson, 2004). In these models, we used annual precipitation and mean temperature of the wettest quarter as climate variables, selected beforehand using a principal component analysis (PCA) applied on all bioclimatic variables. For edaphic peatland conditions, we used *Sphagnum* water content and the first axis of a PCA applied on WEON, WEOC, WEOP and $S_{260\text{-}660}$. For microbial trait strategies, we used the first axis of three PCoAs applied on the CWM of traits of each trait strategy, respectively. The paths of the SEM were fitted as previously described for ANOVAs using *piecewiseSEM* package (Lefcheck, 2016). We selected this approach as it allowed using the Shipley's test of d-separation to assess whether direct or indirect paths are missing from the *a priori* mode. The adequacy of the model was evaluated via several tests including non-significant *Fisher's C* statistic (P >0.05), and low Akaike information criterion (AIC) (Grace et al., 2010).

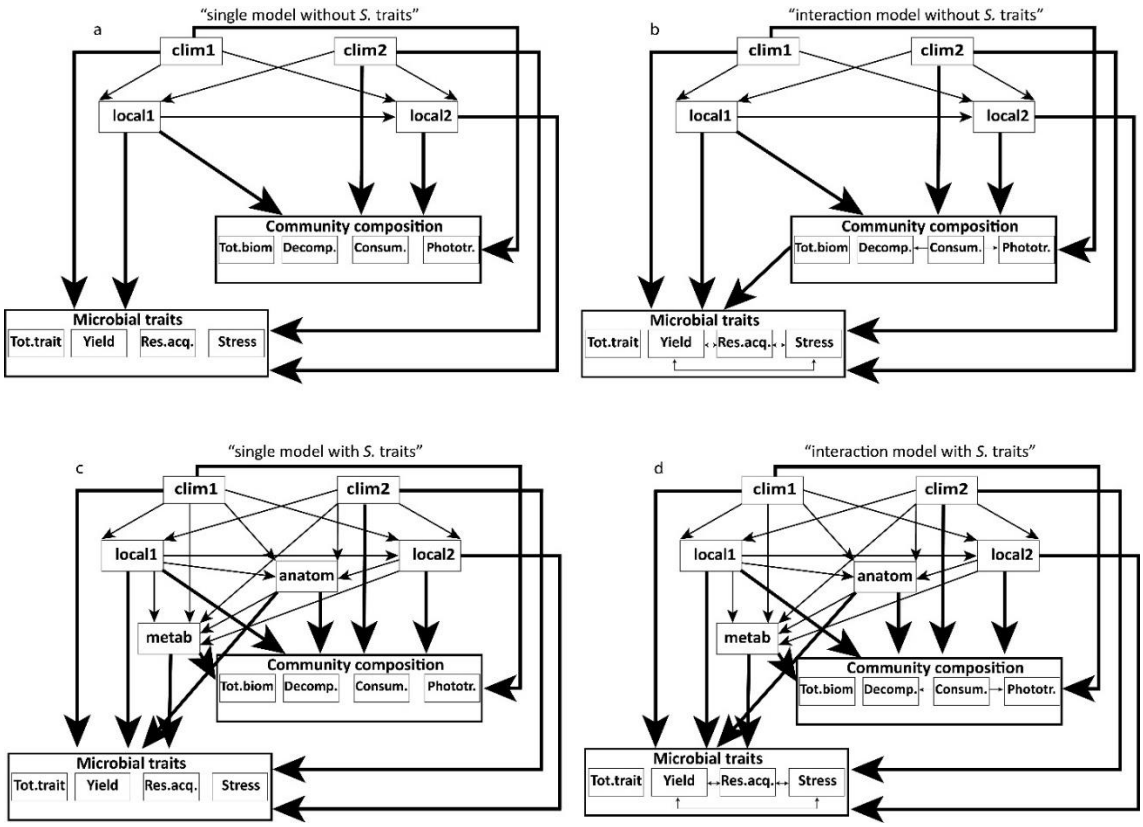


Figure 4-1. A priori conceptual structural equation model (SEM) depicting pathways by which climate and edaphic conditions (standardized data of annual precipitation (clim1), mean temperature of the wettest quarter (clim2), *Sphagnum* water content (local1), PC1 of WEOM chemistry (local2), PCoA1 of *Sphagnum* anatomical and morphological traits (anatom) and metabolites(metab) can affect microbial community composition (PcoA1 of tot.biom=total microbial biomass; Hellinger transformation of decomp.=decomposers, consum.=consumers, phototr.=phototrophs) and traits (PCoA 1 of tot.traits=total traits, yield=growth yield, res.acq.=resource acquisition, stress=stress tolerance). (A) a single model, (B) an interaction model, (C) a single model with *Sphagnum* traits (D) an interaction model with *Sphagnum* traits. Thin lines indicate a single path, while thicker lines indicate that any climatic/edaphic parameter affected each representative of microbial community composition (or the sum of them) and/or microbial trait composition (or the sum of them).

We used two strategies to validate our SEM models and generate statistics of the models' predictive power. The first strategy was inspired by 'null-model' analyses in ecology (Gotelli and Ulrich, 2012), and tests the assumption that the effects of *Sphagnum* traits in predicting microbial community composition and microbial traits are not random and driven by changes in *Sphagnum* traits. To test this assumption, we randomized *Sphagnum* trait matrices to break any structure in the data. We iteratively and randomly shuffled the *Sphagnum* trait matrices ten times before running the SEM models. The second strategy focused on the size of the data set as it can strongly influence SEM modelling (Grabowski and Porto, 2017; Grace et al., 2010). To do so, we iteratively reduced our entire data set by 20% by randomly removing one replicate from the dataset. In other words, we retained four

out of five replicates before running the SEM models. We repeated this step five times, until all possible combinations were covered. For each SEM model we extracted the data relative to the adequacy of the model (*Fisher's C* statistic and *P*-value) and AIC values (see model outputs in Fig. S7 and Tables S11, S12). The sensitivity analyses were performed on the most relevant SEM models, where the benefits gained (ΔR^2) by including *Sphagnum* traits into the models was more that 10%: decomposers single, decomposers interactions, phototrophs single, and yield single.

4.3. Results

Throughout this section we refer to changes in sites (see Table 4-1 for site acronyms), which nevertheless are confounded with *Sphagnum* species identity. Thus, we advise to check the Materials and methods section and Supplementary materials (Fig S1, S2, S3) where we demonstrate that a potential confounding effect of species and site was not an important issue.

4.3.1. *Sphagnum* morphological and anatomical traits and metabolites

PCoA analysis revealed that *Sphagnum* trait composition (anatomical and morphological traits and metabolites) differed among the five sites (Fig. 4-2a). Three distinct groups emerged from the first PCoA axis: a first group composed of *Sphagnum* from FI, a second group composed of EST and SE and a third group with FR and PL. On the second PCoA axis, there was a gradient ranging from FI to FR/PL and then SE/EST. This gradient was not related to any particular climatic and/or edaphic trend. Instead, it showed a clear trend as *Sphagnum* from FI, PL and FR had higher capitulum sizes, water holding-capacity and/or metabolites concentrations (Fig. S4, S5, Table S5), as compared to SE and EST. Specific *Sphagnum* anatomical and morphological traits and metabolites varied between five *Sphagnum* species from three phyla (Fig. 4-2b; Fig. S4, S5). We found that *Sphagnum* from FR and PL produced more total and water-soluble phenols, total flavonoids and tannins than SE and FI (Fig. 4-2b). However, *Sphagnum* from SE, FI and EST produced more polysaccharides, organic acids, symmetric and antisymmetric CH_2 than FR and PL. In terms of anatomical and morphological traits, *Sphagnum* sampled from PL and FI possessed higher capitulum diameter, height and volume than EST and FR. Water holding capacities, hyaline cell surface and chlorocyste width were highest for *Sphagnum* from FI and FR. Even though *Sphagnum* from EST had highest number of hyaline cells per leaf area, its surface of hyaline cells was smallest.

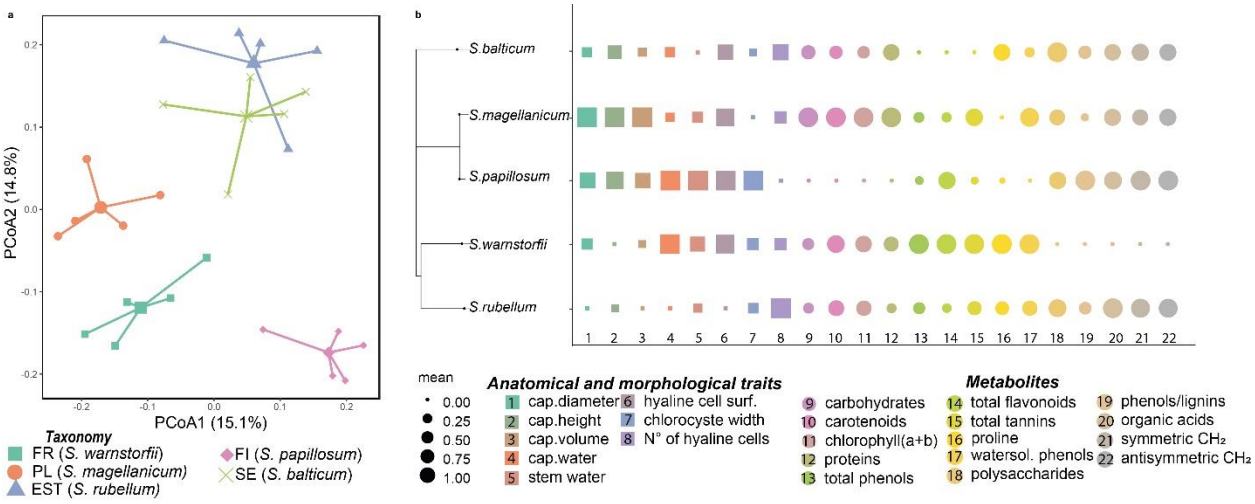


Figure 4-2. *Sphagnum* anatomical and morphological traits and metabolites data. A) Principal coordinates analysis (PCoA) on the Gower dissimilarity matrix of *Sphagnum* anatomical and morphological traits and metabolites for five dominant species collected along a gradient. Groups are colored according to *Sphagnum* species sampled in sites spanning from south to north. B) *Sphagnum* phylogenetic tree and normalized means of *Sphagnum* anatomical and morphological traits and metabolites. The square shape represents mean values of anatomical and morphological traits, while circle shape – mean values of metabolites. The size of mean is represented from the smallest (the smallest circle/square) to the highest (the highest circle/square) values of anatomical and morphological traits and metabolites.

4.3.2. Microbial community composition and trait composition

Microbial community composition and microbial traits differed significantly among the five sites (Fig. 4-3; Fig. S6-S9, Tables S5), and similar to the *Sphagnum* traits composition, no particular climatic and/or edaphic trend was found neither in microbial community composition nor microbial traits (Fig. 4-3). The first PCoA axis showed three distinct groups of microbial community composition with FR and SE aside and a third group composed of PL, FI and EST (Fig. 4-3c). On the second axis, there was a clear separation between SE and the four other sites. Microbial trait composition differed markedly across the five sites (Fig. 4-3d). While no particular variation was observed on the second PCoA axis, sites were well separated along the first PCoA axis (Fig. 4-3d). Overall biomass differed with *Sphagnum* phylogeny. Specifically, the highest biomass of consumers and decomposers was observed in SE and FR (Fig. 4-3a, Fig. S6). Conversely, PL and EST were characterized by low biomass of most microbial groups (Fig. 4-3a, Fig. S6). For community weighted mean (CWM) microbial traits, we found that the microbial traits related to the growth yield strategy were the most abundant in FI and SE, and the least abundant in EST (Fig. 4-3b, Fig. S7). Microbial traits related to resource acquisition peaked in FI and EST, while stress tolerance traits were

the most abundant in SE (Fig. 4-3b, Fig. S8, S9). Despite such differences in microbial biomass and CWMs of traits among sites, *Sphagnum* phylogenetic distances were weakly related to differences in microbial biomasses ($P > 0.1$ in most cases) and in microbial trait composition ($P > 0.1$ in all cases; Table S4). Only the biomass of flagellates ($K = 1.1$, $P = 0.03$; Table S4) was significantly related to *Sphagnum* phylogenetic distances.

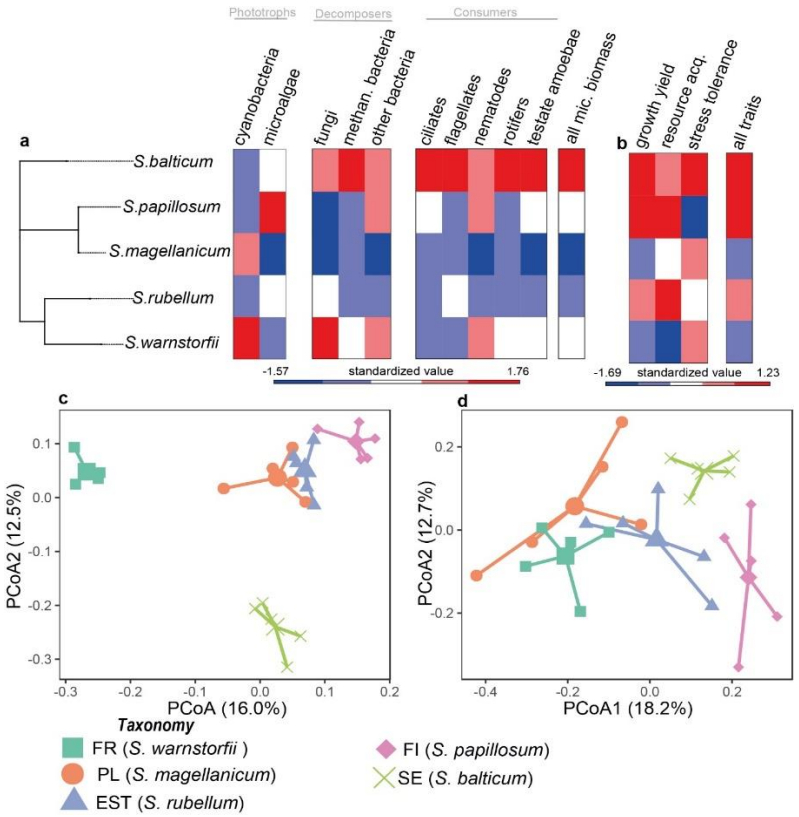


Figure 4-3. Microbial community composition and traits composition. Upper panels: *Sphagnum* phylogenetic tree with the corresponding heatmap showing the dissimilarities in (A) the composition of each trophic group components in which colors represent the standardized value calculated from standardized means of microbial biomass, and (B) the microbial traits composition in which colors represent the standardized value calculated from the first PCoA on the Gower dissimilarity matrix of microbial trait composition. Lower panels: Principal coordinates analysis (PCoA) on the Gower dissimilarity matrix of (C) the microbial community composition based on the abundance of all microbes (micro-eukaryotic species cyanobacteria, fungi and non-photosynthetic bacteria) and (D) the microbial traits composition. Groups are colored according to *Sphagnum* species sampled in sites spanning from south to north.

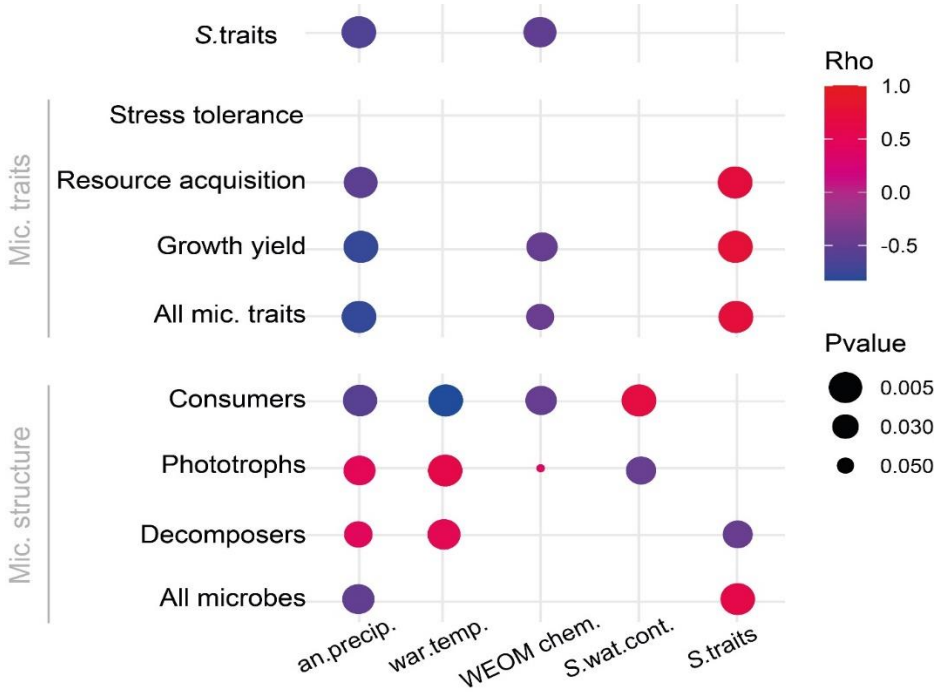
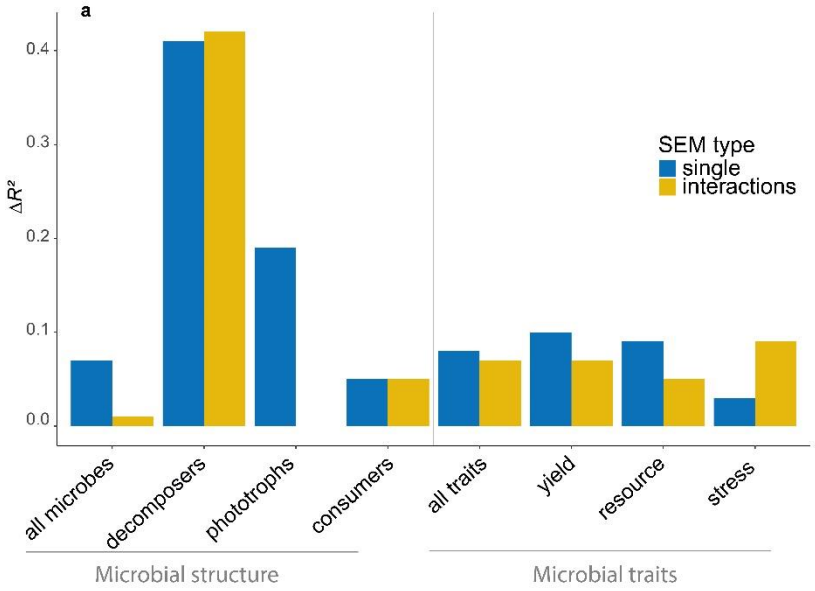


Figure 4-4.Correlation table on the relationships between climatic and edaphic conditions (standardized data of annual precipitation (an. precip.), the mean temperature of the wettest quarter (war. temp.), PC1 of WEOM chemistry (WEOM. chem.), *Sphagnum* water content (S.wat.cont.), PCoA1 of *Sphagnum*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

4.3.3. Predictors of microbial community and microbial traits

Differences in microbial community composition and microbial traits were related to both climatic and edaphic conditions and *Sphagnum* traits (Fig. 4-4). As *Sphagnum* trait composition was also correlated with climatic and edaphic conditions (*i.e.* annual precipitation and WEOM chemistry, Fig. 4-4), we ran structural equation models with and without *Sphagnum* anatomical and morphological traits and metabolites to tease apart the effects attributable to *Sphagnum* traits and metabolites on microbial properties (Fig. 4-5, Table S6-S10). Shifts in microbial community composition and microbial traits across *Sphagnum* species were correlated with multiple climatic and edaphic variables, which together explained 27%-86% of the variation of the biomass of decomposers, phototrophs and consumers, as well as of microbial trait composition (Table S6). When *Sphagnum* anatomical and morphological traits and metabolites were added to the SEM models, prediction accuracies for most microbial biomass and trait compositions increased by 42% (Fig. 4-5), notably for decomposer biomass (+42%), phototrophs (+19%) and traits related to growth yield (+10%). Rigorous sensitivity analyses on SEM models revealed that R^2 improvements provided by the addition of

Sphagnum traits in SEMs were robust and without bias due to possible randomness in the estimations (Fig. S7, S11) or the size of the dataset (Fig. S7, Table S12). Our sensitivity analyses hence indicated that microbial properties can be reasonably predicted from *Sphagnum* traits, and most importantly, that such effects are complementary to environmental (*i.e.* climatic and edaphic conditions) variation.



b

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

Figure 4-5. Outputs of the SEMs when *Sphagnum* traits were included in SEMs for microbial community composition and microbial traits composition: (A) the benefits gained (ΔR2) and (B) Akaike Information Criteria (AIC) values. *Full summed models= Full model with PCoA1 for total microbial biomass and PCoA1 for total microbial traits. All details about SEMs including R2, P-values, Fisher's C, path explanations are provided in Tables S6-S10.

More precisely, most *Sphagnum* metabolites were related to microbial biomasses and/or microbial trait strategies (Fig. 4-6). The biomass of cyanobacteria, some decomposers (*i.e.* fungi and bacteria) and rotifers was positively related to water-soluble phenolic compounds, whereas microalgae and testate amoebae tended to be negatively correlated to phenols (Fig. 4-6). *Sphagnum* anatomical and morphological traits, such as the width of chlorocystes and water-holding capacity, were positively correlated with the biomass of nematodes and some growth yield traits (*i.e.* respiration, biomass, biovolume) and some enzymes. However, methanotrophs were negatively correlated to the same *Sphagnum* traits. Most of the individual microbial traits, especially those related to growth yields (microbial pigments, respiration, size), were negatively correlated to water-soluble phenols, total

tannins, phenols, proteins, carbohydrates and pigments while also being positively correlated to polysaccharides, phenols/lignins, CH_2 compounds. Opposite trends were observed for some resource acquisition traits (mostly enzymes; Fig. 4-6).

Figure 4-6.The relationship between differences in the microbial community composition (sum of Hellinger-transformed microbial biomass per trophic group) and their traits (PCoA1 axes) and individual *Sphagnum* traits. Points represent Spearman correlation coefficients (Rho) and their significance (P<0.05).

4.4. Discussion

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

In contrast to peatland plant species richness and functional diversity (Bjorn J.M. Robroek et al., 2017), no notable latitudinal trends, neither in microbial community composition nor trait composition, were observed. Instead, climatic (*i.e.* the mean temperature of the wettest quarter and annual precipitation) and edaphic (*i.e.* water table depth, *Sphagnum* water content, and nutrient availability) variables were identified as important drivers of microbial community and traits. This corroborates previous studies showing that global and local peatland conditions play deterministic roles in shaping microbial communities and functioning (Elliott et al., 2015; Jassey et al., 2014; Urbanová & Bárta, 2016). However, we show that *Sphagnum* traits, mostly metabolites, were as important as climatic and edaphic conditions in driving microbial community composition and functioning (Fig. 4-4). Our analysis revealed that microbial consumers, as well as growth yield and resource acquisition traits, generally decreased with frequent rainfall, high *Sphagnum* water content, and low nutrient content. Phototrophs and decomposers, however, showed opposite trends. In addition, *Sphagnum* traits were negatively correlated to decomposers, but positively to growth yield and resource acquisition. While correlations between microbial traits, *Sphagnum* traits

and climatic and edaphic factors enabled us to assess the direction of these relationships, the underlying mechanisms remain unknown, since here *Sphagnum* metabolites were also driven by climatic and edaphic conditions. Using the SEM approach and taking into account the response of *Sphagnum* traits to climatic and edaphic conditions, our multi-model comparisons revealed that the addition of *Sphagnum* traits generally did increase the predictive power of SEMs, especially for the biomass of decomposers, phototrophs, and growth yield traits, while avoiding overfitting the models. This suggests that *Sphagnum* anatomical and morphological traits and metabolites are important regulators of *Sphagnum*-microbial interactions.

Overall, *Sphagnum* anatomical and morphological traits were poor predictors of microbial communities. Nevertheless, we found that the biomass of cyanobacteria, large consumers, such as nematodes, and microbial traits related to growth yield (*i.e.* respiration, size and volume) and resource acquisition (*i.e.* some extracellular enzymes) were positively correlated to *Sphagnum* species with high capitulum size, and, hence, high water-holding capacities, and width of chlorocystes (Fig. 4-6). Water held between leaves and hyaline cells of the capitulum provides a habitat for many microorganisms (Vitt, 2000), and allows them to move freely with water exchange between hyaline cells and adjacent photosynthetic cells (Kostka et al., 2016). However, large *Sphagnum* species are known to maintain a more stable water content under unfavorable conditions thanks to the high water-holding capacity traits of their capitula (Jassey & Signarbieux, 2019). Consequently, our findings suggest that microbial communities associated with *Sphagnum* species with high water-holding capacity are better protected from desiccation than for those living in smaller *Sphagnum* species, while the hunting space for large consumers is less limited. Indeed, habitat-size is an important factor structuring microbial communities. For example, Sweeney et al (2020) found that increased root surface area improved opportunities for mycorrhizal fungi colonization in grasslands. Moreover, Delgado-Baquerizo et al. (2018) highlighted habitat-size as a crucial driver of soil bacterial biodiversity and functional diversity.

Comparative effects between *Sphagnum* anatomical and morphological traits and metabolites provide evidence that *Sphagnum* metabolites play a central role in structuring microbial communities and their traits. We found that the biomass of cyanobacteria, fungi, and bacteria, as well as a number of resource acquisition traits, such as extracellular enzymes, were positively correlated to many metabolites, including total carbohydrates, proteins, *Sphagnum* pigments, total phenols and/or tannins (Fig. 4-6). In contrast, the biomass of microalgae and nematodes, and most of microbial growth yield traits (*i.e.* microbial pigments,

respiration, biomass, volume and size), were negatively correlated to *Sphagnum* metabolites (Fig. 4-6). Our findings suggest that *Sphagnum* metabolites have diverse effects on microbial communities and their traits, supporting observations that the degree of host specificity varies despite *Sphagnum* phylogenetic distances (Bragina et al., 2012b). The positive links between decomposers and resource acquisition traits (mostly enzyme activities), and *Sphagnum* pigments, proteins and carbohydrates suggest that the activity of these microorganisms benefit *Sphagnum* growth (Kostka et al., 2016). Alternatively, *Sphagnum* also releases easy-degradable carbohydrates (*i.e.* glucose) that can stimulate decomposers' nutrient mineralization, which directly and positively feeds back to *Sphagnum* growth, the 'host'. However, such beneficial interactions between microbes and plants often involve specific metabolites (Hiruma, 2019). Our findings indeed suggest that *Sphagnum* use an array of specific metabolites to regulate microbial communities and their functions. Polyphenols (*e.g.* *Sphagnum* acids) are released by *Sphagnum* to interact with *Sphagnum* associated microbial communities (Hamard et al., 2019; van Breemen, 1995; Verhoeven and Liefveld, 1997). Polyphenols can be associated with *Sphagnum* cell walls and prohibit microbial breakdown of *Sphagnum* litter (Freeman et al., 2001b; van Breemen, 1995; Verhoeven and Liefveld, 1997; Verhoeven and Toth, 1995) or can be released into the environment to deter or kill microorganisms (Fudyma et al., 2019; Hamard et al., 2019; Mellegård et al., 2009; Opelt et al., 2007b). This likely explains the negative link between phenols and most of the microbial growth traits. Cell-wall carbohydrates (*e.g.* sphagnan) are released slowly into the environment and thus inhibit microbial activity (Stalheim et al., 2009; van Breemen, 1995) either directly by inactivation of extracellular enzymes or indirectly by limiting C and N mineralization and thus microbial growth (Balance et al., 2007; Hájek et al., 2011). However, additional chemical analyses as well as targeted experiments are required to justify this assumption for such *Sphagnum*-microbial interactions.

Our findings demonstrate how soil microbial communities can be structured by *Sphagnum* metabolites. Also, our findings highlight the need for more targeted *Sphagnum* metabolomic analyses to identify the specific compounds involved in *Sphagnum*-microbial relationships (Chiapusio et al., 2018; Fudyma et al., 2019). *Sphagnum* leachates are composed of thousands of compounds (Fudyma et al., 2019; Hamard et al., 2019), and contain not only *Sphagnum* compounds but also microbial derivative compounds (Hamard et al., 2019). We found that *Sphagnum* organic acids, symmetric and asymmetric CH_2 (lipids and fatty acids) were positively related to microbial phototrophic traits such as microbial photosynthetic pigments, photosynthesis efficiency, and C fixation. Microbial phototrophs are highly diverse

and abundant in *Sphagnum* mosses (Jassey et al., 2015), and are an important source of lipids (Griffiths and Harrison, 2009). Hence, these findings suggest that free lipids biomarkers within the *Sphagnum* surface may indicate the activity of photosynthetic microbes associated with *Sphagnum*, which is in line with previous findings on the occurrence of cyanobacterial lipids in peat deposits (Huang et al., 2012). In addition, phototrophic lipids also possess antimicrobial properties (Leflaive and Ten-Hage, 2007), which could explain the negative relationships between lipids and microbial enzyme activities. Further studies are clearly needed to assess how well molecular-derived *Sphagnum* and microbial metabolites can determine microbial community and trait assemblages. In particular, more attention should be given to how to extract and quantify *Sphagnum* metabolites to be able to distinguish the effects of strictly *Sphagnum*-derived metabolites from microbial metabolites on microbial community composition and functioning.

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

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

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

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

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 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). ML was supported by the National Science Foundation, Poland under grant no. UMO-2017/27/B/ST10/02228, within the framework of the project 'Carbon dioxide uptake potential of *Sphagnum* peatlands in the context of atmospheric optical parameters and climate changes' (KUSCO2). BJMR was supported by the British Ecological Society research grant (SR17\1427), the Stiftelsen Anna och Gunnar Vidfelts for biologisk forskning (2018-024-Vidfelts fond) and the Dutch Foundation for the Conservation of Irish bogs. Tallinn University Research Fund and the project "Life Peat Restore" supported MK. We also thank Bruno Leroux from the *Fédération Aude Claire* and the *Syndicat Forestier de Counozouls* for providing the access to the site of Counozouls. We thank three anonymous referees and the associated editor for their helpful and constructive comments, which greatly improved the manuscript.

Author contribution

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

Data availability statement

Raw data for *Sphagnum* traits, microbial communities and traits, as well as environmental data related to this paper can be accessed through the Figshare repository (DOI: 10.6084/m9.figshare.c.5191493).

Supplementary materials

Supplementary methods

Microbial traits measurements

Microbial traits were either directly quantified in the field, in the laboratory, or obtained from literature.

Body size and width (μm) of every species were measured using an inverted microscope connected to a camera. We used cell-shape specific equations to calculate the biovolume (μm^3) for each species based on its body size and width, such as prolate spheroid, cylinder with hemispherical ends, and cylinder (Lyakh A.M., 2012). Twenty individuals per species were measured and averaged as trait. Species specific trait values were based on average measurements on twenty individuals per species.

The photosynthetic efficiency of phototrophic communities was estimated directly in the field. Freshly harvested microbial extracts from 5 *Sphagnum* capitula collected in each plot were shaken in demineralized water for 90 seconds and subsequently filtered; the first time at 100 μm to remove *Sphagnum* remains and a second time onto glass-fiber filters. Then, the glass-fiber filters were incubated in the dark for 15 min and the maximum quantum yield of photosystem II (PSII) were measured using a Phyto-PAM instrument (Walz, Effeltrich, Germany). Following the Phyto-PAM measurement, the glass-fiber filters were stored at -20°C for photosynthetic pigment analyses (see below). We calculated the photosynthetic electron transport (ETR) per cell according to Wilken et al. (2013) to estimate the photosynthetic efficiency of phototrophic communities:

$$ETR = 0.5 \times a \times \frac{Chla}{cell} \times I \times PSII$$

where Chla is the chlorophyll content a microbial extract, cell is the total abundance of phototrophs, I is the light intensity in the field, the factor 0.5 takes into account that two electron excitations at PSI and PSII are required to transport one electron through the Z-scheme of photosynthesis, and a (26.89 m^2 (g Chla)$^{-1}$) is the spectrally averaged (400-700 nm) chlorophyll specific absorption cross section estimated in Falkowski & Raven (2007).

For photosynthetic pigment analysis, the glass-fiber filters were lyophilized and extracted in 625 μL of methanol buffered with 2% of 1 M-ammonium acetate (Sigma-Aldrich,

France). After 2 min in an ultrasound cold-bath at maximum power, samples were kept at -20°C for 15 min before centrifugation (High Conic Rotor, Thermo Scientific, 3220 g, 2°C, and 5 min). Supernatants were collected and the pellets were re-extracted as described above. The pooled supernatants were filtered on PTFE membrane syringe filter (0.2 µm, Ø 13 mm, VWR International, United States) and stored a few days at -80°C before High Performance Liquid Chromatography (HPLC) analysis. To prevent degradation of pigments, all extractions were performed under dark conditions and samples stored on ice during handling. HPLC analyses were performed with a 100 µL-loop auto-sampler and a quaternary solvent delivery system coupled to a diode array spectrophotometer (LC1200 series, Agilent Technologies, USA). The mobile phase was prepared [solvent A: 70:30 (v/v) methanol:1 M ammonium acetate and solvent B: 100% methanol] and programmed (minutes: % solvent A: % solvent B): (0:75:25), (1:50:50), (20:30:70), (25:0:100), (32:0:100) according to Barlow et al. (1997). The column was then reconditioned to original conditions over a further 12 min. Pigment separation was performed through a C8, 3 µm-column (MOS-2 HYPERSIL, Thermo Scientific, USA). The diode array detector was set at 440 nm to detect carotenoids, at 665 nm for chlorophylls and pheopigments. Pigments were identified by comparing their retention time and absorption spectra with those of pure standard pigments (DHI LAB products, Denmark). Each pigment concentration was calculated by relating the peak area of its chromatogram with the corresponding area of calibrated standards using ChemStation software (version A.10.02, Agilent technologies).

Microbial C fixation by phototrophs and microbial respiration were measured directly in the field in respiration chambers using oxygen microsensors (FireStings, PyroScience, USA). Net oxygen exchange (NOE) was measured for 20 min using a transparent chamber while respiration (R, oxygen consumption) was measured for 20 min in a dark chamber. Net microbial C fixation (NMF, or oxygen production) was quantified as: NMF = NOE – R. Microbial C fixation values were then standardized by the total abundance of phototrophs and respiration values by total microbial abundance, and assigned to each microbial species. As microbial metabolic processes relate to the mass of microorganisms (Johnston and Sibly, 2018), we corrected the standardized value of microbial C fixation and respiration per cell by the biomass of each species using the allometric scaling exponent for microbes (0.74) and microfauna (0.66).

We quantified enzymatic activities as a proxy for microbial activities. Specifically, we tested for three hydrolytic and two oxidative C-degrading enzymes, one hydrolytic C/N-

degrading enzyme, three aminopeptidases (N-cycle) and one acid-phosphatase (P-cycle; see Figure S3). Enzyme activities were measured as relative enzyme activity in top *Sphagnum* segments (0-3 cm) under saturating substrate conditions and constant temperature at 25°C. Enzyme activities were quantified in 96-wells microplates following Jassey et al. (2012) and Jassey et al. (2016). Fluorescence of hydrolases was read spectrophotometrically at excitation wavelength 365 nm and emission wavelength 450 nm on a BioTek SynergyMX plate reader (BioTek Instruments Inc, Vermont, USA), while oxidation rates were quantified spectrophometrically at 600 nm. All hydrolitic activities were expressed as micromoles per gram dry weight per min (μmol $min^{-1}g^{-1}$ DW) and all oxidative activities as nanomoles per gram dry weight per min (nmol $min^{-1}g^{-1}$ DW).

Morphology and locomotion traits of microbial species were taken from Biddanda et al. (2015) and Fiore-Donno et al. (2019). Nitrogen fixation and nitrogenase enzyme activity of cyanobacteria were obtained from Eigemann et al. (2019); Issa et al. (2014); and Van Den Elzen et al. (2020). Reproduction ($ind.d^{-1}$) and predation rates (prey ingested per minute; $ind.min^{-1}$) for each microbial group were obtained from literature (Crotty et al. (2013); Gessner (1997); Loka et al. (2016); Rousk & Bååth (2011). The methanotrophic activity per cell of methanotrophs was obtained from Stępniewska et al. (2018). The response of each microbial group to high temperature and desiccation were taken from (Jassey et al. (2015) and Reczuga et al. (2018). Data about the hunting strategy of protists were taken from both literature (Geisen et al., 2015; Gilbert et al., 2003) and personal observations (V. Jassey personal observations).

All community weighted mean of quantitative traits is shown in Figures S4-S6. Raw data for *Sphagnum* traits, microbial communities and traits, as well as environmental data related to this paper can be accessed through the Figshare repository (DOI: 10.6084/m9.figshare.c.5191493).

Supplementary figures

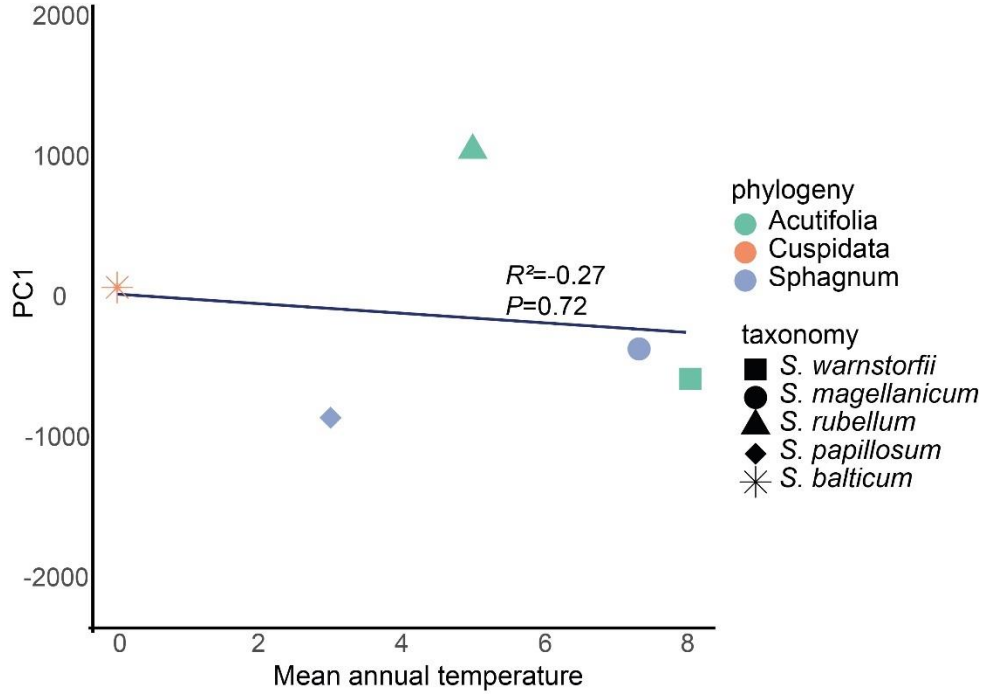


Figure 1. Linear regression analysis on between mean annual temperature in five sites and the first axis of phylogenetic PCA (on all *Sphagnum* traits with *Sphagnum* phylogenetic tree using Brownian motion method). Color codes correspond to *Sphagnum* phylogenetic section (subgenus), icons correspond to *Sphagnum* taxonomy (species), species are listed in the order they were collected in five sites: *Sphagnum* warnstorfii (France), S. magelanicum (Poland), S. rubellum (Estonia), S. papillosum (Finland), S.balticum (Sweden)

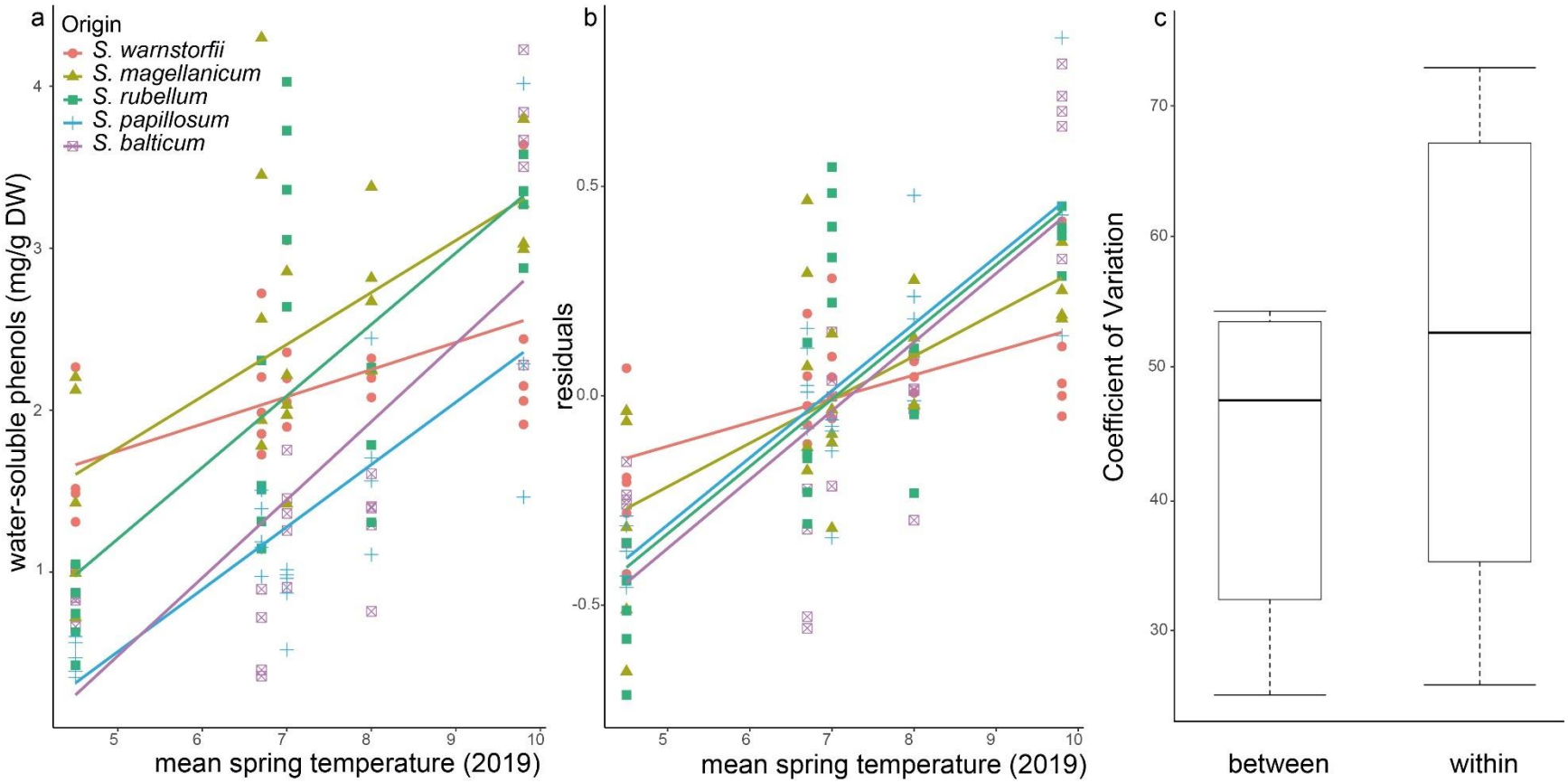


Figure S2. Additional data set of water-soluble phenols concertation in five *Sphagnum* species (the same as used in current study) reciprocally transplanted along a latitudinal gradient (five countries; samples collected in April-May 2019): *Sphagnum warnstorfii* (France), *S. magelanicum* (Poland), *S. rubellum* (Estonia), *S. papillosum* (Finland), *S.balticum* (Sweden). (a) Concentration of water-soluble phenols in five *Sphagnum* species reciprocally transplanted to different sites (LME: $F_{4,107}$=7.9, P<0.001, R^2=0.22), (b) relationship between mean spring temperature and filtered species effect (residuals data, LME: $F_{1,110}$=115.8, P<0.001, R^2=0.5), (c) LME-based confidence intervals variation for all species at every temperature (between) and individual species at different temperatures (within) (Sytiuk et al., unpublished data).

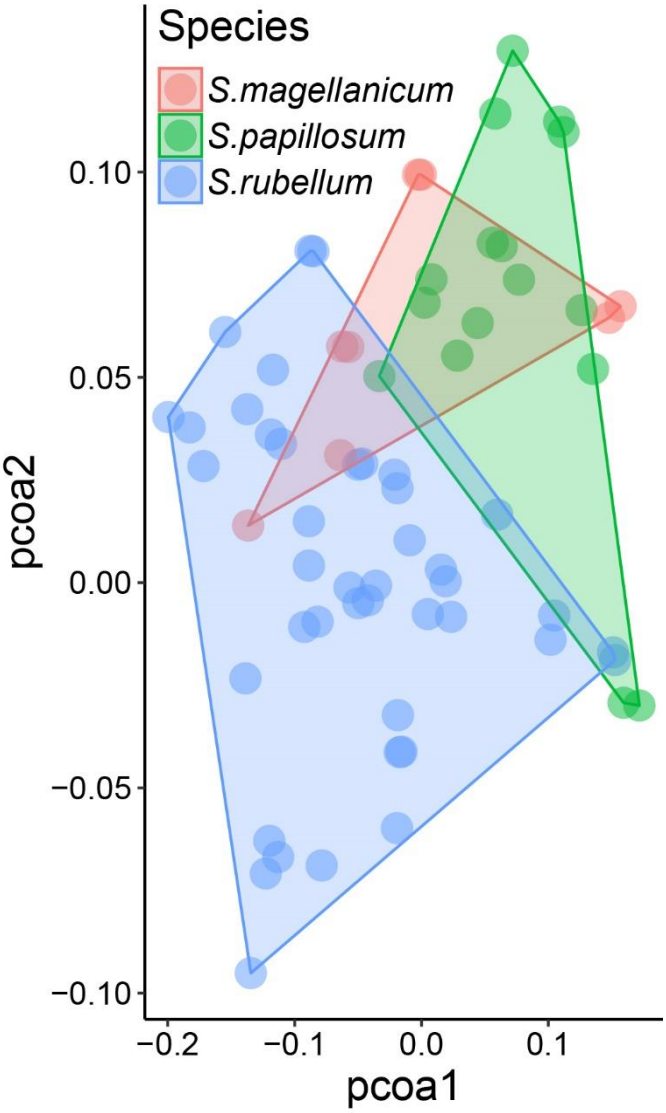


Figure S3. PCoA on metabolomics profiling of three *Sphagnum* species (*S.magellanicum*, *S. rubellum*, *S.papillosum;* Jassey, Allard and Robroek, unpublished data) collected in 56 European *Sphagnum*-dominated peatlands (for sites description see Robroek et al., 2017). *Sphagnum* species were collected in different sites where they were found. We did not find any significant differences among species in terms of metabolite composition (P = 0. 46) .

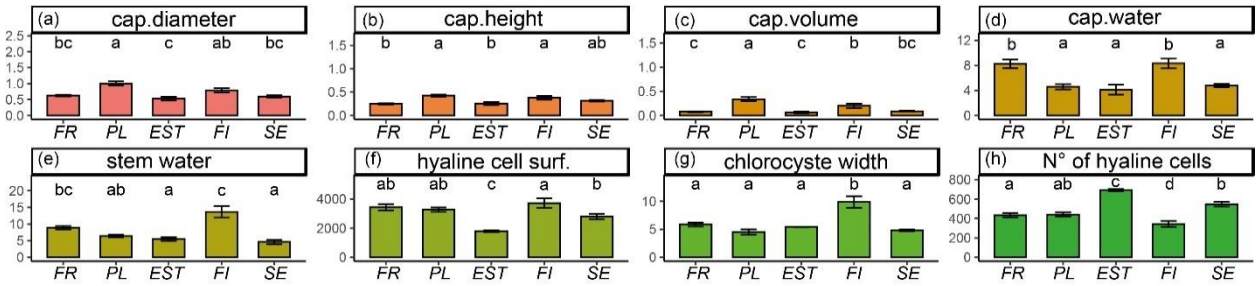


Figure S4. Barplot of anatomical and morphological traits of dominant *Sphagnum* mosses in five sites along the latitudinal gradient. Data represents means and standard errors (SE). *Post-hoc* letters indicate significant differences ($P < 0.05$) between *Sphagnum* species based on Tukey *post-hoc* test. Abbreviations: FR=*Sphagnum warnstorfii* (France), PL=*S. magelanicum* (Poland), EST=*S. rubellum* (Estonia), FI=*S. papillosum* (Finland), SE=*S.balticum* (Sweden). Anatomical traits are given in the following units: capitulum (cap.) diameter and height in cm, volume in cm^3; capitulum and stem water holding capacities in $gH_2O\ g^{-1}$ *Sphagnum* DW, surface of hyaline cell in μm^2, chlorocyste width in μm, number (N°) of hyaline cells in mm^{-2}.

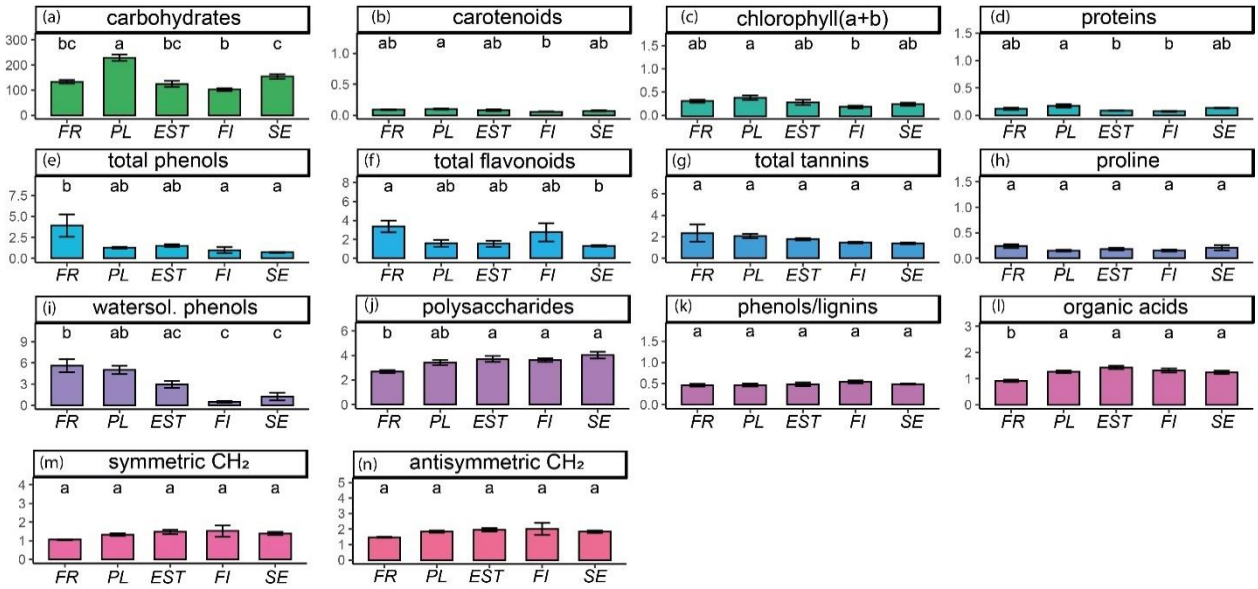


Figure S5. Barplot of metabolites of dominant *Sphagnum* mosses in five sites along the latitudinal gradient. Data represents means and standard errors (SE). *Post-hoc* letters indicate significant differences ($P < 0.05$) between *Sphagnum* species based on Tukey *post-hoc* test. Abbreviations: FR=*Sphagnum warnstorfii* (France), PL=*S. magelanicum* (Poland), EST=*S. rubellum* (Estonia), FI=*S. papillosum* (Finland), SE=*S.balticum* (Sweden), watersol.pehols=water soluble phenols. *Sphagnum* metabolites in panels a-i are expressed in mg of compound g^{-1} *Sphagnum* DW, and panels j-n are expressed as ratio of peaks of compounds to recalcitrant C.

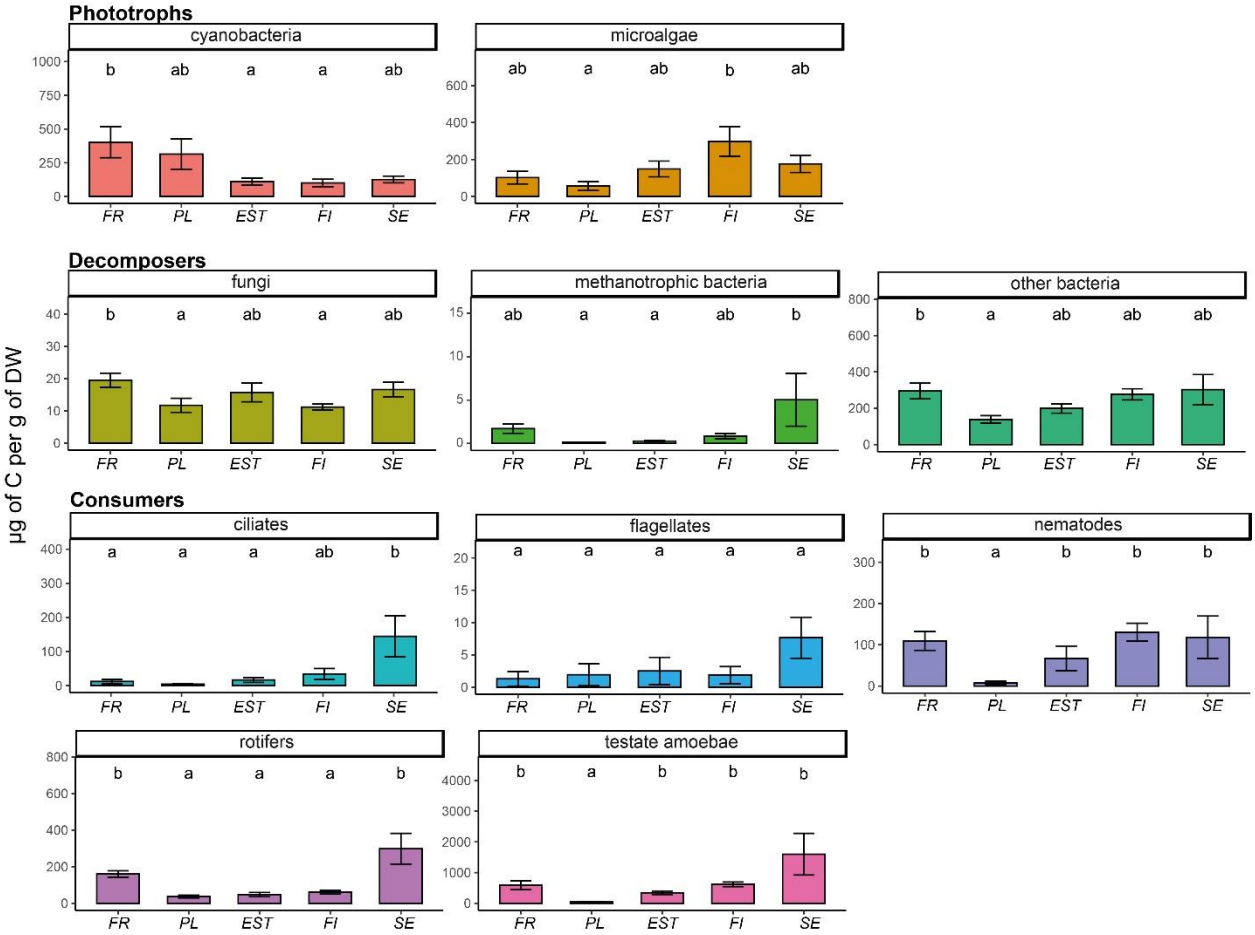


Figure S6. Barplot of microbial biomass in five sites along the latitudinal gradient. Data represents means and standard errors (SE). *Post-hoc* letters indicate significant differences ($P < 0.05$) between *Sphagnum* species based on Tukey *post-hoc* test. Abbreviations: FR=*Sphagnum warnstorfii* (France), PL=*S. magelanicum* (Poland), EST=*S. rubellum* (Estonia), FI=*S. papillosum* (Finland), SE=*S.balticum* (Sweden).

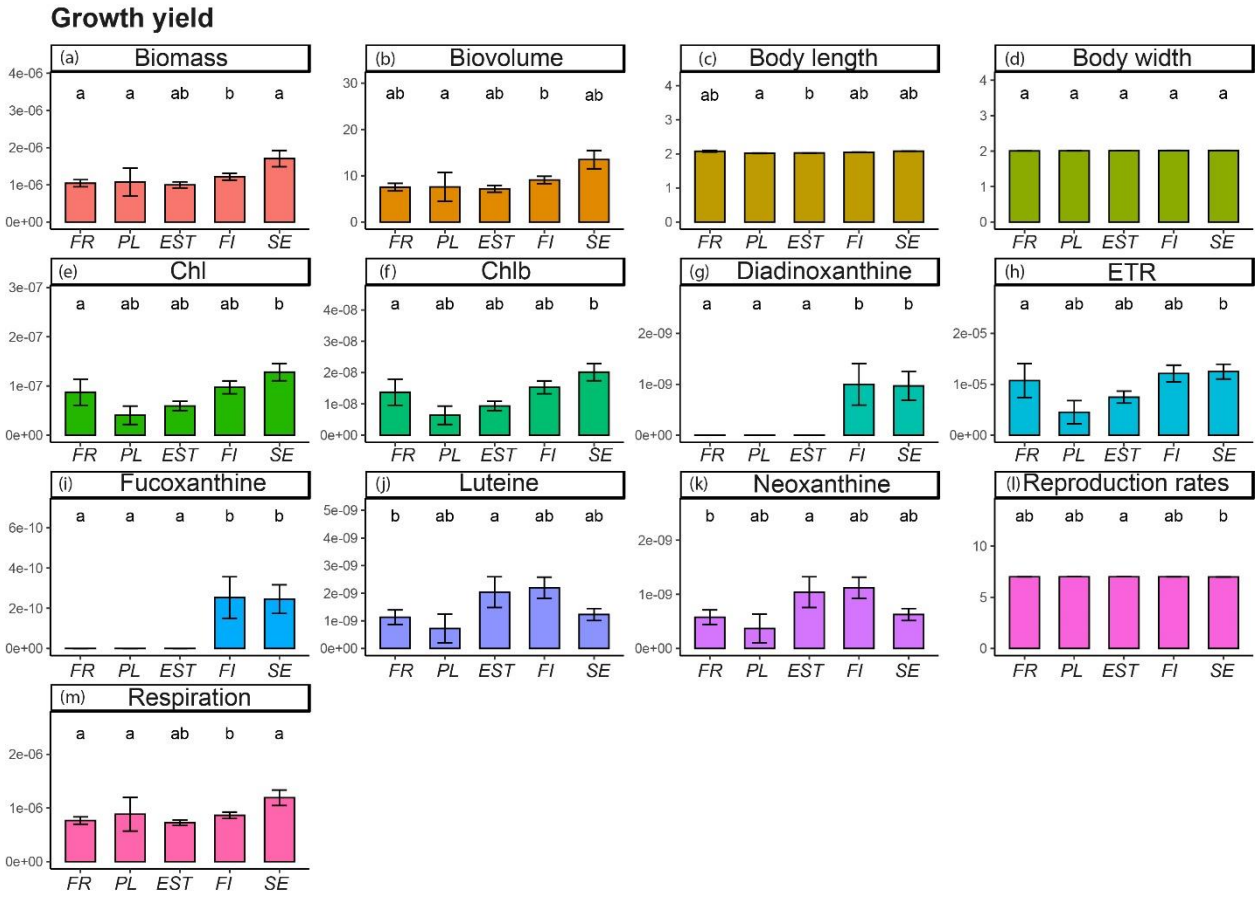


Figure S7. Microbial growth yield trait composition in dominant *Sphagnum* mosses in five sites along the latitudinal gradient. Data represents means and standard errors (SE). *Post-hoc* letters indicate significant differences ($P < 0.05$) between *Sphagnum* species based on Tukey *post-hoc* test. Only quantitative data are displayed. Abbreviations: FR=*Sphagnum warnstorfii* (France), PL=*S. magelanicum* (Poland), EST=*S. rubellum* (Estonia), FI=*S. papillosum* (Finland), SE=*S.balticum* (Sweden). Traits are expressed in following units: biomass in µg C cell^{-1}, biovolume in µm^3, body length and width in µm, Chl (Chlorophyll a + pheophorbid a + pheophytine a) in ng cell^{-1}, microbial pigments (f-k) in ng cell^{-1}, ETR in fmol e$^-$ cell^{-1} s^{-1}, respiration in gCO_2 cell^{-1} s^{-1}, reproduction rates in individual day^{-1}.

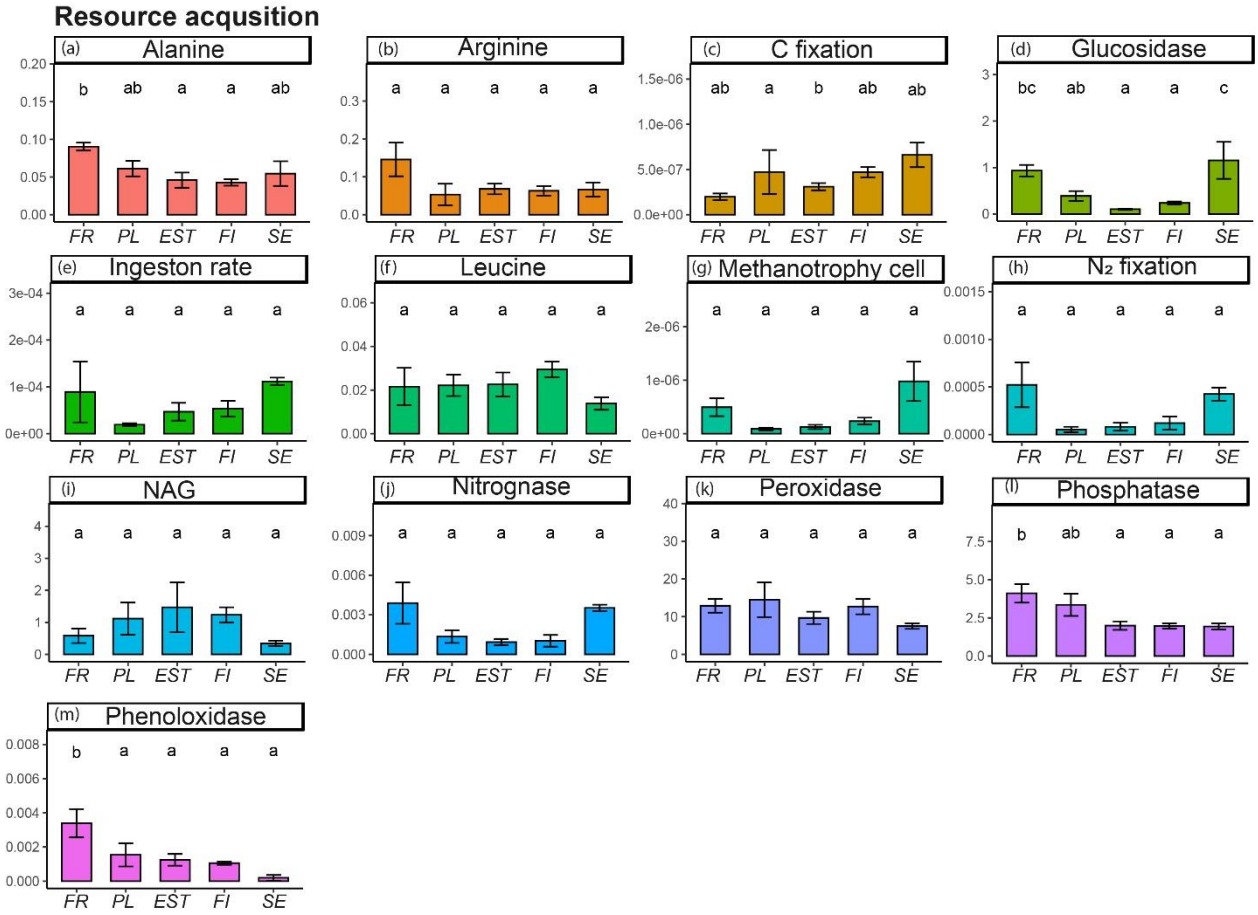


Figure S8. Microbial resource acquisition trait composition in dominant *Sphagnum* mosses in five sites along the latitudinal gradient. Data represents means and standard errors (SE). *Post-hoc* letters indicate significant differences ($P < 0.05$) between *Sphagnum* species based on Tukey *post-hoc* test. Only quantitative data are displayed. Abbreviations: FR=*Sphagnum warnstorfii* (France), PL=*S. magelanicum* (Poland), EST=*S. rubellum* (Estonia), FI=*S. papillosum* (Finland), SE=*S.balticum* (Sweden). Traits are expressed in following units: hydrolases (a,b,d,f,i and L) in μmol min^{-1} g^{-1} DW, C fixation in gCO_2 $cell^{-1}$ s^{-1}, N_2 fixation in nmol $cell^{-1}$ d^{-1}, nitrogenase in nmolC_2H_4 mg^{-1} DW h^{-1}, ingestion rate in consumed cells min^{-1}, methanotrophy cell in nmol h^{-1} $cell^{-1}$, phenoloxidase and peroxidase activities in nmol min^{-1} g^{-1} DW.

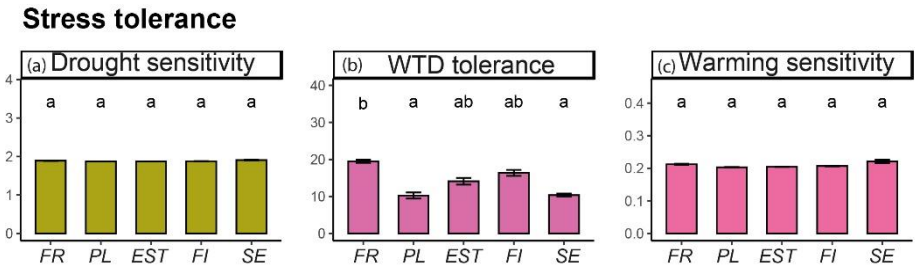


Figure S9. Microbial stress tolerance trait composition in dominant *Sphagnum* mosses in five sites along the latitudinal gradient. Data represents means and standard errors (SE). *Post-hoc* letters indicate significant differences ($P < 0.05$) between *Sphagnum* species based on Tukey *post-hoc* test. Only quantitative data are displayed. Abbreviations: FR=*Sphagnum warnstorfii* (France), PL=*S. magelanicum* (Poland), EST=*S. rubellum* (Estonia), FI=*S. papillosum* (Finland), SE=*S.balticum* (Sweden).

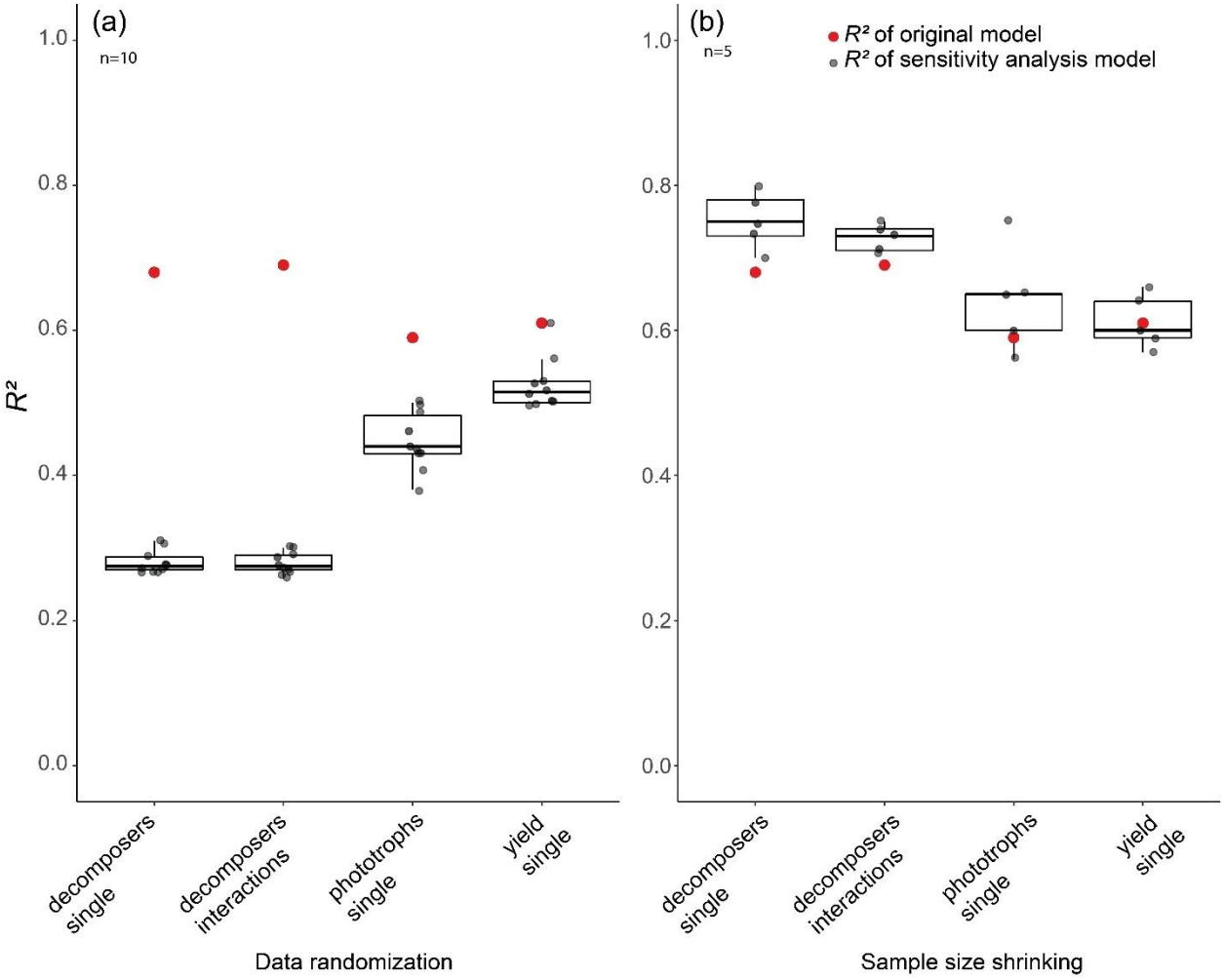


Figure S10. Outputs for two sensitivity analyses with (a) randomized *Sphagnum* trait matrices to break any structure in the data and (b) reduced the entire data set by 20% by randomly removing one replicate from the dataset. Outputs for *Fisher's C* statistic and AIC values are represented in Tables S11-S12.

Supplementary tables

Table S1. Climatic data for the five study sites [France (Counozouls), Poland (Kusowo), Estonia (Männikjärve), Finland (Siikaneva), Sweden (Abisko)] averaged over the period 1960-2018 (WorldClim v2). Sites ordered along the south-north latitudinal gradient.

		France (Counozouls)	**Poland (Kusowo)**	**Esstonia (Männikjärve)**	**Finland (Siikaneva)**	**Sweden (Abisko)**
Annual Mean Temperature	(°C)	7.9	7.3	4.9	2.9	-0.1
Temperature Seasonality (standard deviation *100)	(°C)	54.51	78.52	84.67	86.02	75.15
Max Temperature of Warmest Month	(°C)	21.1	22.4	21.2	20.9	15.5
Min Temperature of Coldest Month	(°C)	-2	-6.8	-9.7	-12.9	-13.3
Mean Temperature of Wettest Quarter	(°C)	9.2	16.9	14.4	12.6	8.9
Mean Temperature of Driest Quarter	(°C)	2	1.8	-1.9	-3.9	-1.5
Mean Temperature of Warmest Quarter	(°C)	15.2	26.9	15.8	14.2	10
Mean Temperature of Coldest Quarter	(°C)	1.5	-3.4	-5.9	-8	-9.3
Annual Precipitation	(mm)	1027	656	623	611	418
Precipitation of Wettest Month	(mm)	11	8.4	7.8	8.1	6.2
Precipitation of Driest Month	(mm)	6.7	3.2	2.9	3	1.8
Precipitation Seasonality (Coefficient of Variation)		1.5	2.7	3.1	3.1	3.8
Precipitation of Wettest Quarter	(mm)	29.2	22.5	21.5	21.9	16.3
Precipitation of Driest Quarter	(mm)	22	10.8	9.6	9.6	6.2
Precipitation of Warmest Quarter	(mm)	24.4	22.5	19.9	21	15.4
Precipitation of Coldest Quarter	(mm)	22.7	12.9	11.5	11.7	8.7

Table S2. Vegetation composition of the five study sites [France (Counozouls), Poland (Kusowo), Estonia (Männikjärve), Finland (Siikaneva), Sweden (Abisko)]. Species relative abundance expressed as % of plants per plot (50 x 30 cm) ± SE. Sites ordered along the south-north latitudinal gradient.

		France (Counozouls)	Poland (Kusowo)	Esstonia (Männikjärve)	Finland (Siikaneva)	Sweden (Abisko)
Mosses	*Polytrichum strictum*	0.36±0.24	0	0	0	0
	Sphagnum balticum	0	0	0	0	61.96±3.21
	Sphagnum rubellum	0	0	34.76±10.19	0	0
	Sphagnum magelanicum	0	37.6±14.2	22.26±4.88	0	0
	Sphagnum fallax	0	25.65±15.82	0	0	0
	Sphagnum fuscum	0	0	20.71±8.71	0	0
	Sphagnum palustre	2.14±1.26	0	0	0	0
	Sphagnum papilosum	0	0	0	73.15±3.15	0
	Sphagnum warnstorfii	30±4.68	0	0	0	0
Vascular plants	*Andromeda polifolia*	0	0.12±0.07	5.65±1.16	3.27±1.05	1.85±0.61
	Empetrum nigrum	0	0	0	0.3±0.13	0.42±0.42
	Vaccinium oxycoccos	0	1.55±0.88	3.81±1.19	1.85±0.8	0
	Carex sp.	6.37±2.02	0	0	0	15.89±3.57
	Drosera rotundifolia	0.3±0.19	0.12±0.07	1.79±0.46	0.71±0.45	0
	Eriophorum vaginatum	0	17.56±1.77	3.57±1.19	6.96±1.29	0
	Molinia caerulea	24.17±5.19	0	0	0	0
	Oxycoccus palustris	0	0.12±0.07	0	0	0
	Potentilla anglica	3.51±1.22	0	0	0	0
	Rubus chamaemorus	0	0	0	0	0.18±0.19
	Ranunculus sp.	15.83±8.46	0	0	0	0
	Litter	15.3±3.14	15.54±7	5±0.96	12.92±1.13	19.11±1.43

Table S3. Water extractable organic (WEOM) chemistry in five peatlands along a latitude gradient collected in early July 2018. Water extractable organic C (WEOC), water extractable organic N (WEON), water extractable P (WEOP) are expressed per *Sphagnum* dry weight (DW), water extractable organic C quality (WEOCq) is based on spectral slopes. Data represents means and standard errors (SE). *F* and *P*-values based on one-way *ANOVA*, *P*-values in bold indicate significance at $P < 0.05$. *Post-hoc* letters indicate significant differences ($P < 0.05$) between sites based on Tukey *post-hoc* test.

	France (Counozouls)		**Poland (Kusowo)**		**Esstonia (Männikjärve)**		**Finland (Siikaneva)**		**Sweden (Abisko)**		$F_{4,16}$-value	*P*
	Mean	*SE*	*Mean*	*SE*	*Mean*	*SE*	*Mean*	*SE*	*Mean*	*SE*		
WEOC (mg C g^{-1}DW)	3.42^{b}	0.43	11.75^{c}	1.74	5.44^{b}	1.01	1.48^{a}	0.24	4.04^{b}	0.49	26.4	**<0.0001**
WEON (mg N g^{-1}DW)	0.09^{ab}	0.008	0.15^{b}	0.024	0.07^{a}	0.014	0.028^{a}	0.004	0.09^{ab}	0.021	8.6	**0.0006**
WEOP (mg PO_4^{3-} g^{-1}DW)	0.024^{b}	0.002	0.007^{ab}	8E-04	0.006^{ab}	0.001	0.005^{a}	5E-04	0.023^{ab}	0.009	5.3	**0.0066**
WEOCq (nm^{-1})	-0.013^{b}	8E-04	-0.015^{a}	2E-04	-0.015^{a}	3E-04	-0.013^{b}	3E-04	-0.013^{b}	3E-04	9.5	**0.0004**

Table S4. Presence/absence of phylogenetic signal for microbial community structure and microbial traits, as a result of phyloSignal test statistics with Blomberg's K index and *P*-value in phylo4d objects. Significant *P* value (< 0.05) marked in bold.

	Phylogenetic signal	K	*P*-value
Microbial community structure			
Phototrophs			
microalgae	Absent	0.0019	1
cyanobacteria	Absent	0.0056	0.67
Decomposers			
fungi	Absent	0.43	0.064
methanotrophic bacteria	Absent	0.10	0.23
other bacteria	Absent	0.0036	0.72
Consumers			
flagellates	**Present**	**1.11**	**0.034**
testate amoebae	Absent	0.015	0.54
ciliates	Absent	0.051	0.52
rotifers	Absent	0.25	0.23
nematodes	Absent	0.0250	0.456
Total biomass	Absent	0.0023	0.95
Microbial traits			
growth yield	Absent	0.0029	0.88
resource acquisition	Absent	0.0079	0.70
stress tolerance	Absent	0.0027	0.83
Total traits	Absent	0.0017	1

Table S5. Summary of linear effect mixed models testing the *Sphagnum* taxonomy (fixed effect) on *Sphagnum* traits, microbial community composition and microbial traits. F and *P*-values based on one-way ANOVA, values in bold indicate significance at $P < 0.05$.

Sphagnum metabolites

	$F_{4,16}$	*P*
total phenols	**5.26**	**0.007**
total flavonoids	**3.09**	**0.046**
total tannins	1.44	0.265
carbohydrates	**18.58**	**<0.001**
carotenoids	2.95	0.053
chlorophyll(a+b)	**3.13**	**0.044**
proline	1.59	0.226
proteins	**5.34**	**0.006**
water-soluble phenols	14.38	**<0.001**
polysaccharides	**6.60**	**0.003**
phenols/lignins	0.75	0.575
organic acids	10.27	**<0.001**
symmetric CH_2	1.69	0.201
antisymmetric CH_2	1.75	0.189

Sphagnum anatomical and morphological traits

	$F_{4,16}$	*P*
capitulum diameter	**27.67**	**<0.001**
capitulum height	**8.53**	**<0.001**
capitulum volume	**23.15**	**<0.001**
capitulum water-holding capacity	**10.61**	**<0.001**
stem water-holding capacity	**18.08**	**<0.001**
chlorocyste width	**14.49**	**<0.001**
number of hyaline cells	**26.40**	**<0.001**
surface of hyaline cell	**13.18**	**<0.001**

Microbial biomass

	$F_{4,16}$	*P*
microalgae	**4.77**	**0.01**
cyanobacteria	**4.78**	**0.01**
flagellates	0.85	0.52

Table S5 continued. Summary of linear effect mixed models testing the *Sphagnum* taxonomy (fixed effect) on *Sphagnum* traits, microbial community composition and microbial traits.

testate amoebae	**17.86**	**<0.001**
nematodes	**7.35**	**0.001**
other bacteria	**3.52**	**0.03**
fungi	**3.43**	**0.03**
methanotrophic bacteria	**4.59**	**0.01**

Microbial growth yield traits

	$F_{4,16}$	P
biomass	**5.03**	**0.008**
biovolume	**5.57**	**0.005**
body length	**3.22**	**0.04**
Body width	2.26	0.108
Chl	**3.6**	**0.028**
Chl b	**3.6**	**0.028**
diadinoxanthine	**20.01**	**<0.001**
ETR	**3.56**	**0.029**
fucoxanthine	**20.01**	**<0.001**
luteine	**3.96**	**0.02**
neoxanthine	**3.96**	**0.02**
reproduction rates	**4.22**	**0.016**
respiration	**5**	**0.008**

Microbial resource acquisition traits

	$F_{4,16}$	P
alanine	**3.46**	**0.032**
arginine	2.08	0.131
C fixation	**5**	**0.008**
glucosidase	**10.52**	**<0.001**
ingeston rate	2.14	0.123
methanotrophy cell	2.98	0.051
N_2 fixation	1.61	0.22
NAG	1.31	0.307
Nitrognase	1.33	0.302
peroxidases	1.24	0.333
phosphatases	**6.22**	**0.003**
phenoloxidases	**8.24**	**<0.001**
Leucine	1.05	0.414

Table S5 continued. Summary of linear effect mixed models testing the *Sphagnum* taxonomy (fixed effect) on *Sphagnum* traits, microbial community composition and microbial traits.

Microbial stress tolerance traits	$F_{4,16}$	P
drought sensitivity	0.46	0.766
water table depth tolerance	**7.03**	**0.002**
warming sensitivity	2.79	0.062

Table S6. Benefits gained (ΔR^2) when *Sphagnum* (*S.*) traits were added to piecewise SEMs. For *a priori* diagrams see Fig.1.

	R^2 without *S.* traits	R^2 with *S.* traits	ΔR^2	Model type
Total microbial structure	0.64	0.57	0.07	single
decomposers	0.68	0.27	0.41	single
phototrophs	0.59	0.4	0.19	single
consumers	0.78	0.73	0.05	single
Total traits composition	0.64	0.57	0.08	single
growth yield	0.61	0.51	0.1	single
resource acquisition	0.51	0.42	0.09	single
stress tolerance	0.32	0.29	0.03	single
Total microbial structure	0.77	0.76	0.01	interactions
decomposers	0.69	0.27	0.42	interactions
phototrophs	0.86	0.87	-0.01	interactions
consumers	0.78	0.73	0.05	interactions
Total traits composition	0.58	0.51	0.07	interactions
growth rate	0.83	0.76	0.07	interactions
resource acquisition	0.82	0.77	0.05	interactions
stress tolerance	0.7	0.61	0.09	interactions

Table S7. Outputs of piecewice SEM first of four models: single model without *Sphagnum* traits. For *a priori* model diagram see Fig. 1. SEMs depict pathways by which climate and local conditions [standardized data of annual precipitation (clim1), maximum temperature of the warmest quarter (clim2), *Sphagnum* water content (local1), PC1 of WEOM chemistry (local2), PCoA1 of *Sphagnum* anatomical and morphological traits (anatomical) and metabolites] can affect microbial community structure [PCoA1 for total microbial biomass (microbial BM); Hellinger transformation for decomposers, consumers, phototrophs] and microbial traits [PCoA axes 1 for total microbial traits (microbial traits), growth yield (yield), resource acquisition (resource), stress tolerance (stress)]. Significant paths marked in bold, * P<0.05, ** P<0.01, *** P < 0.001.

Decomposers biomass (*Fisher's C* = 2.571, *P*-value = 0.0632, *Df* = 4)

	Std.Error	*Std.Estimate*	
clim2→decomposers	**0.025**	**0.6892**	*
local1→decomposers	0.0391	-0.2889	
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***

Phototrophs biomass (*Fisher's C* = 14.952, *P*-value = 0.134, *Df* = 10)

	Std.Error	*Std.Estimate*	
clim1→phototrophs	0.0297	0.2471	
local1→phototrophs	**0.0467**	**0.5904**	**
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***

Consumers biomass (*Fisher's C* = 12.551, *P*-value = 0.128, *Df* = 8)

	Std.Error	*Std.Estimate*	
clim1→consumers	**0.03**	**-0.2975**	*
local1→consumers	**0.0629**	**-0.354**	*
clim2→consumers	**0.0405**	**-0.5599**	**
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***

Growth yield (*Fisher's C* = 8.601, *P*-value = 0.57, *Df* = 10)

	Std.Error	*Std.Estimate*	
clim1→yield	**0.0296**	**-0.6085**	***
local1→yield	**0.0464**	**-0.4056**	*
clim2→local1	**0.0992**	**0.6676**	

Table S7 continued. Outputs of piecewice SEM first of four models: single model without *Sphagnum* traits.

clim2→local2	**0.1413**	**-0.71**	***

Stress tolerance (*Fisher's C* = 15.364, *P*-value = 0.119, *Df* = 10)

	Std.Error	*Std.Estimate*	
clim1→stress	0.0377	0.333	
local1→stress	0.0595	-0.3173	
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***

Resource acquisition (*Fisher's C* = 17.463, *P*-value = 0.133, *Df* = 12)

	Std.Error	*Std.Estimate*	
clim1→resource	**0.0224**	**-0.6554**	***
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***

Overall microbial composition (*Fisher's C* = 23.068, *P*-value = 0.01, *Df* = 10)

	Std.Error	*Std.Estimate*	
clim1→microbial BM	**0.0227**	**0.3392**	*
local1→microbial BM	**0.0355**	**0.6918**	***
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***

Overall microbial trait composition (*Fisher's C* = 11.432, *P*-value = 0.325, *Df* = 10)

	Std.Error	*Std.Estimate*	
clim1→microbial traits	**0.0224**	**-0.6342**	***
local1→microbial traits	**0.0351**	**-0.3702**	*
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***

Table S8. Outputs of piecewice SEM second of four models: single model with *Sphagnum* traits. For *a priori* model diagram see Fig. 1. SEMs depict pathways by which climate and local conditions [standardized data of annual precipitation (clim1), maximum temperature of the warmest quarter (clim2), *Sphagnum* water content (local1), PC1 of WEOM chemistry (local2), PCoA1 of *Sphagnum* anatomical and morphological traits (anatomical) and metabolites] can affect microbial community structure [PCoA1 for total microbial biomass (microbial BM); Hellinger transformation for decomposers, consumers, phototrophs] and microbial traits [PCoA axes 1 for total microbial traits (microbial traits), growth yield (yield), resource acquisition (resource), stress tolerance (stress)]. Significant paths marked in bold, * P<0.05, ** P<0.01, *** P < 0.001.

Consumers biomass (*Fisher's C* = 16.441, *P*-value = 0.172, *Df* = 12)

	Std.Error	*Std.Estimate*	
anatomical→consumers	**0.1379**	**-0.2302**	*
clim1→consumers	**0.0279**	**-0.2451**	*
local1→consumers	**0.0603**	**-0.4423**	**
clim2→consumers	**0.0398**	**-0.443**	**
clim2→anatomical	0.0572	0.4771	
local1→anatomical	0.0895	-0.3858	
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***

Phototrophs biomass (*Fisher's C* = 18.567, *P*-value = 0.55, *Df* = 20)

	Std.Error	*Std.Estimate*	
metabolites→phototrophs	0.2172	0.4079	
anatomical→phototrophs	0.1204	0.2769	
clim1→phototrophs	**0.0343**	**0.4536**	*
local1→phototrophs	**0.0443**	**0.7516**	***
clim1→metabolites	**0.0256**	**-0.6143**	***
local1→metabolites	**0.0401**	**-0.3332**	*
clim2→anatomical	0.0572	0.4771	
local1→anatomical	0.0895	-0.3858	
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***

Decomposers biomass (*Fisher's C* = 13.751, *P*-value = 0.468, *Df* = 14)

	Std.Error	*Std.Estimate*	
metabolites→decomposers	**0.0795**	**-0.7055**	***
clim2→decomposers	**0.017**	**0.9284**	***
local1→decomposers	**0.0282**	**-0.6745**	**
clim1→metabolites	**0.0256**	**-0.6143**	***

Table S8 continued. Outputs of piecewice SEM second of four models: single model with *Sphagnum* traits.

local1→metabolites	**0.0401**	**-0.3332**	*
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***

Growth yield (*Fisher's C* = 13.509, *P*-value = 0.487, *Df* = 14)

	Std.Error	*Std.Estimate*	
metabolites→yield	**0.2192**	**0.4558**	*
clim1→yield	0.035	-0.3286	
local1→yield	0.0457	-0.2567	
clim1→metabolites	**0.0256**	**-0.6143**	***
local1→metabolites	**0.0401**	**-0.3332**	*
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***

Stress tolerance (*Fisher's C* = 17.742, *P*-value = 0.219, *Df* = 14)

	Std.Error	*Std.Estimate*	
metabolites→stress	0.326	0.2052	
clim1→stress	0.0506	0.4591	
local1→stress	0.0668	-0.2467	
clim1→metabolites	**0.0256**	**-0.6143**	***
local1→metabolites	**0.0401**	**-0.3332**	*
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***

Resource acquisition (*Fisher's C* = 18.845, *P*-value = 0.277, *Df* = 16)

	Std.Error	*Std.Estimate*	
metabolites→resource	**0.1549**	**0.4132**	*
clim1→resource	**0.0261**	**-0.403**	*
clim1→metabolites	**0.0256**	**-0.6143**	***
local1→metabolites	**0.0401**	**-0.3332**	*
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***

Overall microbial composition (*Fisher's C* = 24.193, *P*-value = 0.043, *Df* = 14)

	Std.Error	*Std.Estimate*	
anatomical→microbial BM	**0.0992**	**0.2818**	*

Table S8 continued. Outputs of piecewice SEM second of four models: single model with *Sphagnum* traits.

clim1→microbial BM	**0.0212**	**0.2943**	*
local1→microbial BM	**0.0328**	**0.7103**	***
clim2→anatomical	0.0572	0.4771	
local1→anatomical	0.0895	-0.3858	
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***

Overall microbial trait composition (*Fisher's C* = 14.434, *P*-value = 0.418, *Df* = 14)

	Std.Error	*Std.Estimate*	
metabolites→microbial traits	**0.171**	**0.4027**	*
clim1→microbial traits	**0.0273**	**-0.3869**	*
local1→microbial traits	0.0357	-0.2387	
clim1→metabolites	**0.0256**	**-0.6143**	***
local1→metabolites	**0.0401**	**-0.3332**	*
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***

Table S9. Outputs of piecewice SEM third of four models: interaction model without *Sphagnum* traits. For *a priori* model diagram see Fig. 1. SEMs depict pathways by which climate and local conditions [standardized data of annual precipitation (clim1), maximum temperature of the warmest quarter (clim2), *Sphagnum* water content (local1), PC1 of WEOM chemistry (local2), PCoA1 of *Sphagnum* anatomical and morphological traits (anatomical) and metabolites] can affect microbial community structure [PCoA1 for total microbial biomass (microbial BM); Hellinger transformation for decomposers, consumers, phototrophs] and microbial traits [PCoA axes 1 for total microbial traits (microbial traits), growth yield (yield), resource acquisition (resource), stress tolerance (stress)]. Significant paths marked in bold, * P<0.05, ** P<0.01, *** P < 0.001.

Full model, microbial and traits interactions (*Fisher's C* = 38.656, *P*-value = 0.194, *Df* = 32)

	Std.Error	*Std.Estimate*	
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***
local1→decomposers	0.0449	-0.2376	
clim2→decomposers	**0.0299**	**0.7505**	*
consumers→decomposers	0.1187	0.1267	
local2→phototrophs	**0.0225**	**0.3329**	*
consumers→phototrophs	**0.0812**	**-1.1473**	***
local1→consumers	**0.0629**	**-0.354**	*
clim1→consumers	**0.03**	**-0.2975**	*
clim2→consumers	**0.0405**	**-0.5599**	**
decomposers→yield	**0.3209**	**-0.4086**	*
phototrophs→yield	0.3031	0.3723	
consumers→yield	0.2774	0.5143	
stress→yield	0.1264	-0.0968	
resource→yield	**0.2113**	**0.627**	***
local2→yield	0.0376	0.1946	
clim2→yield	0.0506	0.162	
decomposers→resource	0.2006	0.1072	
phototrophs→resource	0.2202	-0.135	
consumers→resource	0.182	-0.161	
stress→resource	**0.089**	**0.43**	**
yield→resource	**0.1255**	**0.6143**	**
local2→resource	0.025	-0.26	
clim1→resource	**0.0222**	**-0.4849**	**
decomposers→stress	0.4066	0.2655	
phototrophs→stress	0.4803	-0.2705	
consumers→stress	0.3994	-0.1702	
resource→stress	**0.3864**	**0.827**	**
yield→stress	0.328	-0.1421	
local2→stress	0.0528	0.3105	

Table S9continued. Outputs of piecewice SEM third of four models: interaction model without *Sphagnum* traits.

clim1→stress	**0.04**	**0.7923**	**

Full model on summed microbial biomass and traits (summed) (*Fisher's C* = 15.003, *P*-value = 0.241, *Df* = 12)

	Std.Error	*Std.Estimate*	
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***
local1→microbial BM	0.0354	0.2869	
clim2→microbial BM	**0.0228**	**0.6077**	***
clim1→microbial BM	**0.017**	**0.4209**	***
microbial BM→microbial traits	0.2147	-0.1084	
local1→microbial traits	0.0526	-0.2952	
clim1→microbial traits	**0.0258**	**-0.5975**	**

Table S10. Outputs of piecewice SEM fourth of four models: interaction model with *Sphagnum* traits. For *a priori* model diagram see Fig. 1. SEMs depict pathways by which climate and local conditions [standardized data of annual precipitation (clim1), maximum temperature of the warmest quarter (clim2), *Sphagnum* water content (local1), PC1 of WEOM chemistry (local2), PCoA1 of *Sphagnum* anatomical and morphological traits (anatomical) and metabolites] can affect microbial community structure [PCoA1 for total microbial biomass (microbial BM); Hellinger transformation for decomposers, consumers, phototrophs] and microbial traits [PCoA axes 1 for total microbial traits (microbial traits), growth yield (yield), resource acquisition (resource), stress tolerance (stress)]. Significant paths marked in bold, * P<0.05, ** P<0.01, *** P < 0.001.

Full model, microbial and traits interactions (*Fisher's C* = 37.507, *P*-value = 0.862, *Df* = 48)

	Std.Error	*Std.Estimate*	
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***
clim1→metabolites	**0.0256**	**-0.6143**	***
local1→metabolites	**0.0401**	**-0.3332**	*
clim2→anatomical	0.0572	0.4771	
local1→anatomical	0.0895	-0.3858	
local1→decomposers	**0.0304**	**-0.5871**	**
clim2→decomposers	**0.0199**	**1.0472**	***
consumers→decomposers	0.0763	0.2354	
metabolites→decomposers	**0.0792**	**-0.72**	***
local2→phototrophs	**0.0232**	**0.3337**	*
consumers→phototrophs	**0.0883**	**-1.1723**	***
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***
clim1→metabolites	**0.0256**	**-0.6143**	***
local1→metabolites	**0.0401**	**-0.3332**	*
clim2→anatomical	0.0572	0.4771	
local1→anatomical	0.0895	-0.3858	
local1→decomposers	**0.0304**	**-0.5871**	**
anatomical→phototrophs	0.0718	-0.0163	
metabolites→phototrophs	0.0893	0.0752	
local1→consumers	**0.0666**	**-0.5532**	**
clim1→consumers	**0.0363**	**-0.3763**	*
clim2→consumers	**0.0408**	**-0.3953**	*
anatomical→consumers	0.1392	-0.2207	
metabolites→consumers	0.2292	-0.2215	
decomposers→yield	**0.2679**	**-0.3649**	*
phototrophs→yield	0.2516	0.3872	
consumers→yield	0.231	0.5925	
stress→yield	0.1061	-0.1452	
resource→yield	**0.1774**	**0.6828**	***

Table S10 continued. Outputs of piecewice SEM fourth of four models: interaction model with *Sphagnum* traits.

local2→yield	0.0312	0.1949	
clim2→yield	0.0421	0.1156	
anatomical→yield	**0.088**	**0.2742**	*
decomposers→resource	0.1804	0.1623	
phototrophs→resource	0.1971	-0.2248	
consumers→resource	0.1658	-0.3411	
stress→resource	**0.0792**	**0.4023**	**
yield→resource	**0.1197**	**0.7658**	***
local2→resource	0.0221	-0.2553	
clim1→resource	**0.0207**	**-0.3743**	*
anatomical→resource	**0.0684**	**-0.2453**	*
decomposers→stress	0.4184	0.306	
phototrophs→stress	0.5016	-0.3684	
consumers→stress	0.4286	-0.2049	
resource→stress	**0.4423**	**0.7504**	*
yield→stress	0.3543	-0.3668	
local2→stress	0.0493	0.3526	
clim1→stress	**0.0376**	**0.8255**	***
anatomical→stress	0.1591	0.1633	
metabolites→stress	0.2948	0.3833	
clim2→yield	**0.0421**	**0.1156**	
anatomical→yield	**0.088**	**0.2742**	*
decomposers→resource	0.1804	0.1623	
phototrophs→resource	0.1971	-0.2248	
consumers→resource	0.1658	-0.3411	
stress→resource	**0.0792**	**0.4023**	**
yield→resource	**0.1197**	**0.7658**	***
local2→resource	0.0221	-0.2553	
clim1→resource	**0.0207**	**-0.3743**	*
anatomical→resource	**0.0684**	**-0.2453**	*
decomposers→stress	0.4184	0.306	
phototrophs→stress	0.5016	-0.3684	

Full model on summed microbial biomass and traits (summed) (*Fisher's C* = 26.49, *P*-value = 0.436, *Df* = 26)

	Std.Error	*Std.Estimate*	
clim2→local1	**0.0992**	**0.6676**	***
clim2→local2	**0.1413**	**-0.71**	***
clim1→metabolites	**0.0256**	**-0.6143**	***
local1→metabolites	**0.0401**	**-0.3332**	*
clim2→anatomical	0.0572	0.4771	

Table S10 continued. Outputs of piecewice SEM fourth of four models: interaction model with *Sphagnum* traits.

local1→anatomical	0.0895	-0.3858	
anatomical→microbial BM	0.0859	0.1219	
local1→microbial BM	**0.0372**	**0.3382**	*
clim2→microbial BM	**0.0247**	**0.5427**	**
clim1→microbial BM	**0.0174**	**0.3928**	**
microbial BM→microbial traits	0.1985	-0.1477	
local1→microbial traits	0.0517	-0.1329	
clim1→microbial traits	0.0304	-0.33	
metabolites→microbial traits	**0.1738**	**0.4138**	*

Table S11. Outputs of piecewice SEM sensitivity analysis with randomized *Sphagnum* trait matrices to break any structure in the data

Decomposers single

model	*Fisher's C*	*Df*	*P*	AIC
original	**13.751**	**14**	**0.468**	**51.751**
1	17.218	14	0.245	55.218
2	22.206	14	0.074	60.206
3	17.579	14	0.227	55.579
4	16.022	14	0.312	54.022
5	15.765	14	0.328	53.765
6	16.35	14	0.292	54.35
7	19.907	14	0.133	57.907
8	18.056	14	0.204	56.056
9	18.939	14	0.167	56.939
10	19.145	14	0.159	57.145

Decomposers interaction

original	**37.507**	**48**	**0.862**	**185.507**
1	47.584	48	0.49	195.584
2	50.069	48	0.391	198.069
3	48.086	48	0.469	196.086
4	57.748	48	0.158	205.748
5	51.142	48	0.351	199.142
6	60.233	48	0.111	208.233
7	56.5	48	0.187	204.5
8	51.62	48	0.334	199.62
9	63.646	48	0.065	211.646
10	48.841	48	0.439	196.841

Phototrophs single

original	**18.567**	**20**	**0.55**	**68.567**
1	26.077	20	0.163	76.077
2	29.014	20	0.087	79.014
3	21.962	20	0.343	71.962
4	17.623	20	0.612	67.623
5	24.633	20	0.216	74.633
6	26.219	20	0.159	76.219
7	21.184	20	0.386	71.184
8	23.544	20	0.263	73.544
9	25.429	20	0.186	75.429
10	28.008	20	0.109	78.008

Table S11 continued. Outputs of piecewice SEM sensitivity analysis with randomized *Sphagnum* trait matrices to break any structure in the data

Yield single				
model	*Fisher's C*	*Df*	*P*	AIC
original	**13.509**	**14**	**0.487**	**51.509**
1	16.316	14	0.294	54.316
2	19.092	14	0.161	57.092
3	16.206	14	0.301	54.206
4	10.507	14	0.724	48.507
5	12.87	14	0.537	50.87
6	11.603	14	0.638	49.603
7	11.562	14	0.641	49.562
8	12.954	14	0.53	50.954
9	12.924	14	0.533	50.924
10	14.02	14	0.448	52.02

Table S12. Outputs of piecewice SEM sensitivity analysis with reduced the entire data set by 20% by randomly removing one replicate from the dataset.

Decomposers single

model	*Fisher's C*	*Df*	*P*	AIC
original	**13.751**	**14**	**0.468**	**51.751**
1	10.988	14	0.687	48.988
2	13.913	14	0.456	51.913
3	14.179	14	0.436	52.179
4	9.201	14	0.818	47.201
5	5.73	14	0.973	43.730

Decomposers interaction

original	**37.507**	**48**	**0.862**	**185.507**
1	39.861	48	0.792	187.861
2	25.719	48	0.997	173.719
3	40.731	48	00762	188.731
4	42.063	48	0.714	190.063
5	51.914	48	0.324	199.914

Phototrophs single

original	**18.567**	**20**	**0.55**	**68.567**
1	19.906	20	0.594	67.906
2	15.876	20	0.724	65.876
3	14.905	20	0.782	64.905
4	22.098	20	0.335	72.098
5	20.065	20	0.454	70.065

Yield single

model	*Fisher's C*	*Df*	*P*	AIC
original	**13.509**	**14**	**0.487**	**51.509**
1	12.214	14	0.589	50.214
2	14.175	14	0.437	52.175
3	20.376	14	0.119	58.376
4	12.361	14	0.577	50.361
5	19.442	14	0.149	57.442

Chapter 5. Climate change and seasonality effects on *Sphagnum* metabolite plasticity and their linkages with peatland carbon uptake

In this chapter, I explored how seasonal patterns of *Sphagnum* metabolites respond to climate changes, and how they influence peatland C uptake in return. My main questions were: what are the patterns of *Sphagnum* metabolites from different species in response to climate seasonality? When facing a new climate, will the plastic response of *Sphagnum* species follow the same directions? How climate-induced shifts in *Sphagnum* metabolites will feedback to ecosystem processes of carbon assimilation?

To fulfill this aim, I used a reciprocal transplantation along a latitudinal gradient spanning five countries (thus emulating shifts in climate conditions) with diverse environmental conditions to evaluate the responses of metabolites and gross ecosystem productivity (GEP) in five *Sphagnum* species. In addition to the reciprocal transplantation experiment, I performed seasonal monitoring to investigate how transplanted cores respond to altered climate seasonality. To characterize *Sphagnum* metabolite plasticity, we used reaction norms that are the graphical representation of the phenotype variation in the response to environmental changes.

All five *Sphagnum* species, when transplanted to new sites, showed similar responses of metabolite concentrations and GEP over all seasons. In addition to seasonal variability, transplantation towards warmer conditions benefited to *Sphagnum* metabolites and GEP, which all increased. *Sphagnum* species were very plastic in response to temperature and precipitation and their reaction norms had similar slope and curvature. Reaction norms of *S. balticum* (Sweden) and *S. papillosum* (Finland) were grouped together, while those of *S. warnstorfii* (France), *S. magellanicum* (Poland) and *S. rubellum* (Estonia) were closer to each other, but the distance between reaction norm curves were changing over the time. I found that *Sphagnum* metabolite plasticity led to increased C uptake, especially in the early and late growing season. This suggests that important linkages between *Sphagnum* metabolites and C-related processes were the most prominent in spring and autumn.

This chapter shows that our results bring information about the dynamics of *Sphagnum* metabolites, not only at their home site, but also when transplanted along a latitudinal gradient to emulate new climates and seasonal patterns. These results have important implications for understanding the plasticity of *Sphagnum* metabolites and how it will feedback to C assimilation in peatlands under future climate warming.

Climate change and seasonality effects on *Sphagnum* metabolite plasticity and their linkages with peatland carbon uptake

Anna Sytiuk[1]*, Regis Céréghino[1], Samuel Hamard[1], Honorine Geissel[1], Ellen Dorrepaal[3], Martin Küttim[4], Mariusz Lamentowicz[5], Bjorn J.M. Robroek[6,7], Eeva-Stiina Tuittila[8], Vincent E.J. Jassey[1]

In preparation for Journal of Ecology

[1]Laboratoire Ecologie Fonctionnelle et Environnement, Université de Toulouse, UPS, CNRS, Toulouse, France,[3]Climate Impacts Research Centre, Department of Ecology and Environmental Science, Umeå University, SE-981 07, Abisko, Sweden,[4]Institute of Ecology, School of Natural Sciences and Health, Tallinn University, Uus-Sadama 5, 10120 Tallinn, Estonia,[5]Climate Change Ecology Research Unit, Faculty of Geographical and Geological Sciences, Adam Mickiewicz University in Poznań, Bogumiła Krygowskiego 10, 61-680 Poznań, Poland,[6]Aquatic Ecology & Environmental Biology, Institute for Water and Wetland Research, Faculty of Science, Radboud University Nijmegen, AJ 6525 Nijmegen, The Netherlands,[7]Biological Sciences, Faculty of Natural and Environmental Sciences, Institute for Life Sciences, University of Southampton, Southampton SO17 1BJ, UK, [8]School of Forest Sciences, Joensuu campus, University of Eastern Finland, Finland.

Abstract

Peatlands store one third of global carbon, which is due to *Sphagnum* mosses presence that easily facilitate peatland harsh environmental conditions and shape their habitat by possessing unique morphological and biochemical (metabolites) traits. Phenotypic plasticity allows organism to cope with rapid environmental changes. Uncertainties in the response of peatlands facing climate changes questions how *Sphagnum* traits, *e.g.* metabolites, feedback to peatland primary productivity. We used a reciprocal transplantation along a latitudinal gradient spanning five countries (thus emulating shifts in climate conditions) to evaluate the responses of metabolites and gross ecosystem productivity (GEP) in five *Sphagnum* species. All five *Sphagnum* species, when transplanted to new sites, showed similar responses of metabolites concentrations and GEP over all seasons. When *Sphagnum* were transplanted to warmer sites they exhibited higher rates of GEP and metabolite concentrations. We found that five *Sphagnum* species were very plastic in response to temperature and precipitation and their reaction norms had similar slope and curvature, suggesting that species originating from similar environments show similar responses to new climate conditions. We show important linkages between *Sphagnum* metabolites and C-related processes, which were the most prominent in spring and autumn. Our results bring information about the dynamics of *Sphagnum* metabolites, not only at their home site, but also when transplanted along a latitudinal gradient to emulate new climates and seasonal patterns. Our results have important implications for understanding the plasticity of *Sphagnum* metabolites and how it will feedback to C assimilation in peatlands under future climate warming.

Key words: *Sphagnum*, metabolites, reciprocal transplantation, climate change, trait plasticity, reaction norms

5.1. Introduction

Global temperature has increased by 1°C compared to the pre-industrial era (Arndt et al., 2020) and precipitation patterns have been also facing interannual and seasonal variability, resulting in more frequent extreme events (Fischer and Knutti, 2016; Medvigy and Beaulieu, 2012). Rapid climate warming and associated environmental changes are anticipated to influence most of the biomes in the northern hemisphere, with the most pronounced effects occurring at high northern latitudes (Ljungqvist et al., 2016; Swindles et al., 2019). Range shifts associated with climatic changes have been demonstrated for many plant species in the short (Chen et al., 2011) and the long term (Lamentowicz et al., 2019). The drift of seasonal events and variability of season duration can affect the plant's adaptation to established seasonal variability (Stevenson et al., 2015; Visser and Both, 2005). Subsequently, phenological mismatches can arise between a species and its environment or even between multiple species (Both et al., 2009; Visser and Both, 2005). As climate may affect plant development, directly or indirectly, and therefore phenology, as signals for the begging of development (Dahl et al., 2013). Such phenological responses can be driven either by genetic changes in response to selection (Visser, 2008) or by phenotypic plasticity, *i.e.* a single genotype produces alternative phenotypes in response to different environments (Fusco and Minelli, 2010; West-Eberhard, 2008). Also, phenotypic plasticity can serve as a source of sufficient phenotypic variation that may induce adaptive divergence and, subsequently, evolution and speciation (West-Eberhard, 2008). Numerous studies reported that plant are plastic for many ecological traits related to plant anatomy, morphology, physiology as well as developmental timing and reproduction (Sultan, 2000). In the past two decades and in the face of a warming world, plant phenotypic plasticity has become an important subject in ecological and evolutionary research and researches aim to understand the potential role of plasticity for species and population adaptations and resilience (Chevin and Lande, 2011). A precursor in answering this question is to characterize reaction norms (Arnold et al., 2019; Toftegaard et al., 2016), which are the graphical representation of the phenotype variation in the response to environmental changes, including rapid climate changes (Pigliucci, 2001; Sultan, 1987). Plastic responses to environmental changes can be evaluated with reaction norms *via* changes in slope and curvature (Ghalambor et al., 2007; Murren et al., 2014). Merilä and Hendry (2014) assumed that phenological response to climate change in a short-term to medium-term can become apparent mostly due to changes along a plastic response shape (phenotypic plasticity), while long-term responses in shapes can become apparent due to genetic changes. In addition, the response of populations and species as well as traits to

climate change may significantly differ in the extent of their plastic response shapes (Sultan, 2001; Valladares et al., 2000).

Shifts in plant physiology but also in plant community composition (Alexander et al., 2015; Harrison, 2020; Parmesan and Yohe, 2003) are expected to affect ecological processes of carbon cycling and energy balance, with further consequences for atmospheric carbon balances (Goud et al., 2018) that are driven by plants in most of ecosystems around the globe (Elmendorf et al., 2012). Understanding how the functional properties of plants respond to and affect their environment is an important task of functional ecology (Calow, 1987b). By determining essential properties of plant ecophysiology, morphology and life-history strategies, plant functional traits offer a help in determination of how plants respond to environmental factors, influence other trophic levels and affect ecosystem processes (Díaz et al., 2004; Garnier and Navas, 2012b; Grime, 2006; Lavorel and Garnier, 2002). Many morphological and chemical plant traits are commonly used by ecologists (*e.g.* plant height, leaf nitrogen content, specific leaf area; Díaz et al., 2016) to acquire a mechanistic framework for understanding the ecosystem processes related to soil carbon sequestration (De Deyn et al., 2008; Garnier and Navas, 2012b). However, their explanatory power is sometimes insufficient to explain most of the ecosystem properties and thus the prediction of ecosystem processes is limited (Plas et al., 2020). To cope with these limits, recent studies suggested that the use of plant metabolites can improve predictions of ecosystem processes (Sytiuk et al., 2021; Walker et al., 2022, 2019).

Plant kingdom produces a tremendous diversity of metabolites, with an estimated range of 200 000 to 1 000 000 compounds and they serve as substrates or products for enzymatic reactions (Wang et al., 2019). A single plant is capable to produce a set of diverse metabolites — collectively called the metabolome — ranging 5 000 to 10 000 metabolites (Fernie et al., 2004). Metabolites play diverse role in plant growth, survival and coping with environmental stresses (Berini et al., 2018). For example, plants respond to abiotic and biotic factors, such as drought or herbivore attacks, by producing specialized metabolites like alkaloid, terpenoid, and phenolic compounds (*e.g.* Kapoor et al., 2020; Mithöfer and Boland, 2012; Peters et al., 2019; van Dam and Bouwmeester, 2016). Besides, metabolites are mediators of plant-soil interactions by influencing microbial activities with possible consequences for ecosystem processes (Iason et al., 2012b; van Dam and Bouwmeester, 2016). Therefore, plant metabolites can be a key for understanding plant performances in ecosystems, and ultimately ecosystem processes directly or indirectly driven by plants such

as ecosystem C uptake and/or litter decomposition (Chomel et al., 2016; Whitham et al., 2006).

The diversity and the dynamic of metabolites within vascular plants have been somehow more explicitly characterized (Bakhtiari et al., 2021; Defossez et al., 2021; Obata and Fernie, 2012; Turner et al., 2016), compared to non-vascular plants such as mosses. Yet mosses significantly contribute to aboveground biomass and soil carbon sequestration in boreal ecosystems such as peatlands and boreal forests (Tan and Pócs, 2000; Turetsky, 2003), where 65% of global soil organic carbon is locked belowground (Hengl et al., 2014; Hugelius et al., 2020). This ability of peatland to store atmospheric carbon is due to accumulation of partially decomposed organic matter, *i.e.* dominated by remnants of *Sphagnum* mosses (Rydin and Jeglum, 2013). *Sphagnum* mosses are keystone species that easily facilitate peatland harsh environmental conditions and shape their habitat by possessing unique morphological and biochemical peculiarities (Rydin and Jeglum, 2013; Turetsky, 2003). *Sphagnum* mosses can directly affect carbon flux in the ecosystem *via* their metabolism and growth rates (Turetsky, 2003). They have high capillarity system favoring water-logged conditions and resulting in anoxia. *Sphagnum* also produces plethora of metabolites (Fudyma et al., 2019; Hamard et al., 2019) involved in specific and/or multiple functions that presumably maintain *Sphagnum* growth, defense and interact with the environment and/or with other organisms in the environment (Erb and Kliebenstein, 2020; Isah, 2019; Khare et al., 2020; Massalha et al., 2017; Tissier et al., 2014; Wink, 2010; Yang et al., 2018). For particularly, primary metabolites (carbohydrates, carotenoids) are mostly related to the growth and photosynthesis (*e.g.* Granath et al., 2009; Hájek et al., 2011), while specialized metabolites (phenols, proline, flavonoids, tannins, proline) are related to litter-resistance to decomposition and tolerance to abiotic stresses (Cornelissen et al., 2007; Xie and Lou, 2009). However, the same group of metabolites can be involved in multiple processes, like carbohydrates and polyphenols that can support the maintenance of the integrity of plant cell-structure and the internal regulation of plant cell physiology (Ferrer et al., 2008; Roberts et al., 2012; Rudolph and Samland, 1985; Tissier et al., 2014; Turetsky et al., 2008) thus assigning recalcitrance properties to the litter which delay the microbial breakdown (Fudyma et al., 2019; Hamard et al., 2019; Turetsky, 2003; van Breemen, 1995). Thus, *Sphagnum* mosses produce metabolites to interact with its environment, which in its turn feedbacks to ecosystem processes. Nevertheless, the production of *Sphagnum* metabolites can be affected by ongoing climate changes, which can influence *Sphagnum* interactions with its environment and then cascade to ecosystem processes. The mechanism by which *Sphagnum* metabolites respond to climate changes

remains virtually unknown and challenging for studying (Chiapusio et al., 2013), as most of studies to date are concentrated on the effect of the climate change on vegetation communities and ecosystem functions (*e.g.* Binet et al., 2017; Bragazza et al., 2016; Dieleman et al., 2016b; Jassey et al., 2013; Jassey and Signarbieux, 2019; Robroek et al., 2009).

The effect of warming on *Sphagnum* phenols showed contrasting effects of warming with either no direct effect (Jassey et al., 2016; Jassey et al., 2013; Reczuga et al., 2018), or decreasing concentrations along warming gradient (Dorrepaal et al., 2005; Jassey et al., 2011a). *Sphagnum* pigments had different responses to warming depending on species microhabitat preference (Rastogi et al., 2020). The dynamic of other compounds under environmental changes is virtually unknown. However, (Ludwiczuk et al., 2013) showed different metabolite profiles for the same specimen of liverwort *Conocephalum conicum* collected from contrasting environments. This suggests that phenotypic traits possess a variety of plastic response shapes under changing climate (Arnold et al., 2019). Despite the importance of peatlands in carbon storage, important peatland-specific processes that regulate carbon accumulation are not widely used in current climate models (Frolking et al., 2013; Limpens et al., 2008) and the direction of cycle feedback to climate remains uncertain (Frolking et al., 2011). Therefore, there is an urgent need to understand how *Sphagnum* metabolites dynamic responds to climate changes in order to erase uncertainties in the response of peatlands under climate changes.

In this study, we explored how seasonal patterns of *Sphagnum* metabolites respond to climate changes, and how this influence peatland C uptake. To do so, we conducted a reciprocal transplantation experiment in five *Sphagnum*-dominated peatlands representing a wide range of local and reginal conditions (Sytiuk et al., 2021). Peat mesocosms were reciprocally transplanted along a latitudinal gradient from northern Sweden to southern France (Fig. 1a). Reciprocal transplantations provide relevant insight about species and ecosystem responses to changes in climate. Transplanting peat-mesocosms from the same site will remove the confounding effects between geography and climate in the responses, which can be an issue in disentangling those effects (Ågren and Schemske, 2012). In addition to reciprocal transplantation experiment, a seasonal monitoring was performed to investigate how transplanted cores respond to altered climate seasonality.

As previously showed for nine bryophytes but excluding *Sphagnum* (Peters et al., 2018), we hypothesize that (1) *Sphagnum* metabolites from different species will follow similar trends in response to climate seasonality, and that environmental filtering is more important

than taxonomy in determining *Sphagnum* metabolite profiles. (2) More likely climate change will affect the seasonal patterns of *Sphagnum* metabolites as climate change and seasonal interactions can significantly affect species plastic responses. The mismatches in seasonal events, changes in season duration and variability can alter the relative timescales between the organism and seasonal variability (Stevenson et al., 2015). Subsequently, plant traits display a variety of plastic response shapes to changing climate. (3) As mosses, similarly to other plants, simultaneously perform many diverse and often contending tasks to support their fitness, thus leading to trade-offs when the optimal performance of one task is completed at the cost of sub-optimal performance of another task (Kleessen et al., 2014), we hypothesize that climate change will intensify trade-offs of resource partioning between carbon uptake and subsequent growth, and the production of specialized metabolites used for defense. More precisely, we expect that the launch of defense mechanisms against abiotic or biotic stress will be necessary for *Sphagnum* survival, at the cost of *Sphagnum* growth.

By linking a latitudinal gradient of climate conditions to metabolites dynamics in a transplant experiment we were able to not only document the effect of climate seasonality and changes *Sphagnum* biochemical traits, but relate those shifts to ecosystem process.

5.2. Materials and methods

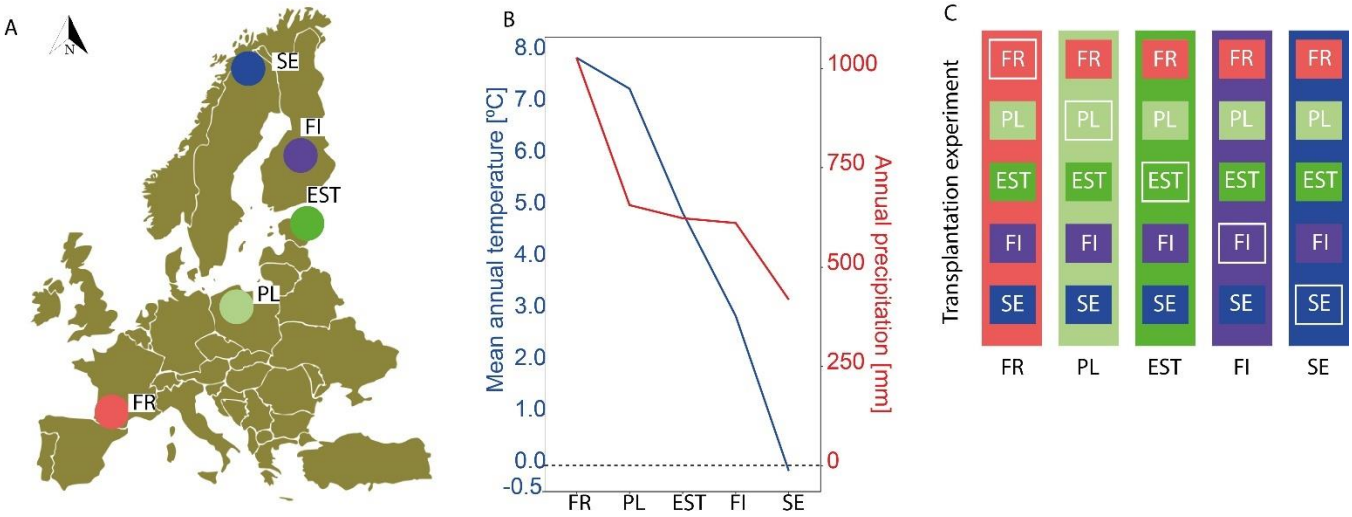


Figure 5-1. (A) Location of five sites along a latitudinal gradient. Site are represented in different colors: FR=Red, France; PL=light green, Poland; EST=dark green, Estonia; FI=purple, Finland; SE=dark blue, Sweden. (B) Mean annual temperature (in Celsius, dark-blue line), total precipitation (in mm, dark-red line) averaged over the period 1960-2018 (WorldClim v2, Fick and Hijmans (2017). Sites ordered along the south-north latitudinal gradient from France to Sweden. (C) Schematic of peat cores reciprocal transplant experiment. Twenty-five mesocosms were collected at each site, five of them stayed at the site of the origin, while other mesocosms were dispatched among the four other sites (5 sites x 5 boxes x 5 replicate plots= 125 boxes).

5.2.1. Experimental set-up and sampling

A multi-sites reciprocal transplant experiment was conducted over five European peatlands spanning along a 3000 km (as the crow flies) latitudinal gradient from northern Sweden to southern France (Fig. 5-1A). These peatlands belong to different ecological classes: Poland and Finland — ombrotrophic bogs, France— moderately rich fens, Estonia — poor fen and Sweden — aapa mire, which are located in diverse environmental and climatic zones and present contrasting local and regional conditions (Fig.5-1B, Table S1): higher mean annual temperature and annual precipitation in France (7.9 °C and 1027 mm, respectively), while low in Sweden (-0.1 °C and 419 mm). The highest temperature seasonality is in Finland (86) and Estonia (85), while the lowest in France (55, Table S1). The highest precipitation seasonality is in Sweden (3.8), while the lowest in France (1.5, Table S1). More details on local and regional conditions can be found in Sytiuk et al. (2022, 2021).

Sphagnum moss was a dominant species across the five sites (see Sytiuk et al., 2021): *S. warnstorfii* (France), *S. magellanicum* (Poland), *S. rubellum* (Estonia), *S. papillosum* (Finland) and *S. balticum* (Sweden). Peat cores (60 x 40 x 20 cm) together with plant cover were sampled

in each site (on lawns) in June-July 2018 and encased into polyvinyl chloride boxes of corresponding size. In each site, five homogeneous blocks have been defined; in each block, five plots with homogeneous *Sphagnum* carpet have been selected (25 plots per site in total). Five mesocosms (one from each block) stayed at their original location (control), while other mesocosms were dispatched among the four other sites and thus experienced warmer/wetter or colder/drier climate, depending on the site origin (Fig. 5-1C, 5 sites x 5 boxes x 5 replicate plots= 125 boxes). In addition, we selected 5 untouched plots, one in each block, as control of the box effect in each site.

After 10 months of adaptation, we performed a seasonal monitoring in each site. Three sampling campaigns of three weeks each were performed in spring, summer and autumn 2019 across all sites. In each plot, we collected a single *Sphagnum* species, which was dominant at the site on origin: *S. warnstorfii* (French boxes), *S. magellanicum* (Polish boxes), *S. rubellum* (Estonian boxes), S. *papillosum* (Finish boxes) and *S. balticum* (Swedish boxes) for measuring metabolites content. For each campaign of measurements and in each plot, *Sphagnum* mosses were sampled at three permanently marked spots (ca. 3–5 shoots per spot). This sampling design allowed us to obtain a composite sample, which represents the entire box. After sampling, the living top of the *Sphagnum* shoots (0–3 cm) were cut immediately, pooled, homogenized and then dispatched for the different laboratory analyses. We could not sample in Sweden in autumn because the soil was already frozen and sampling could damage our plots.

The effect of the box was insignificant for the most of the species and metabolites over three seasons ($P>0.05$, see Fig. S2,3 and Table S2) as well as for CO_2 fluxes (Fig. S4, Table S3).

5.2.2. Environmental local and regional data

Daily air temperature, precipitation and photosynthetically active radiation (PAR) were measured at hourly intervals at the height 30 cm above the ground using data loggers. Then, the temperature was averaged per day, precipitation and PAR were summed per day. The climatic variables of the sites were characterized by mean values of the 30 days period preceding each sampling campaign (Table S1/Fig.S4). As PAR and mean temperature were positively correlated, as well as precipitation had equal negative correlation with both parameters (Fig S5), we decided not to use PAR in further statistical analyses.

In addition to climatic data, we further monitored water-extractable organic matter (WEOM) in each plot. Briefly, and according to Jassey et al. (2018), *Sphagnum* shoots (3g of fresh weight, 0-3 cm to the capitula) were soaked in 30 mL of demineralized water following by 90 min of shaking at 150 rpm. Then, *Sphagnum* shoots were dried at 60°C for 48 hours and weighted to obtain dry mass (mg/g DW). Whatman filter (1 µm pore size) were used to filter the water extract and dissolved organic carbon and nitrogen (WEOC and WEON respectively) were quantified using a TOC analyser.

Samples for pH in boxes was collected in October 2021 at three receptor sites (Finland, Estonia and France). They were stored at 4°C for two day prior to measurement. Then pH was measured at the lab at 20 °C. pH values in the boxes from the same site dispatched along the gradient were not affected by the receptor site (P>0.05, Fig. S3, Table S6).

5.2.3. *Sphagnum* metabolites analyses

We quantified a set of eight *Sphagnum* moss metabolites according to (Sytiuk et al., 2022). Briefly, *Sphagnum* mosses were frozen, lyophilized, ground and stored at −20°C before performing metabolites quantification. Then, we used 1) a 99.9% methanol extraction for quantifying *Sphagnum* pigments (chlorophyll a, b and total carotenoids), 2) a 50% methanol extraction for quantifying total phenols, flavonoids, tannins and carbohydrates, 3) a water extraction for quantifying water-extractable total phenols, 4) a sulfosalicylic acid extraction for quantifying proline. All metabolites were quantified using spectroscopy at different wavelengths (chlorophyll a, b and carotenoids at 480, 652, and 665 nm; total carbohydrates at 490 nm; total phenols at 760 nm; total flavonoids at 595 nm; total tannins at 500 nm; total proline at 510 nm).

5.2.4. Gross ecosystem productivity measurements

Measurements of plant photosynthesis were taken in each plot during each field campaign in optimal sunlight (09:30 to 13:00) using a portable TARGAS-1 infrared gas analyzer (PP-System, USA) equipped with a CPY-5 transparent canopy chamber. Gas flux rates were measured under airtight seal within the chamber through the use of a custom-made PVC collar installed in each plot. The record of CO_2 concentrations was set every second during 70 seconds in order to avoid the build-up of heat and condensation inside the chamber. Net ecosystem exchanges (NEE) was measured with the transparent chamber, whereas ecosystem

respiration (RECO) was assessed using overshadowed chamber. All fluxes were measured at ambient temperature and light conditions at each site. We calculated CO_2 fluxes as a linear change in CO_2 concentration (ppm) over the measurement period using the *R* package *gasfluxes* (Fuss et al., 2020), taking into account ambient atmospheric pressure, gas temperature, the chamber volume, PVC-tube surface area, light intensity. Gross ecosystem productivity (GEP), CO_2 uptake as a result of photosynthesis, was calculated as the difference between NEE and RECO. Negative values for CO_2 fluxes indicate C uptake, while positive values C release. GEP data was standardized by relative vascular plant cover to obtain comparable fluxes among boxes.

5.2.5. Statistical analyses

All statistical analyses were performed in *R* 3.5.3 (R Core Team, 2019) using specific packages, as indicated below. Linear mixed effects models (LME) were used to assess effect of box origin, receptor site and season (fixed effect) on the *Sphagnum* metabolites, GEP, *Sphagnum* water content and WEOM data. The models were fitted with plot nested with season and origin as a random effect on the intercept (Pinheiro & Bates, 2000). LME on mean temperature and PAR was performed on daily data along three seasons and using country*season as fixed effect and day as a random effect. Tukey's multiple comparison test was used for post hoc analyses of differences among the levels of the fixed effects in the final model.

Missing data for *Sphagnum* metabolites in Sweden in autumn sampling campaign created a protentional confounding effect in the data between season and receptor site, which made impossible to apply origin*season*receptor as fixed effect. To overcome this issue and check the effect origin*season*receptor on metabolites, LME models were performed only for four sites (excluding Sweden) and four species only (excluding *S. balticum* as dominant in Sweden). In parallel, linear models (Lm) without accounting for random effect were run accounting for five sites and species. Similar results were found using both approaches, we therefore used LME models to assess the response of *Sphagnum* species (see statistical outputs in Table S6, S7). Normality and homogeneity assumptions of the data, as well as model residuals, were assessed using a Shapiro test and diagnostic plots. Log_{10}-transformations of the data were applied if needed in order to meet these assumptions.

A principal component analysis (PCA) was performed on *Sphagnum* metabolites (standardized data) to assess the seasonal as well transplantation effects (*i.e.* site origin,

receptor site, season) on *Sphagnum* metabolites. Site scores from the PCA were extracted for the two first axes to determine correlations metabolites between climatic variables and GEP.

We calculated the seasonality of the transplantation effect by extracting the mean temperature and precipitation of the coldest site (Sweden, as reference site) from other four site to obtain delta temperature and delta precipitation. We further used a redundancy analysis (RDA) to assess how environmental parameters (temperature, precipitation, delta temperature ad delta precipitation, WEOM) drive the distribution of *Sphagnum* metabolites (standardized transformation) in the ordination space and with which axes those parameters are correlated. Adjusted R^2 was used to estimate the proportion of explained variance (Peres-Neto et al., 2006). The significance of each explanatory variable included in RDA was tested using 1000 permutations. Variance partitioning (*vegan* package, Oksanen et al. (2019)) were used to determine the relative importance of environmental variables on *Sphagnum* metabolites.

We used random regression mixed models (RRMMs, *lme4* package) to quantify the variation in phenotype for each *Sphagnum* species and the overall average for all species in response to reciprocal transplantation (*i.e.* reaction norms), which were graphically represented as phenotype plotted against an environmental parameter. We followed a methodology described in Arnold et al. (2019) to select the best model which represents reaction norms of each *Sphagnum* species. As showed by RDA analysis, shifts in metabolites was mostly driven by temperature on axis 1 and precipitation on axis 2. We therefore built two separate models: (1) PC1 and (2) PC2 on metabolites as response variable and cumulated temperature (1) and precipitation (2) as fixed variables.

We added in the random effect cumulative temperature or precipitation (*i.e.* receptor) and *Sphagnum* origin to account for spatial differences among five receptor sites and differences in five *Sphagnum* species. Maximum likelihood (REML=FALSE) was used to fit models and ensure that models with different fixed effects can be compared directly (Zuur et al., 2009). Additionally, we compared the fit of the models through R^2 values (Nakagawa and Schielzeth, 2013), Akaike Information Criterion (AIC) (Burnham and Anderson, 2004) comparing a log-likelihoods of the models and a likelihood ratio test.To evaluate a quadric-fixed effect of the precipitation on PC2 on metabolites, a random effect of *Sphagnum* origin to vary both in slope and intercept, while for the effect of temperature on PC1 on metabolites — the random effect is additionally varied in the curvature. Using *predict* function, we could predict y-values over the continuous x-axis and then plot the fixed effect of the appropriate

model either of temperature or precipitation (the predicted averaged reaction norm of five species). *Sphagnum* origin was included in random effects allowed to predict the reaction norm for every *Sphagnum* species.

5.3. Results

5.3.1. Seasonal variation of local and regional parameters

The mean temperature was different between site and seasons (LME country*season, $F_{4,277}$=8.7, P< 0.0001). The lowest mean temperature was in spring in Sweden (1.3 ℃) and the highest in Estonia (8.1 ℃; ANOVA P < 0.0001). Sweden was the coldest in summer (11.1 ℃) and Poland the warmest (19.8 ℃; ANOVA P < 0.0001). In autumn, France and Sweden had the lowest temperature with 2.9 ℃ and 5.3 ℃, respectively, while Poland was the warmest with 8.9 ℃ on average (ANOVA, P<0.0001). The mean cumulative PAR showed diverse values in five sites and different seasons (LME country, $F_{4,277}$=9.9, P<0.0001, season $F_{4,180}$=85, P<0.0001). PAR was the lowest in Poland in spring with 6890 μmol photons/m²/day, while the highest in Estonia with 9483 μmol photons/m²/day (ANOVA P=0.04). In summer, France had the lowest PAR (8634 μmol photons/m²/day), whereas Poland the highest (13320 μmol photons/m²/day; ANOVA p<0.0001). France had the lowest PAR in autumn (201 μmol photons/m²/day), while Estonia – the highest (4256 μmol photons/m²/day; ANOVA p<0.0001).

Poland had the lowest precipitation amount in spring (11 mm), while Sweden had the lowest amount in summer and autumn (29 and 64 mm, respectively). However, Sweden was the wettest site in spring (129 mm), whereas Estonia in summer and France in autumn (69 and 201 mm, respectively) were the wettest sites (Fig. S4). Water content of five *Sphagnum* species significantly differed between receptor sites and seasons (receptor*season LM $F_{7,234}$=10.7, P<0.0001, Fig. S7), while no differences when species origin, receptor site and season were combined (origin*receptor*season LM $F_{27,234}$=0.7, P>0.9). In spring, *Sphagnum* water content in all species did not significantly differ between receptor sites with the overall mean of 15.8 ± 1.3 g H_2O/ g DW (receptor LM $F_{4,95}$=2, P=0.1). In summer, water content in all *Sphagnum* species transplanted to Sweden (6.4±0.34 3 g H_2O/ g DW) and Poland (7.5±0.16 3 g H_2O/ g DW) was the lowest, and the highest in France (13.8±0.8 g H_2O/ g DW) and Estonia (13±1.2 g H_2O/ g DW, receptor LM $F_{4,82}$=20.4, P<0.0001). In autumn, the highest water content was in *Sphagnum* all species (except S. *balticum*) collected in Poland (on average 24.7±1.5 g H2O/ g DW, receptor LM $F_{3,66}$=7, P=0.0003), while the average water content for the other sites was 19 ± 1.1 g H_2O/ g DW for all species (excluding measurement in Sweden due to frozen moss under ice layer).

Water-extractable organic carbon and nitrogen (WEOC and WEON, respectively) extracted from all five *Sphagnum* species varied along receptor site and season (LM

season*receptor C: $F_{7,261}$=10.1, P<0.0001; N: $F_{7,261}$=12.3, P<0.0001; Fig S8 and S9), while no differences when species origin, receptor site and season were combined (origin*receptor*season C: LM $F_{28,261}$=0.6, P>0.97; N: $F_{28,261}$=0.7, P=0.9). In spring, WEOC and WEON were the lowest in all *Sphagnum* species transplanted to France (on average 1.3±0.05 mgC/mg DW and 0.04±0.004 mgN/mg DW, respectively, LM receptor C: $F_{4,261}$=21.9, P<0.0001; N: $F_{4,261}$=12.7, P<0.0001), while the highest WEOC was in Poland (on average 5.7±0.8 mgC/mg DW) and WEON in Estonia (on average 0.2±0.03 mgN/mg DW). In summer, WEOC content was remarkably the highest in *Sphagnum magellanicum* transplanted to other sites, especially to Sweden (maximum 19.8±3.1 mgC/mg DW, average of *S. magellanicum* 13.6 ± 1.81 mgC/mg DW), while the other four species transplanted to Poland were high (on average 7.7 ± 0.4 mgC/mg DW). The lowest content of WEOC extracted from all *Sphagnum* species was in Estonia (on average 4.5±0.9 mgC/mg DW, LM receptor: $F_{4,92}$=8.9, P<0.0001). WEON was the highest in *Sphagnum* transplanted to France (on average 0.47±0.08 mgN/mg DW), while the lowest in Poland (on average 0.14±0.01 mgN/mg DW, LME receptor: $F_{4,92}$=11.7, P<0.0001). In autumn, WEOC and WEON did not vary significantly between receptor sites (average of 7.42±0.6 mgC/mg DW and 0.26±0.02 mgN/mg DW, LM P>0.05).

All statistical details can be found in Table S5,S6.

5.3.2. Seasonal and transplantation effect on *Sphagnum* metabolites

For all metabolites and all *Sphagnum* species, we found a strong seasonal effect (LM origin*season, P < 0.05 for all metabolites; Fig. 5-2, Fig. S7-15, Table S7). The PCA analysis clearly showed three separate groups according to seasons (Fig 2A, LM season: P<0.05, Table S7). Overall, our findings showed greater concentrations of specialized metabolites (*i.e.* total tannins, phenols, flavonoids, proline and water-soluble phenols) and pigments (*i.e.* chlorophyll a, b and carotenoids) in summer (Fig 5-2G, Fig S10-18), while concentrations of carbohydrates tended to decrease along with season. RDA analysis revealed that seasonal variations of metabolites were mostly driven by mean annual temperature on the first axis and precipitation on the second axis, which together explained 7% of total variation (Fig. S19,20). In addition to seasonal variations, the PCA analysis showed a neat transplantation effect on metabolites from all *Sphagnum* species (Fig. 5-2B), with similar patterns among all species (LM receptor*season P<0.05, Table S7, S8; Fig. 5-2C). The RDA confirmed these patterns and showed that transplantation effect (delta temperature and delta precipitation)

over seasons was similar across seasons (Fig. S19,20) and explained 6% of total metabolite variation. Overall, WEOC and WEOC were poorly connected to metabolite variation and explained only 3 % of the overall variance (Fig. S20). Important to mention that WEOM and WEON can be partially cofounded with metabolites, as they were extracted from *Sphagnum*, thus they were not used for further statistical analyses.

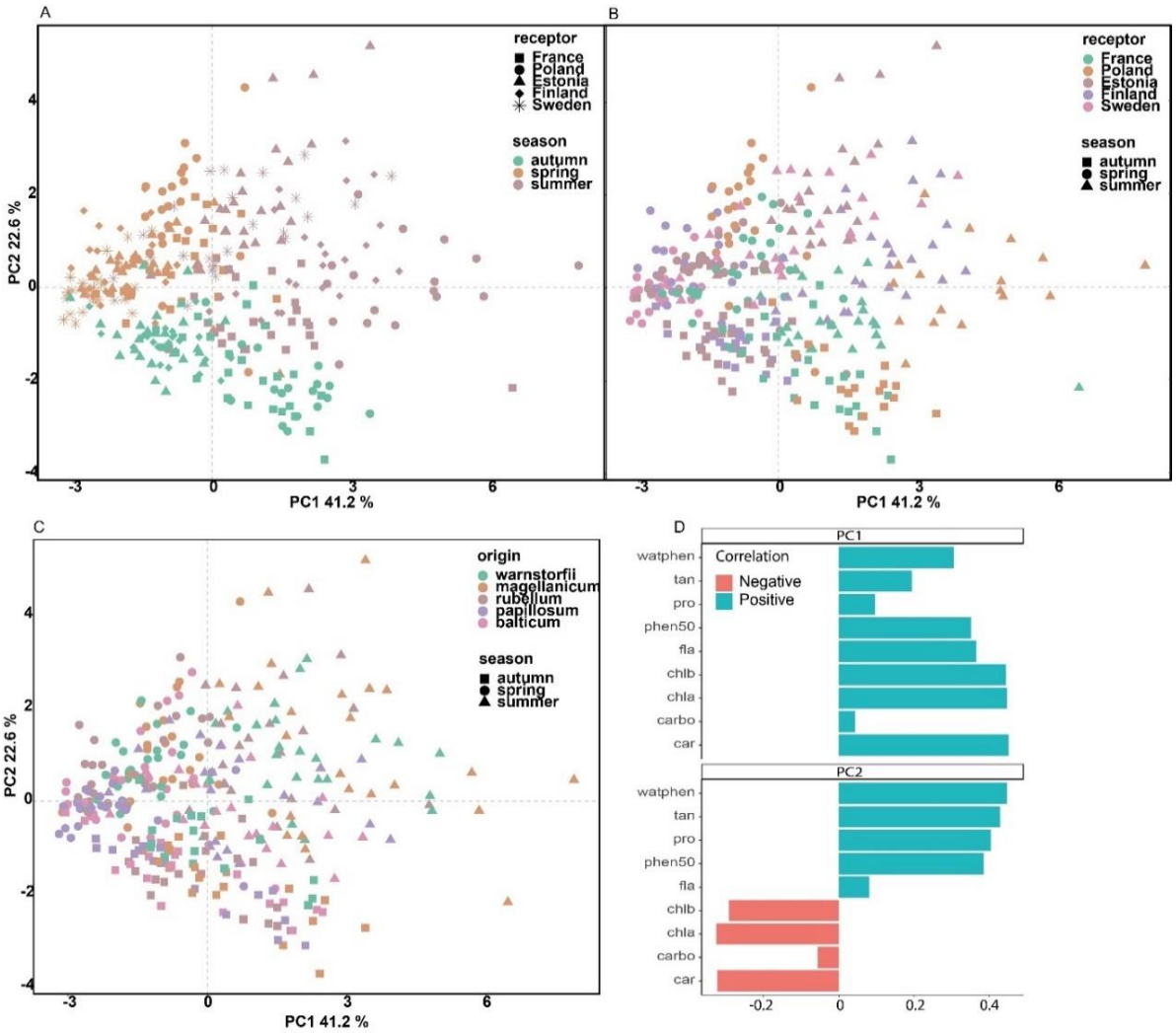


Figure 5-2. PCA of standardized metabolites data collected along the latitudinal gradient over three seasons for (A) receptor sites presented as shapes and seasons as color, (B) receptor sites presented as colors and seasons as shapes, (C) transplanted species presented as color and seasons as shapes, (D) the loadings of each variable (metabolite) on the two PCA axes.

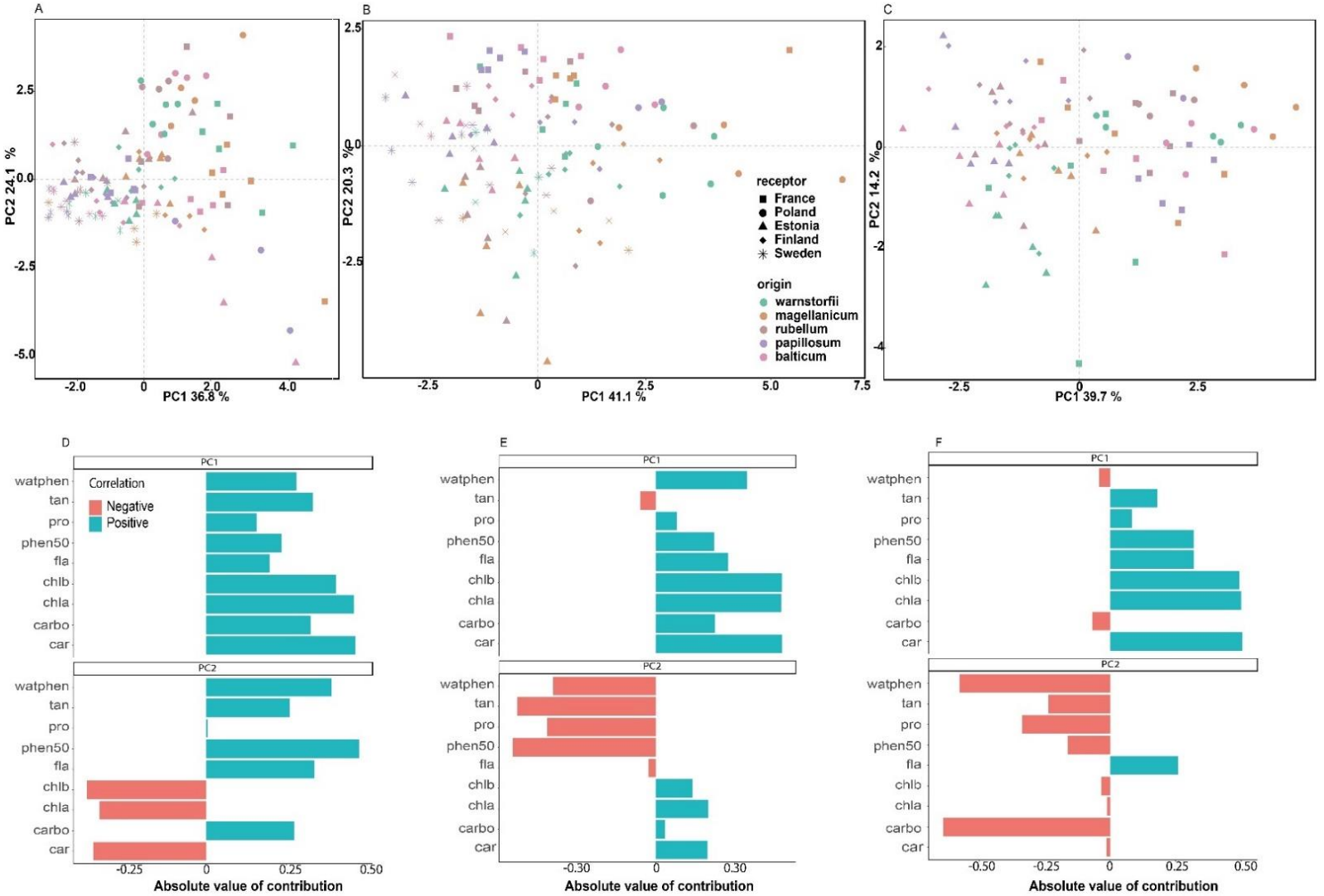


Figure 5- 3. PCA of standardized metabolites data collected along the latitudinal gradient presented per each season for (A-C) receptor sites presented as shapes and transplanted species as color in spring, summer and autumn, respectively, (D-F) the loadings of each variable (metabolite) on the two PCA axes in spring, summer and autumn, respectively

In spring, the PCA ordination showed that all species transplanted to France and Poland (warmer sites) had higher concentrations of total carbohydrates, flavonoids, phenols, tannins, pigments and water-soluble phenols, while most of the metabolites had low concentrations in Estonia/Finland/Sweden (Fig 5-3A, axis 1). In summer, the PCA showed similar patterns on axis 2, although the variability among receptor sites increased. Overall, the concentrations of water-soluble phenols, total carbohydrates, flavonoids, pigments were higher in all species transplanted to Poland/France than in other sites (Fig 5-3b). On the opposite, the concentrations of proline and total tannins were the highest in Sweden and Estonia (*S. warnstorfii*, *S. magellanicum*), and the lowest in France, Poland and Finland for all species. In autumn, the transplantation effect was still markable with a separation between France/Poland and Estonia/Finland on axis 1. Again, all species followed the same trend with low concentration of carbohydrates in all *Sphagnum* species in Poland, and high concentrations of pigments, total flavonoids and phenols in Poland/France (Fig. 5-3C).

5.3.3. Dynamic of *Sphagnum* metabolites plasticity along the latitudinal gradient

The quadratic regression between *Sphagnum* metabolites (*i.e.* PCA scores on axes 1 and 2) and cumulative temperature and precipitation showed that metabolites from five *Sphagnum* species had similar reaction norms (slope and curvature) when transplanted along the gradient (Fig. 5-4A, 5-4B, Table S9). Average curves of *Sphagnum* metabolites (PC1) showed a positive correlation with temperature and that *S. magellanicum* exhibited the highest rates of metabolite plasticity along the temperature gradient (R^2=0.29, Fig 5-4A). The mean reaction norms (of five *Sphagnum* species) as well as individual reaction norms peaked in Estonia in autumn with +7.9°C. *Sphagnum* metabolites (PC2) reaction norms showed a negative correlation with precipitation and *S. warnstorfii/S. rubellum* had the highest plasticity along a precipitation gradient (Fig. 5-4B, R^2=0.48). The mean and individual reaction norms were at the maximum in Finland/Estonia in spring with 31-40 mm.

The curves of reaction norms of *S. balticum* (Sweden) and *S. papillosum* (Finland) were grouped together, while those of *S. warnstorfii* (France), *S. magellanicum* (Poland) and *S. rubellum* (Estonia) were closer to each other, but the distance between response shapes and forms were changing over the time.

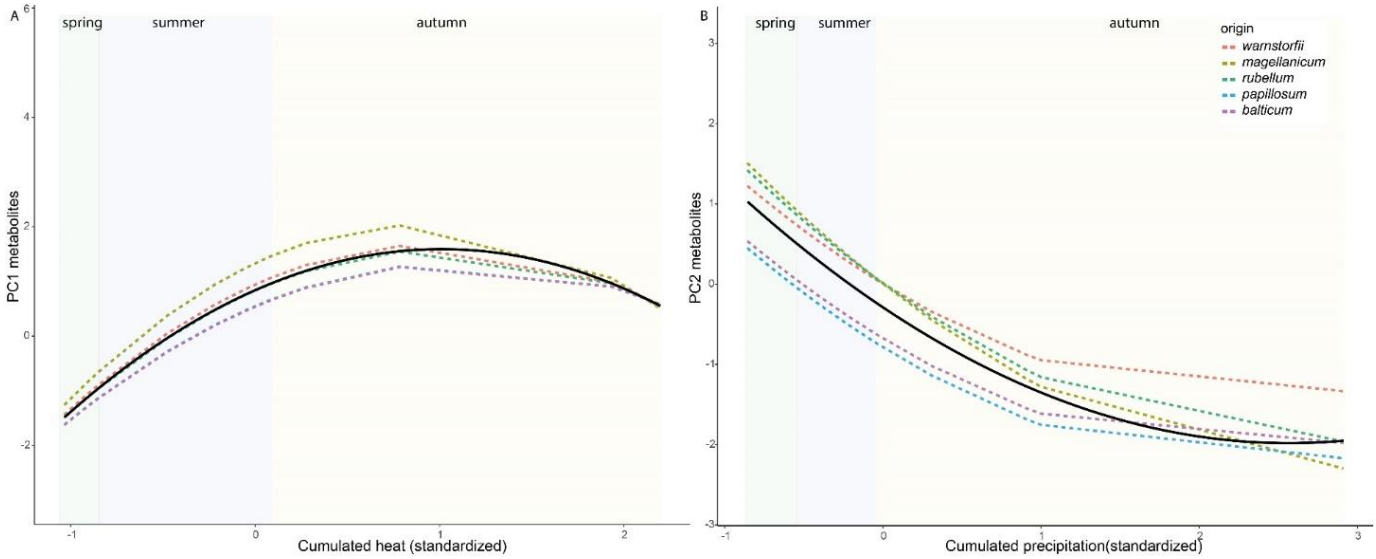


Figure 5-4. (A) Metabolites dynamic across mean-centered cumulative temperatures of the receptor sites for five *Sphagnum* species (three seasons). The thick black line represents the quadratic regression model fit of the overall effect of the receptor sites cumulative temperature (the predicted average population-level reaction norm), and dashed colored lines represent each *Sphagnum* species' modelled reaction norm from the random regression mixed-effects model that accounts for differences in intercept, slope, and quadratic curvature. (B) Metabolites dynamic across mean-centered cumulative precipitation of the receptor sites for five *Sphagnum* species (three seasons). The thick black line represents the quadratic regression model fit of the overall effect of the receptor sites precipitation (the predicted average population-level reaction norm), and dashed colored lines represent each *Sphagnum* species' modelled reaction norm from the random regression mixed-effects model. The observations are absent in Sweden in autumn for all species (frozen site).

5.3.4. Gross ecosystem productivity (GEP) dynamic

As showed for *Sphagnum* metabolites, GEP clearly evidenced seasonal patterns with an increase of C uptake in boxes at the peak of the growing season (summer) for all *Sphagnum* species at their sites of origin (LM origin*season $F_{8,251}$= 5.4, P=<0.0001). Besides seasonal variations, GEP also exhibited transplantation effects, but that effect was season dependent (Fig. 5-5; receptor*season, $F_{8,191}$=7.5, P < 0.0001). The overall response of GEP was driven by changes in delta temperature and delta precipitation (LM delta temperature * delta precipitation $F_{1,270}$=6.2, P=0.01), while neither WEOC nor WEON affect GEP rates along the gradient (P>0.05).

In spring, all species transplanted to warmer climate systematically showed higher GEP values (average 14.7 ± 1.1 mg CO_2 m^{-2} h^{-1}, LM temperature $F_{1,117}$=13.6, P=0.0003; LM temperature*precipitation $F_{1,117}$=2.8, P=0.1) when compared to the coldest conditions (Sweden; average 6.1 ± 0.9 mg CO_2 m^{-2} h^{-1}). In summer, similar patterns as in spring were observed with an increase of GEP values (+80% on average, 25.2± 1.5 mg CO_2 m^{-2} h^{-1} on

average) in most of the sites (Fig. 5-5), at the exception of boxes transplanted to Poland that showed low values of GEP (15± 2.4 mg CO_2 m^{-2} h^{-1} on average, LM precipitation $F_{1,114}$=7.7, P=0.006; LM precipitation*temperature $F_{1,114}$=2.7, P=0.11). In autumn, GEP rates decreased and were similarly low to those in spring (-82% comparing to summer). The highest fluxes were in all species transplanted to Estonia (23.4± 4.3 mg CO_2 m^{-2} h^{-1} on average), and the lowest when transplanted to Sweden (2.1± 0.4 mg CO_2 m^{-2} h^{-1} on average) and Poland (2± 0.4 mg CO_2 m^{-2} h^{-1} on average, LM precipitation*temperature $F_{1,83}$=23, P<0.0001).

All statistical details can be found in Table S10.

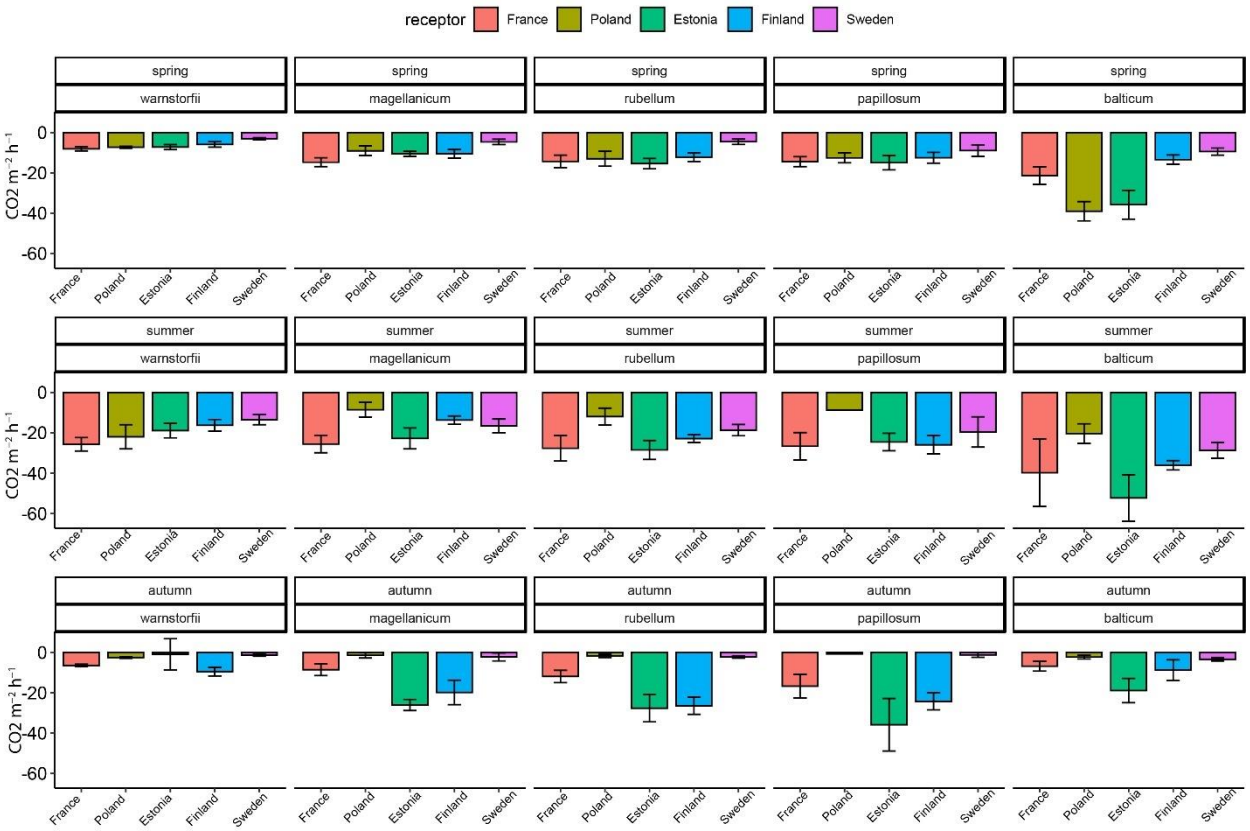


Figure 5-5. Gross ecosystem productivity (GEP, g C m^{-2} d^{-1}) dynamic of boxes transplanted to five receptor sites along the gradient over three seasons. Receptor sites are colored and names are ordered according to south-north gradient (from warmer to colder). Each value represents the mean ± SE (n = 5). Negative value represents uptake of carbon into the system, while positive represent the losses of carbon in the system.

5.3.5. Linkages between *Sphagnum* metabolites and ecosystem functioning under warming

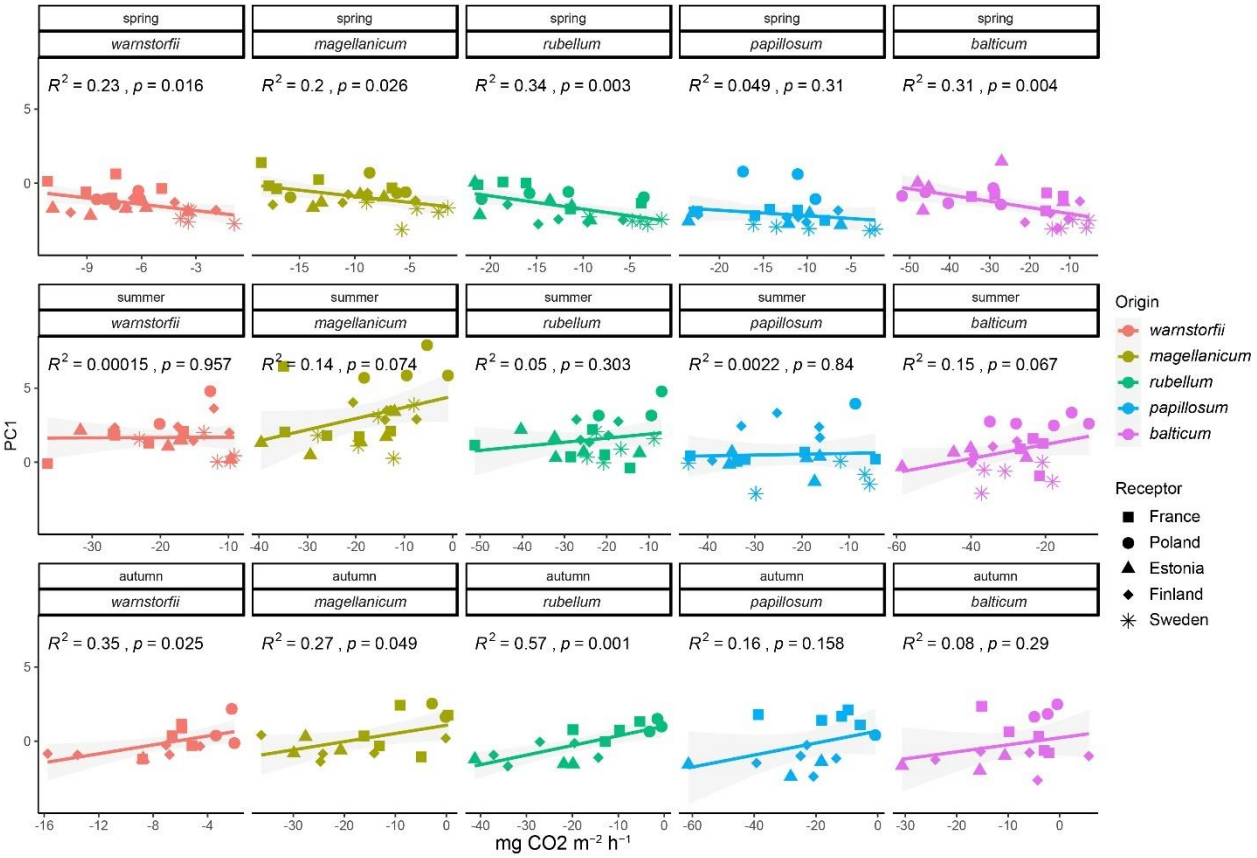


Figure 5- 6. Correlation between metabolites (PC1) and GEP of boxes transplanted to five receptor sites along the gradient over three seasons. Receptor sites represent as shapes and transplanted species represented as colors. Both species and receptor sites are ordered according to south-north gradient (from warmer to colder).

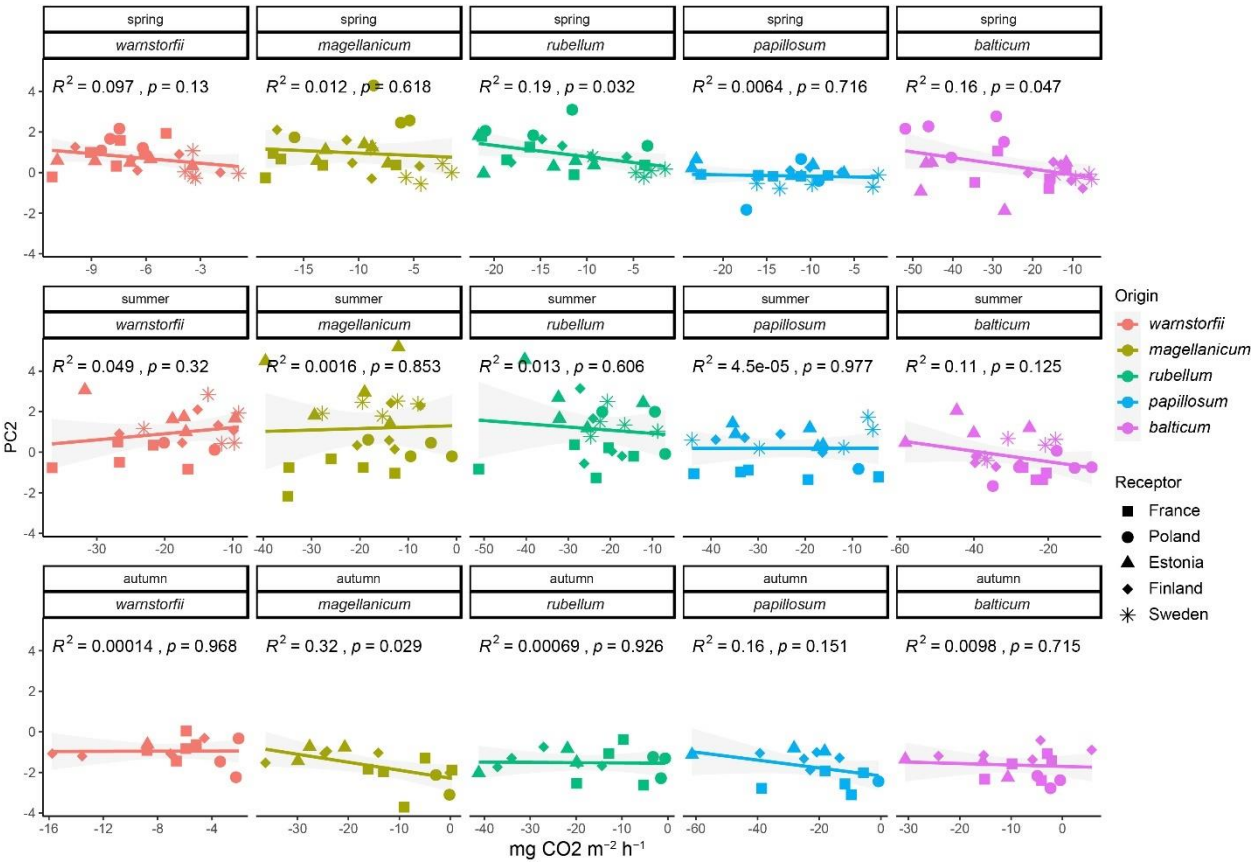


Figure 5-7. Correlation between metabolites (PC2) and GEP of boxes transplanted to five receptor sites along the gradient over three seasons. Receptor sites represent as shapes and transplanted species represented as colors. Both species and receptor sites are ordered according to south-north gradient (from warmer to colder).

We found important linkages between *Sphagnum* metabolites and GEP in response to transplantation, but the direction of the relationships depended on season (Fig. 5-6, 5-7). The overall relationship between GEP and the first PCA axis on metabolites was significant (LME: $F_{1,232}$=5.3, P=0.02), while less significant with the second PCA axis (LME: $F_{1,232}$=0.16, P=0.7, Table S11). More particularly, *Sphagnum* metabolites were negatively correlated to GEP in spring for all *Sphagnum* species, excluding *S. papillosum* for PC1 and *S. warnstorfii*, *S. magellanicum* and *S. papillosum* for PC 2 (Fig. 5-6, 5-7). In other words, ecosystem C uptake increased along with increasing concentrations of carbohydrates (in *S. magellanicum and S. warnstorfii*), proline (in *S. balticum*), flavonoids (in *S. warnstorfii* and *S. rubellum*) and total phenols (in *S. balticum and S. rubellum)* and water-soluble phenols (*S. balticum*, Fig. S21-S29). In summer, the relationship between GEP and metabolites was absent (P>0.05) for all the species, while in autumn the patterns were the opposite to spring with mostly positive correlations. To wit, C uptake increased along with decreasing concentration of carotenoids

(*S. magellanicum* and *S. rubellum*), chlorophyll a and b (*S. magellanicum*, *S. rubellum* and *S. papillosum*), flavonoids (*S. rubellum*), tannins (*S. rubellum*) and increasing of carbohydrates (*S. balticum*, Fig. S21-S29).

5.4. Discussion

We found that *Sphagnum* metabolite concentrations and gross ecosystem productivity (GEP) exhibited low rates when transplanted to colder sites over all seasons. Additionally, the highest concentrations of most metabolites and GEP were observed at the peak of growing season (summer) whatever *Sphagnum* origin and receptor site. More interestingly, our data showed important linkages between *Sphagnum* metabolites and C-related processes, assuming that climate-induced shifts in *Sphagnum* metabolites can feedback to ecosystem processes of carbon assimilation. Carbon cycle and related processes, which strongly affect climate, is in turn impacted by chemical matrices into which plants store carbon (Iason et al., 2012b). We caution that we focused only on the plasticity of five *Sphagnum* species during one growing season (spring-autumn 2019). Nevertheless, this work provides the first demonstration that plastic responses of *Sphagnum* metabolites to climate warming can be linked to ecosystem processes related to carbon cycling.

Sphagnum metabolites from five species showed similar response to seasonal variability, with the maximum concentrations in summer. Previous findings showed similar trends for polyphenols, where a decrease in *S. fallax* and *S. magellanicum* could be observed by the end of the growing season (Chiapusio et al., 2018). Klavina et al. (2018) showed for *S. fallax* and *S. magellanicum* increasing polyphenols and carbohydrates from spring to mid-summer, with a decrease in autumn. Mandi et al. (2022) found that concentrations of phenols, flavonoids and terpenoids in moss *Hypnum cupressiforme* were at the maximum in summer. Additionally, Peters et al. (2018) showed the number of biochemical features in nine bryophytes was the highest in summer in any species. This increase in metabolites in summer could be related to more intense biological activity of *Sphagnum* during summer (Lambers et al., 2008; Rousk et al., 2017; Thakur and Kapila, 2017). More precisely, higher concentrations of these metabolites in summer could enable to cope with abiotic stress as high temperature and light irradiation, and drought (Iason et al., 2012b), and biotic stresses as increased herbivory pressure and competition with other plants (Chen et al., 2021; Chiapusio et al., 2013; Glime, 2006; Whitehead et al., 2018). Additionally, the response of bryophytes and their metabolites to seasonal variability may also depend not only of environmental factors, but

also on moss ecological life-style strategies, *i.e.* competitive, stress-tolerant or fast-growing species (CSR triangle *sensu* Grime (1977)) (Peters et al., 2018).

We found that *Sphagnum* had lower concentrations of chlorophyll a, b and carotenoids, flavonoids in spring, carbohydrates – in summer, and specialized metabolites like tannins, phenols and proline were low in autumn. Low rates of chlorophyll and carotenoids in spring, can be due to remaining acclimation of photosynthetic apparatus to winter dormancy, therefore low CO_2 fixation can be compensated by using capitulum storage accumulated previously in autumn (Hájek, 2014). Besides, lower concentration of flavonoids in any *Sphagnum* species in spring may evidence that photosynthetic cells of moss did not face an oxidative stress from the accumulation of reactive oxygen species (ROS) (Elstner, 1982), as flavonoids play role of an antioxidant and limit oxidative stress in plants (Choudhury et al., 2013; Das and Roychoudhury, 2014; Noctor et al., 2018). Low concentrations of carbohydrates in summer, but high in spring and autumn, can be explained by a seasonality in resource allocation to photosynthetic capacity (Hájek, 2014). At the end of growing season, photosynthates can be stored in capitula in the form of carbohydrates, and thus these compounds provide cellular osmotic protection against freezing in winter (Skre et al., 1983). We can assume that the increase of metabolites at the beginning of the growing season and gradual decrease towards its end may reflect their active participation in the growth process.

In addition to seasonal variability, we found that transplantation towards warmer conditions benefited to *Sphagnum* metabolites, which all increased in concentrations. Specifically, temperature was positively correlated with PC1 on metabolites (mostly chlorophyll a, b and carotenoids, total and water-soluble phenols, tannins and flavonoids), while precipitation was negatively correlated with PC2 on metabolites (mostly total and water-soluble phenols, tannins and proline) over the seasons. The increasing concentration of metabolites along with warming was also reported in other studies on *Sphagnum* phenols (Jassey et al., 2016) and carotenoids (Rastogi et al., 2020), while decreasing of *Sphagnum* phenols (Klavina et al., 2018; Reczuga et al., 2018b) with higher precipitation, but increasing chlorophyll a and b (Rastogi et al., 2020). The positive effect of warming on chlorophyll and carotenoids concentrations could be due to stimulation of the activity of certain enzymes (*e.g.* Rubiso) involved in chlorophyll production (Rastogi et al., 2020) and thus higher photosynthesis. The activity of Rubisco was strongly corelated with the net CO_2 uptake (Björkman, 1981). Indeed, we observed higher rates of GEP along with higher concentrations of chlorophyll and carotenoids. The increase of metabolites (phenols, flavonoids and tannins) with increasing temperature can be due to direct response of *Sphagnum* to elevated

temperatures by accumulating those compound for plant protection or due to indirect effect of increasing competition with vascular plants (Chiapusio et al., 2018; Liu et al., 2019), or restraining higher microbial activities (Fudyma et al., 2019; Hamard et al., 2019; Verhoeven and Liefveld, 1997). Nevertheless, some studies showed contrasting effects of warming with either no direct effect of warming on metabolites concentration (Jassey et al., 2013), suggesting warming could affect qualitative production of polyphenols as was showed for dwarf shrubs (Hansen et al., 2006); or decreasing concentrations along warming gradient, more likely reflecting a stronger nutrient limitation on growth in the subarctic area (Dorrepaal et al., 2005; Jassey et al., 2011a). Negative correlation between proline and precipitation was also found for two mosses *Pogonatum cirratum* and *Hypnum plumaeforme* (Liu et al., 2016). The accumulation of proline in plant tissues is the response to osmotic stress and it serves as scavenger of ROS to provide cell protection against drought and/or salinity (Hayat et al., 2012; Kishor and Sreenivasulu, 2014; Okumoto et al., 2015; Verbruggen and Hermans, 2008). We acknowledge that we did not measure the effect of pore water chemistry and pH on *Sphagnum* metabolites across all sites and seasons. However, we found no effect on site pH on transplanted boxes in autumn, which allows us to suggest that boxes experienced their 'home' pore water conditions. Alternatively, we did not find the effect of WEOM on *Sphagnum* metabolites and GEP, but WEOM can be confounded with some of *Sphagnum* metabolites as both are extracted from *Sphagnum* moss *per se*.

Using random regression models (RRMM) with quadric function, were able to assess the variation in phenotype in response to transplantation along the gradient of each *Sphagnum* species and the average response of five species by using reaction norms (plotted phenotype as PC axis on metabolites against environmental parameters as temperature and precipitation). It was found that the reaction norms of *Sphagnum* metabolites (PC1) in response to temperature were positive parabolic curve, with the maximum at +7.9°C (autumn, Estonia). Conversely, response of *Sphagnum* metabolites (PC2) to cumulative precipitation was negative parabolic curve with the maximum reaction norm at 11 and 31 mm (spring, Poland and Finland). We assume that those climatic parameters represent benign conditions and *Sphagnum* high performance reflects a favorable phenotypic response for all metabolites (PC1) to temperature, and mostly secondary metabolites (PC2) to precipitation. The diverse direction of reaction norms to temperature and precipitation could be related to the fact that most mosses are considered to have broad physiological optima and being not genetically specialized ecotypes (Såstad et al., 1999).

Interestingly, reaction norms of *S. balticum* (Sweden) and *S. papillosum* (Finland) were grouped together, while those of *S. warnstorfii* (France), *S. magellanicum* (Poland) and *S. rubellum* (Estonia) were closer to each other, but the distance between reaction norm curves were changing over the time, as mentioned in Sultan (2000). This suggests that species originating from similar environments can possess similar responses to new climate conditions. For example, along elevation gradients, species which located at similar elevation showed some similarities in their metabolomic profiles (Bakhtiari et al., 2020; Defossez et al., 2021; Fernandez-Conradi et al., 2021). More likely, species metabolome, when moved to new conditions, tends to switch towards local optima, suggesting the advantage to adopt similar phenotype, but only if transplanted species had dissimilar phenotype from the members of a new community (Muscarella and Uriarte, 2016). Contrary it can be also suggested, that transplanted species have already similar phenotype as new community (*i.e.* divergence hypotheses, Valladares et al. (2006)). The evolution of reaction norms in the environments with distinguishable seasonal variability within generation of the plant depends on the character of traits, *i.e.* either labile – changing during lifetime or nonlabile - incapable of being affected by environmental changes after some critical period (Via, 1994). Limpens et al. (2017) found that most of *Sphagnum* metabolites were driven by either environment or microtopography, but not by *Sphagnum* phylogeny suggesting traits lability. More importantly, plant metabolites are known to respond rapidly and reversibly to environmental stresses in order to support plant homeostasis , as it serves as primary mechanism by which plant adapt to climate variability (Metlen et al., 2009). The prediction of differences in reaction norms is uncertain, as some studies suggested that the maximum differences in reaction norms can be detected in the most stressful environment, due to higher rates of evolution (Hoffmann and Parsons, 1991), while other authors suggested that the maximum differences will occur under the most favorable conditions, if the optimal response can only take place under benign conditions (Kéry et al., 2000).

Similarly to *Sphagnum* metabolites, gross ecosystem productivity (GEP) showed seasonal variability, with the maximum C uptake in summer, as it was shown in other studies on peatlands (*e.g.* Bubier et al., 1998; Gavazov et al., 2018; Jassey and Signarbieux, 2019; Korrensalo, 2017; Lafleur et al., 2001; Tian et al., 2020; Walker et al., 2017). Besides seasonal variability, GEP rates in spring and summer were the highest when transplanted to France (4.8 C, 92 mm and 15.2 C, 37 mm, respectively) and Estonia (8 C, 40 mm and 15.8 C, 69 mm, respectively), while lowest in Sweden (1.3 C, 128 mm and 11 C, 29 mm, respectively) and Poland (6 C, 11mm and 19.8 C, 60mm, respectively). In autumn, GEP was high in boxes

transplanted to Estonia and Finland (>+7.3C), the warmest sites with moderate amount of precipitation (73-105 mm) comparing with other sites. We could suggest that GEP rates upon transplantation were driven by compromises between temperature and precipitation. More precisely, the impact of increasing temperature can be modulated by alteration of water levels and/or moisture content (Buttler et al., 2015; Elmendorf et al., 2012). Radu and Duval (2018) showed that decreasing precipitation led to drop of productivity of *Sphagnum* carpet, suggesting that frequent precipitations support sufficient carpet moisture needed for moss photosynthesis. Also, some studies found that rising temperature can increase *Sphagnum* photosynthesis and biomass production under wet and cool season, where vascular plant growth was reduced (Buermann et al., 2018; Laine et al., 2019; Robroek et al., 2007). Jassey and Signarbieux (2019) showed that climate warming started to have negative effect when bog transited to dry periods, suggesting that low soil moisture decreased *Sphagnum* productivity and cancelled the positive effect of warming on productivity in wet periods. Even though studies showed contrasting effect of climate change on *Sphagnum* ecophysiology with further consequences for C processes (Breeuwer et al., 2009; Dorrepaal et al., 2003; Gunnarsson et al., 2004; Renato, 1995; Robroek et al., 2007) *Sphagnum* can stabilize community productivity via differences in the magnitude of their response to climate changes (Jassey and Signarbieux, 2019).

Contrary to our hypothesis, we did not observe trade-offs between C uptake and metabolites production, but we quantified a shift in a suite of primary and secondary metabolites, alongside local rates of gross ecosystem productivity. More precisely, C uptake increased with increasing carbohydrates, proline, flavonoids and phenols concentrations in spring, while in autumn C uptake increased along the decreasing concentration of carotenoids, chlorophyll a and b, tannins and increasing of carbohydrates. Our results suggest that the phenotypic control of resource allocation to metabolites formation is exercised by the levels and balance of environmental resources available for synthesis of metabolites and for competing growth (Bryant et al., 1983; Coley et al., 1985; Jones and Hartley, 1999). In spring, positive correlation between *Sphagnum* metabolism and C assimilation was observed, suggesting that, water supply prevails on evapotranspiration, thus creating the optimum conditions for growth and production, whereas in summer it can be restricted by drought (Brock and Bregman, 1989; Gaberščik and Martinčič, 1987). Besides, we found that C uptake was increasing in spring along with flavonoids and phenols especially when transplanted to warmer sites. The compounds are generally known to participate in plant defense (against pathogens/herbivores) and interactions with other plants. It is generally assumed that plant

performance is resource- restricted and demands allocation of resources to either growth or chemical and structural defense, something known as a growth-defense trade-off (Herms and Mattson, 1992). Thus, it was expected that species transplanted to warmer site face stressful condition, and thus compromising between growth and defense. Contrary to our findings, warming was shown to have negative effect on phenols content in peatland species (Veteli et al., 2007), including *Sphagnum* (Jassey et al., 2011a), suggesting a potential trade-off between growth and production of carbon-containing metabolites, with lesser investment into phenols production (Mattson et al., 2005; Veteli et al., 2007), but more intense growth. Nevertheless, the results on simultaneous increase of C uptake and phenolic compounds can be related that some other resources (different to C) may limit plant production, and the growth is restricted leading to high levels of C and the excess of C is redirected to synthesis of C-containing metabolites like phenols (Graglia et al., 2001). In autumn, increasing C uptake was along with decreasing pigments content, but increasing carbohydrates concentration. This indicates that photosynthates were stored in form of carbohydrates to support osmotic protection during pre-winter freezing (Hájek, 2014; Skre et al., 1983) without suppressing benefits of C assimilation during the day. Thus, our finding show important linkages between *Sphagnum* metabolism and C-related processes are season dependent although the exact mechanisms behind these linkages remain unclear and require further studies.

To sum up, our reciprocal transplant experiment revealed that all five *Sphagnum* species, when transplanted to new sites, showed similar responses of metabolites concentrations (biochemical traits) over all seasons, suggesting that environment filtering prevails on phylogeny in driving biological activities and that these traits are evolutionary labile (Limpens et al., 2017; Piatkowski and Shaw, 2019). Our results further show that *Sphagnum* metabolic plasticity lead to increased C uptake, especially in early and late growing season. We found that *Sphagnum* metabolites were very plastic in response to temperature and precipitation and their reaction norms had similar slopes and curvatures, suggesting that shift in phenotypes across the gradient mirror a set of phenotypes that maximizes fitness in different environments (Henn et al., 2018). Also, we reported linkages between *Sphagnum* metabolites and C-related processes, assuming that climate-induced shifts in *Sphagnum* metabolites can feedback to ecosystem processes of carbon assimilation. Indeed, Moor et al., (2015) reported that changes in community-weighted mean traits led to ambiguous consequences for carbon sequestration.

Our results shed interesting new light on the dynamics of *Sphagnum* metabolites not only at their home site, but also when transplanted along a latitudinal gradient. A caveat is

that we measured five *Sphagnum* species at a single stage of its life cycle (one year) along one gradient, and only quantified ecosystem CO_2 exchange at a local scale and did not account for the effect of other parameters related to local conditions (porewater chemistry and pH) and plant physiology (photosynthesis, capitulum size). As such, further (long-term) studies are required to account for the potential effect of the pure and combined effects of other parameters. Nevertheless, we could evaluate the plastic responses of *Sphagnum* metabolites and we observed season-specific relationships between metabolites and ecosystem productivity. Moreover, abiotic filters such temperature or water availability, which are limiting for successful survival strategies, promote traits convergence to a new local phenotype (Keddy, 1992; Violle et al., 2012). Our results have important implications for understanding the plasticity of *Sphagnum* metabolites and how it will feedback to C assimilation in peatlands under future climate warming.

Supplementary materials

Supplementary figures

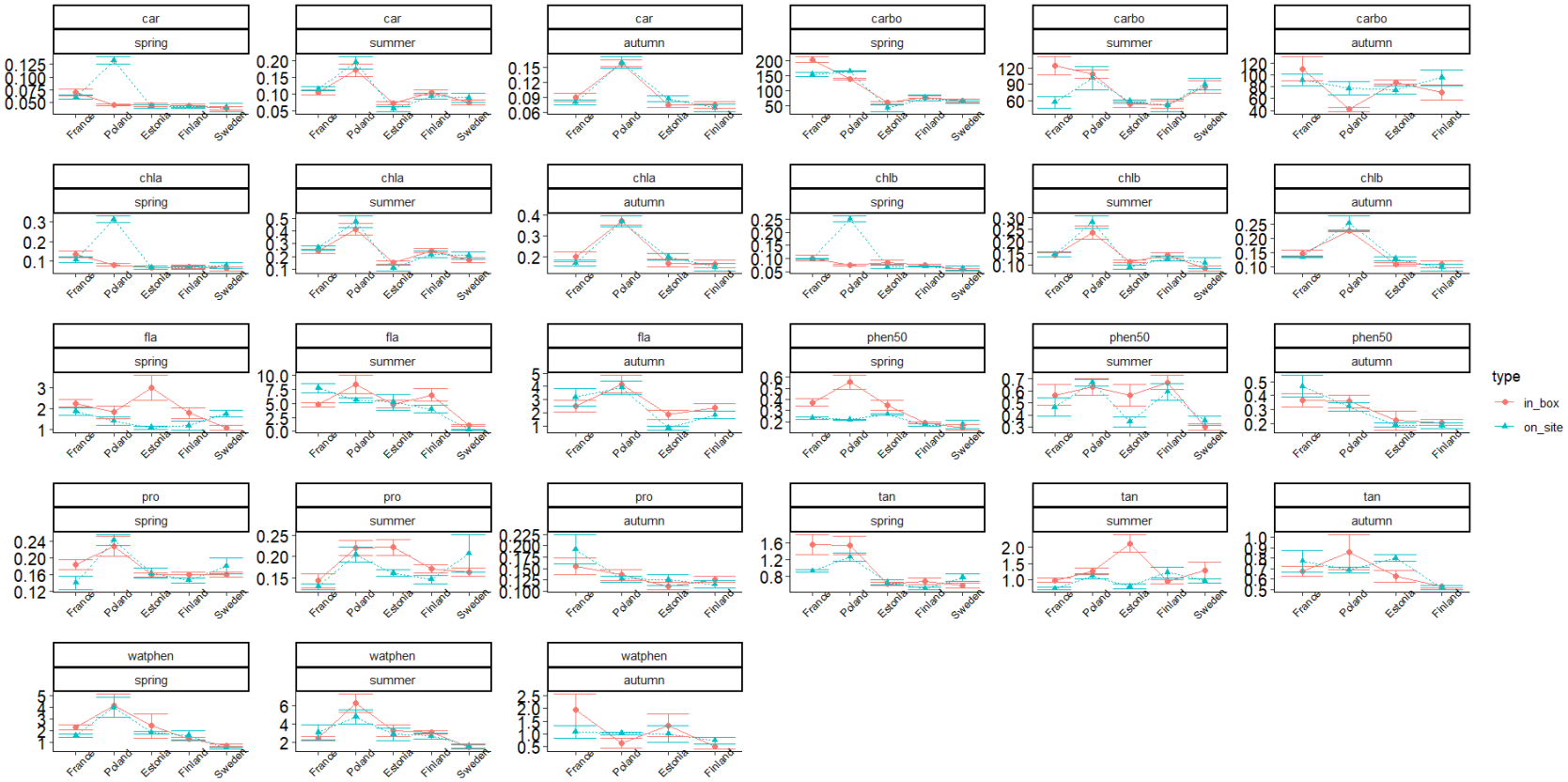


Figure S1. *Sphagnum* metabolites content in the boxes (which stayed at their site of origin) and at the control plots on the sites (outside the boxes) over three seasons. Pale red color corresponds to the samples collected from the boxes and pale blue — samples outside the boxes. Abbreviations: car-carotenoids, carbo—carbohydrates, chla—chlorophyll a, chlb—chlorophyll b, fla—total flavonoids, phen50—total phenols, pro—proline, tan—total tannins, watphen—water-soluble phenols

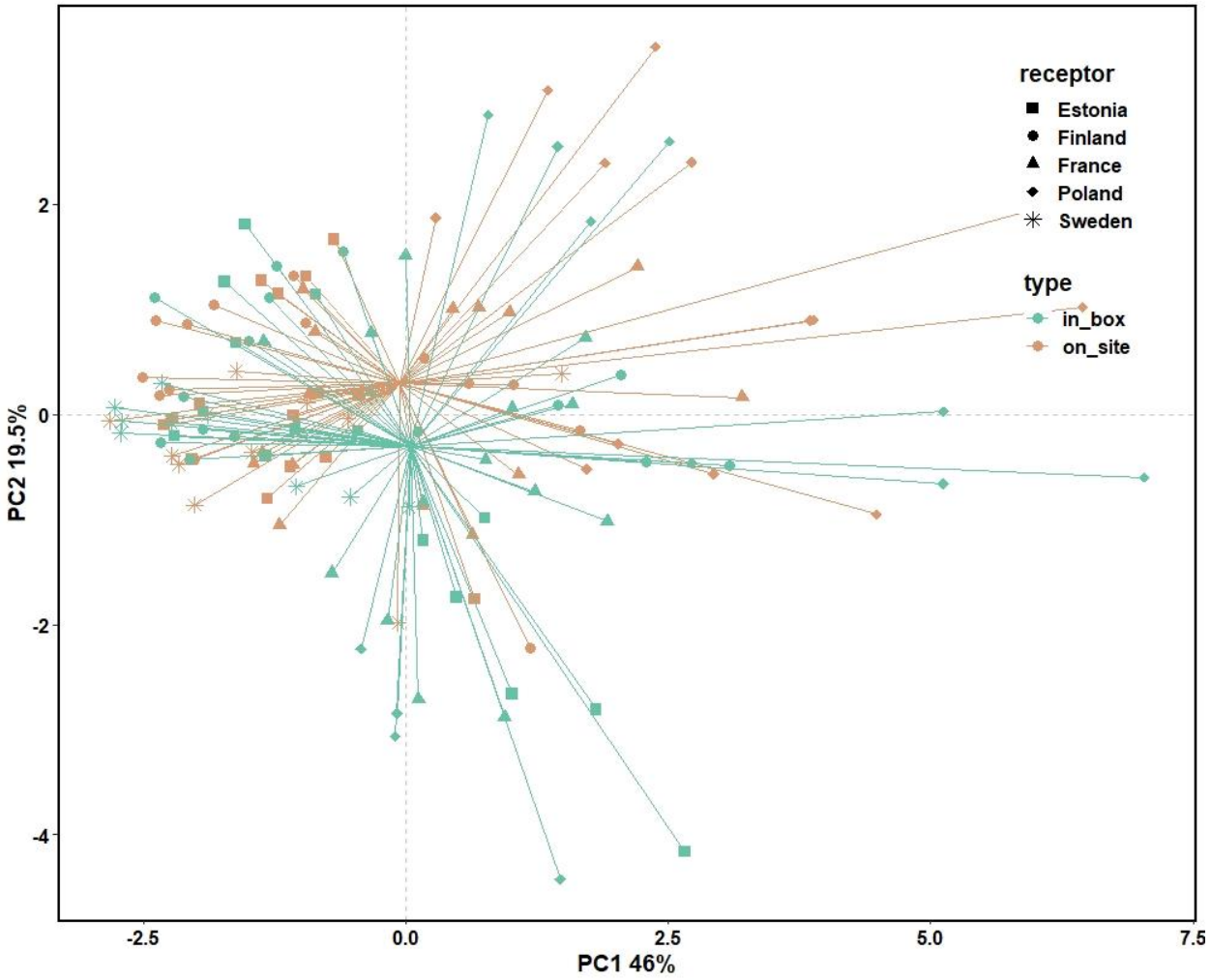


Figure S2. PCA on *Sphagnum* metabolites over three seasons in the boxes (which stayed at their site of origin) and at the control plots on the sites (outside the boxes). Pale color corresponds to the samples collected from the boxes and orange — samples outside the boxes.

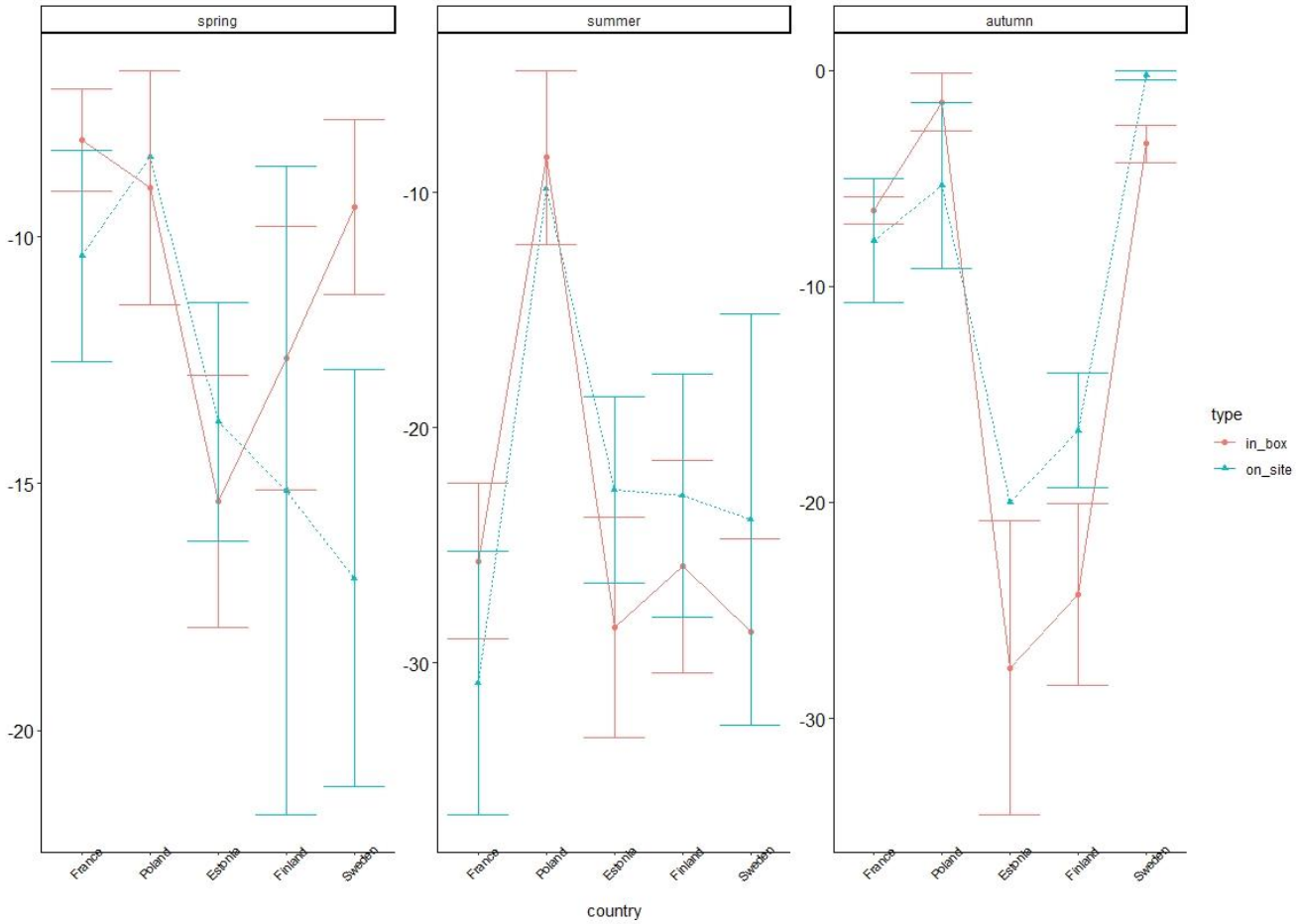


Figure S3. Dynamic of gross primary productivity measured in the boxes (which stayed at their site of origin) and at the control plots on the sites (outside the boxes) over three seasons. Pale red color corresponds to the samples collected from the boxes and pale blue — samples outside the boxes.

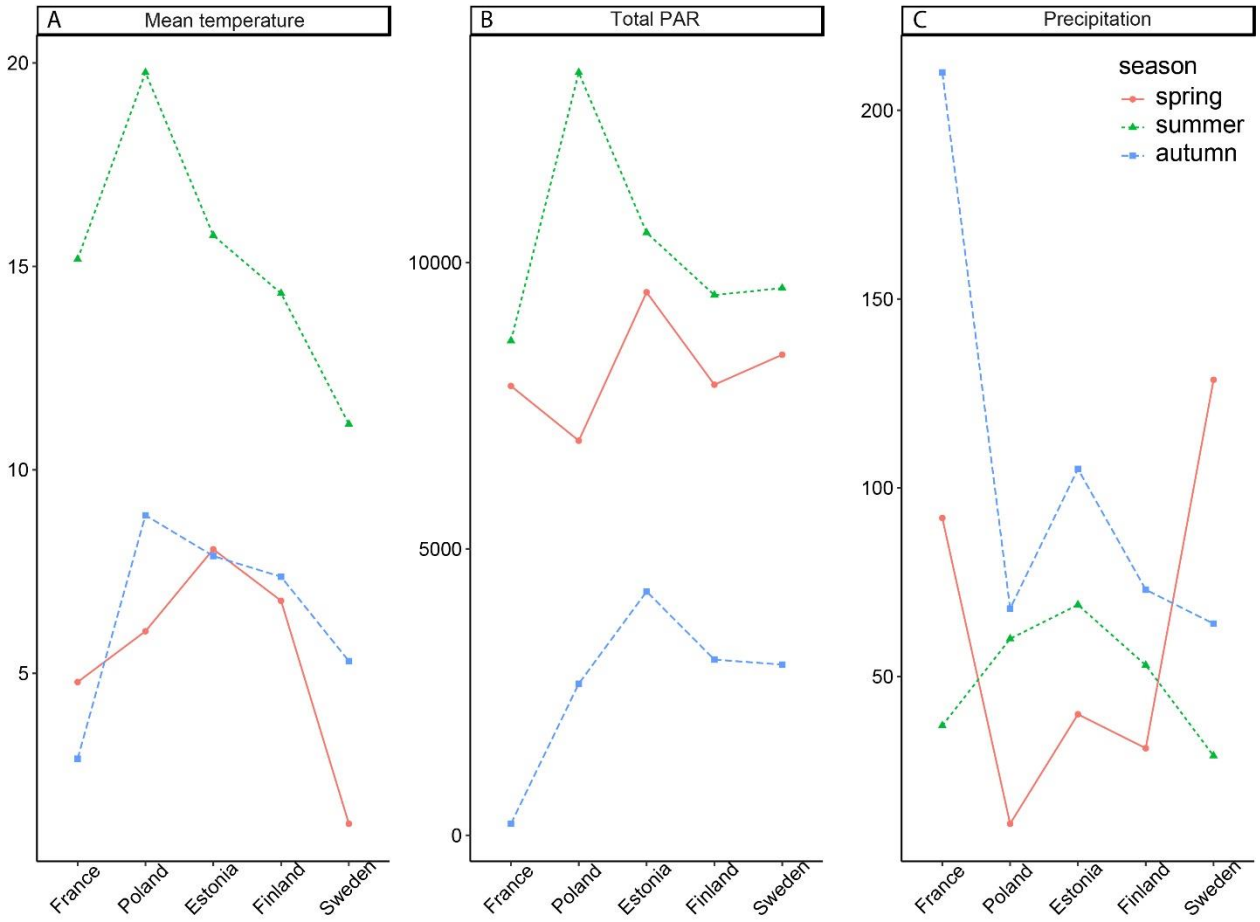


Figure S4. (A) Temperature, (B) Total PAR, (C) Precipitation. Climatic variables are characterized by mean values of the 30 days period preceding each sampling campaign. Colors of lines correspond to seasons.

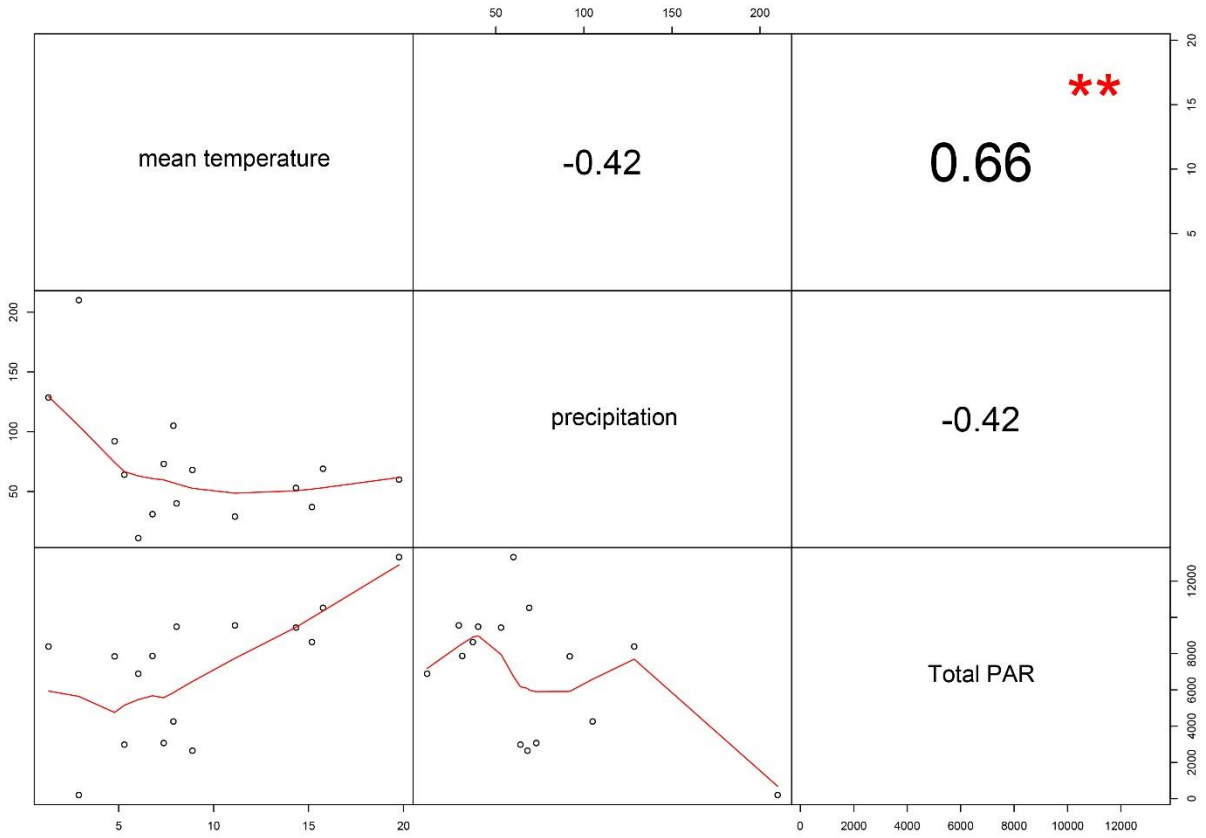


Figure S5. Correlation plot between climatic variables (characterized by mean values of the 30 days period preceding each sampling campaign). Asterix correspond to significant correlation between variables.

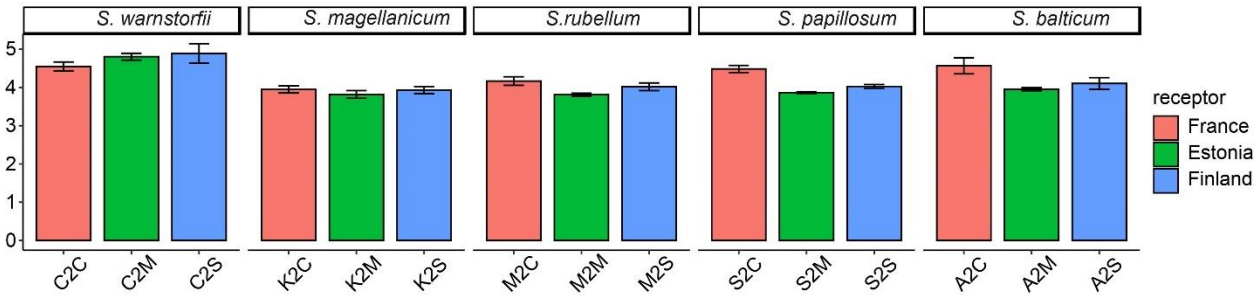


Figure S6. pH values in the boxes from the same site dispatched along the gradient.

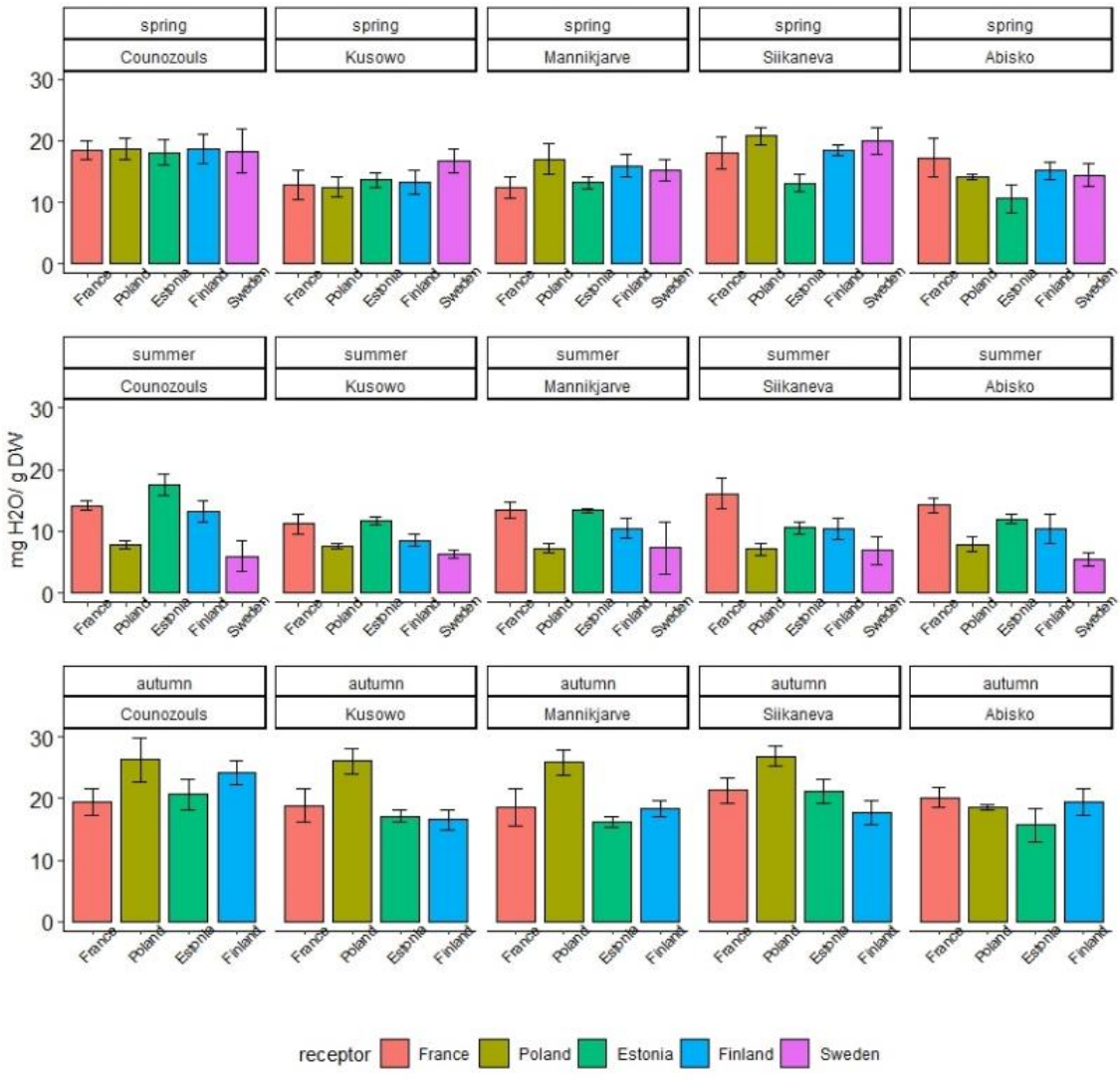


Figure S7. Barplot of water content in the *Sphagnum* collected in five sites along the gradient over three seasons. Data represents means and standard errors (SE)

Figure S8. Barplot of water-extractable organic carbon in the *Sphagnum* collected in five sites along the gradient over three seasons. Data represents means and standard errors (SE).

Figure S9. Barplot of water-extractable organic nitrogen in the *Sphagnum* collected in five sites along the gradient over three seasons. Data represents means and standard errors (SE).

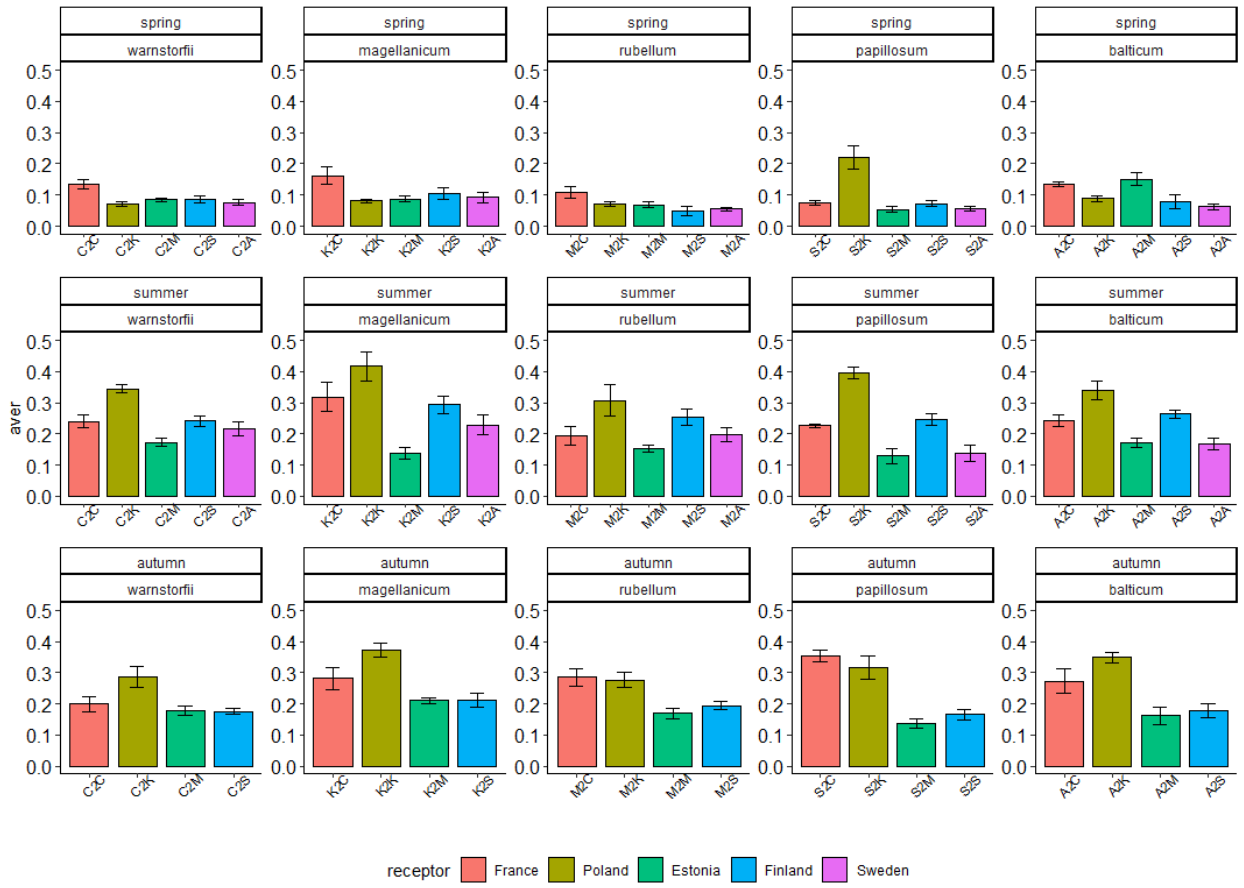


Figure S10. Barplot of chlorophyll a content in the *Sphagnum* collected in five sites along the gradient over three seasons. Data represents means and standard errors (SE).

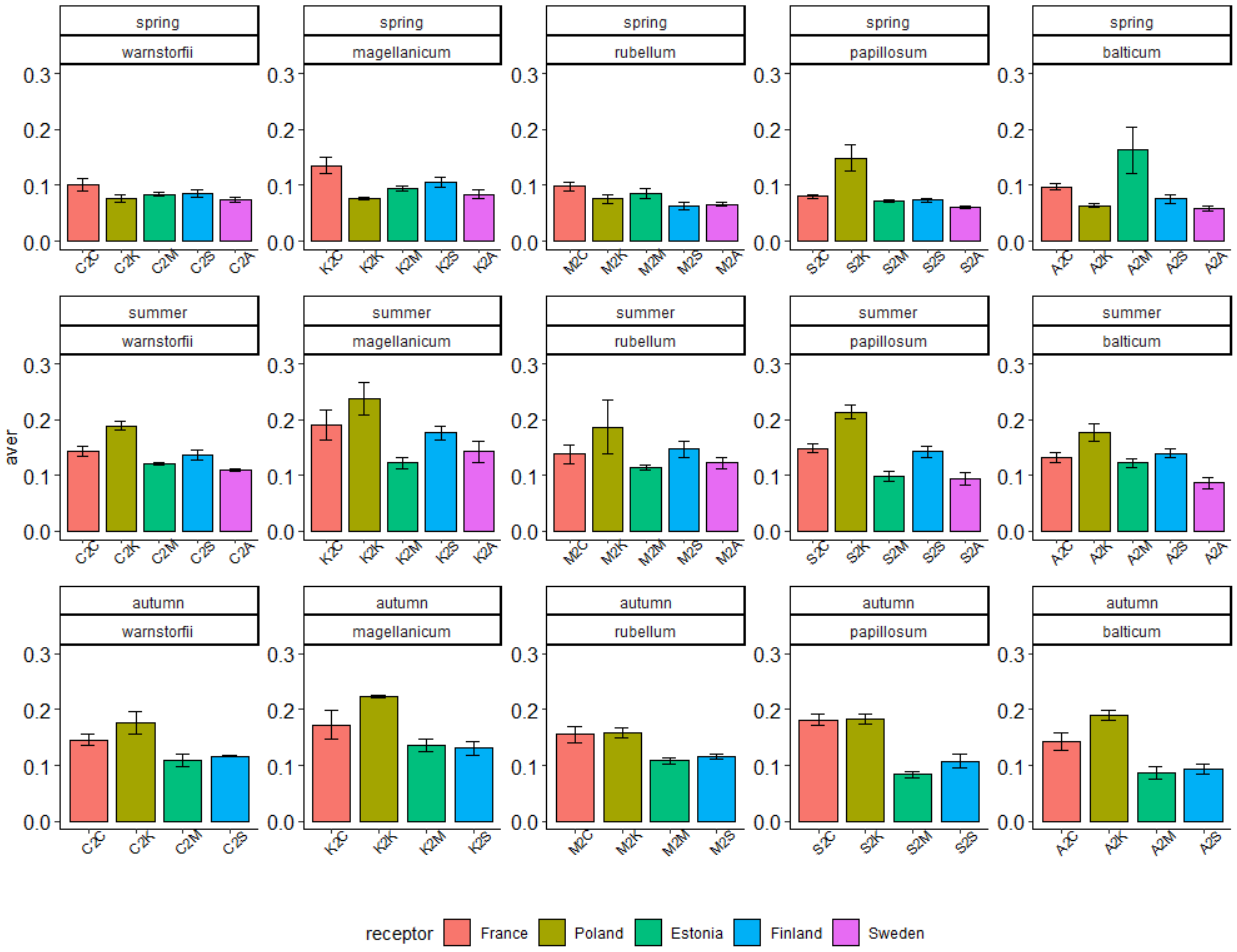


Figure S11. Barplot of chlorophyll b content in the *Sphagnum* collected in five sites along the gradient over three seasons. Data represents means and standard errors (SE).

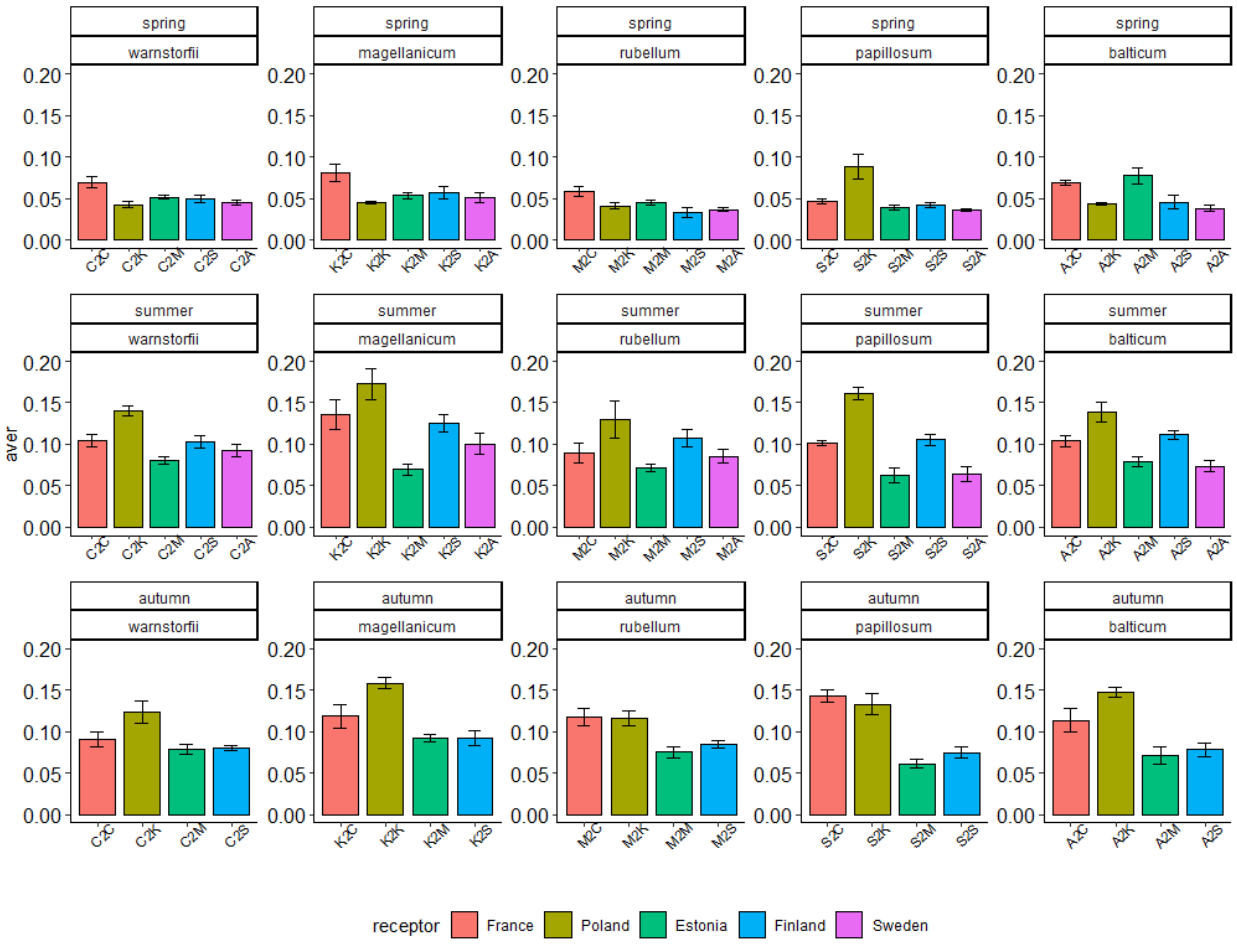


Figure S12. Barplot of carotenoids content in the *Sphagnum* collected in five sites along the gradient over three seasons. Data represents means and standard errors (SE).

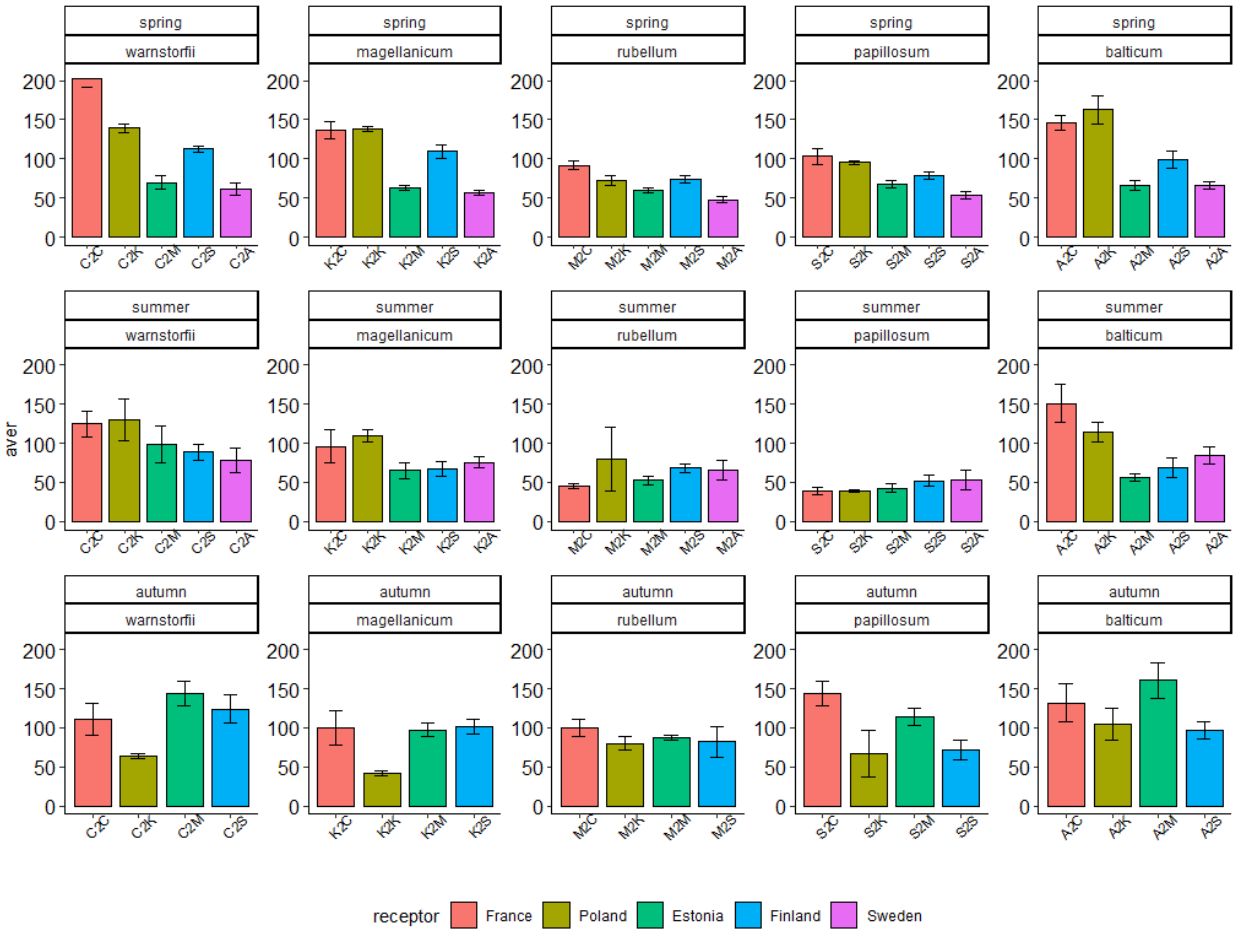


Figure S13. Barplot of total carbohydrates content in the *Sphagnum* collected in five sites along the gradient over three seasons. Data represents means and standard errors (SE).

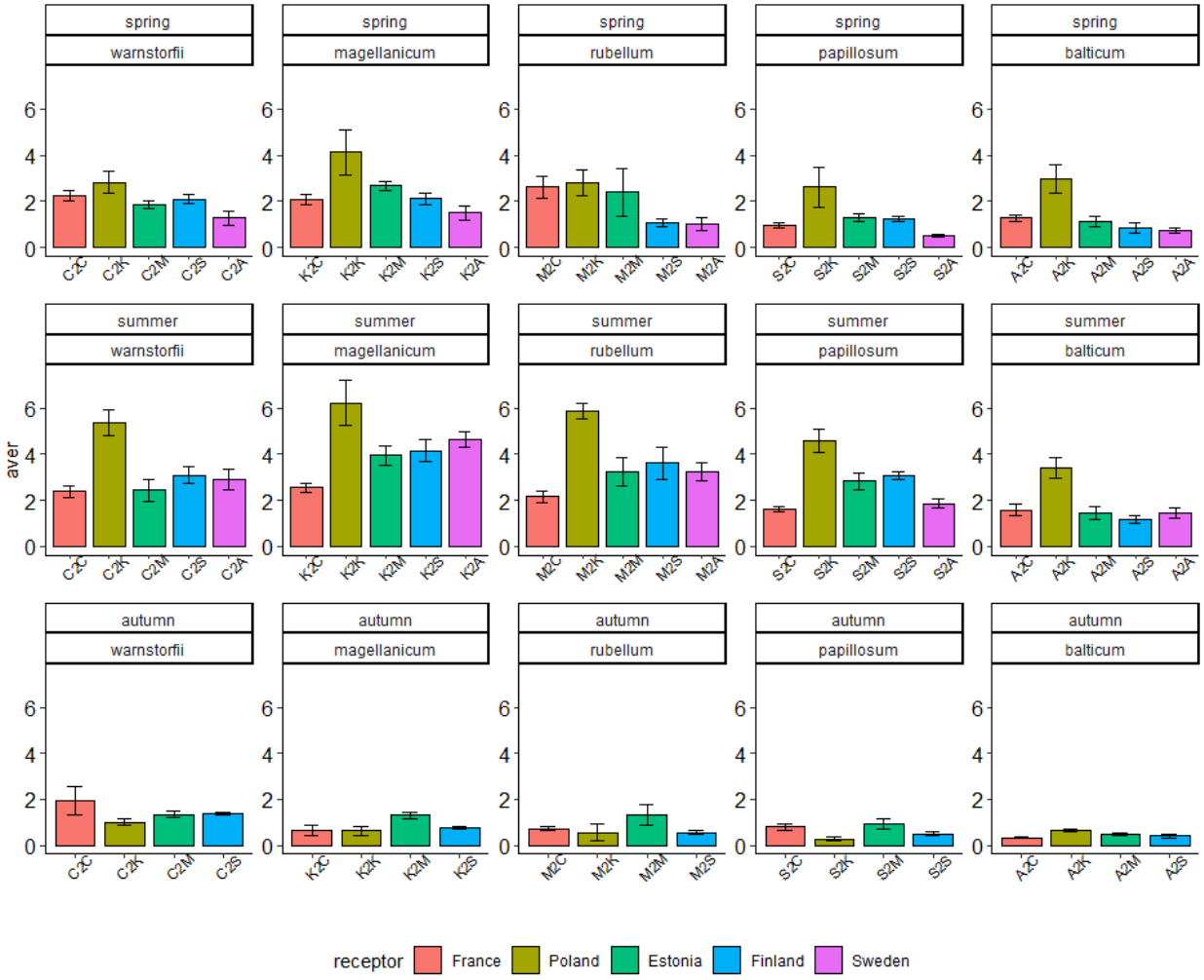


Figure S14. Barplot of water-soluble phenols content in the *Sphagnum* collected in five sites along the gradient over three seasons. Data represents means and standard errors (SE).

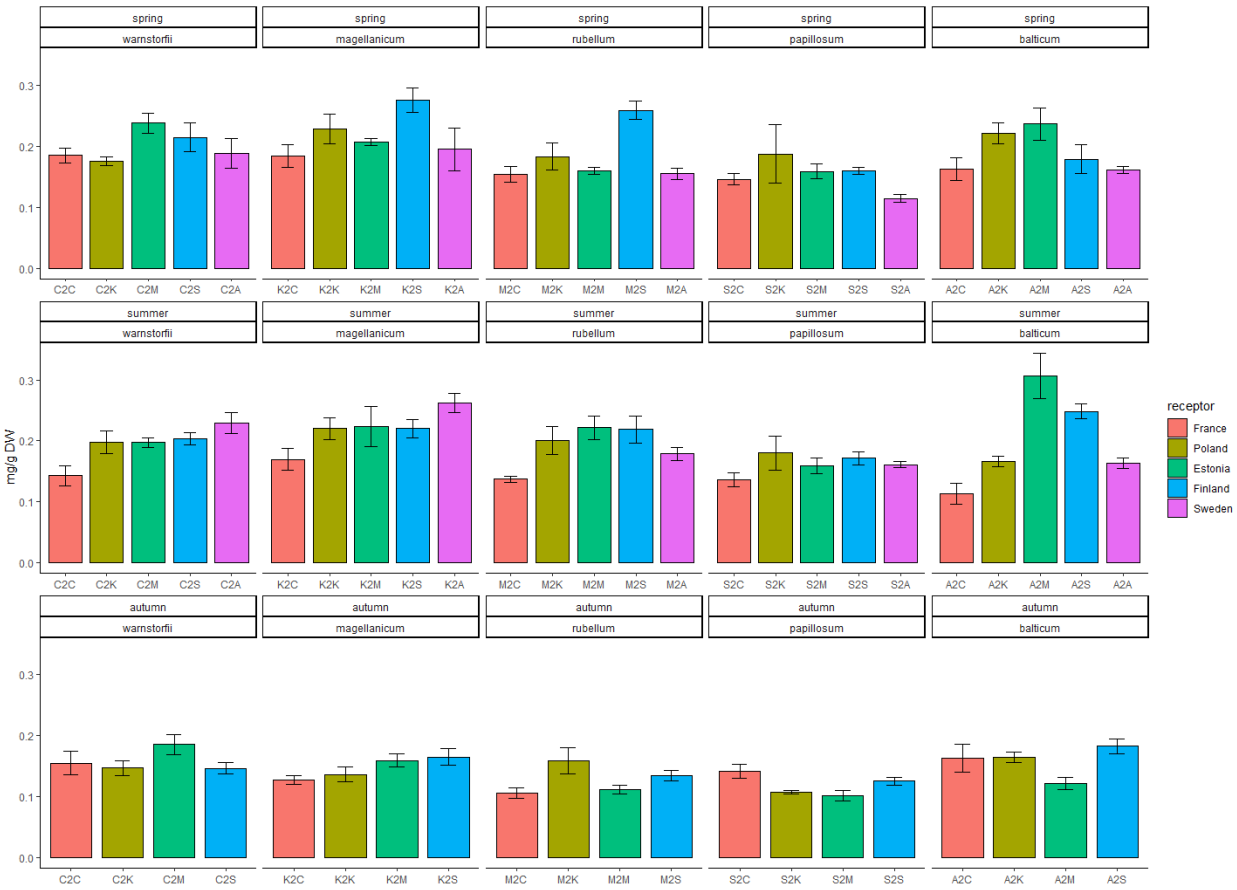


Figure S15. Barplot of proline content in the *Sphagnum* collected in five sites along the gradient over three seasons. Data represents means and standard errors (SE).

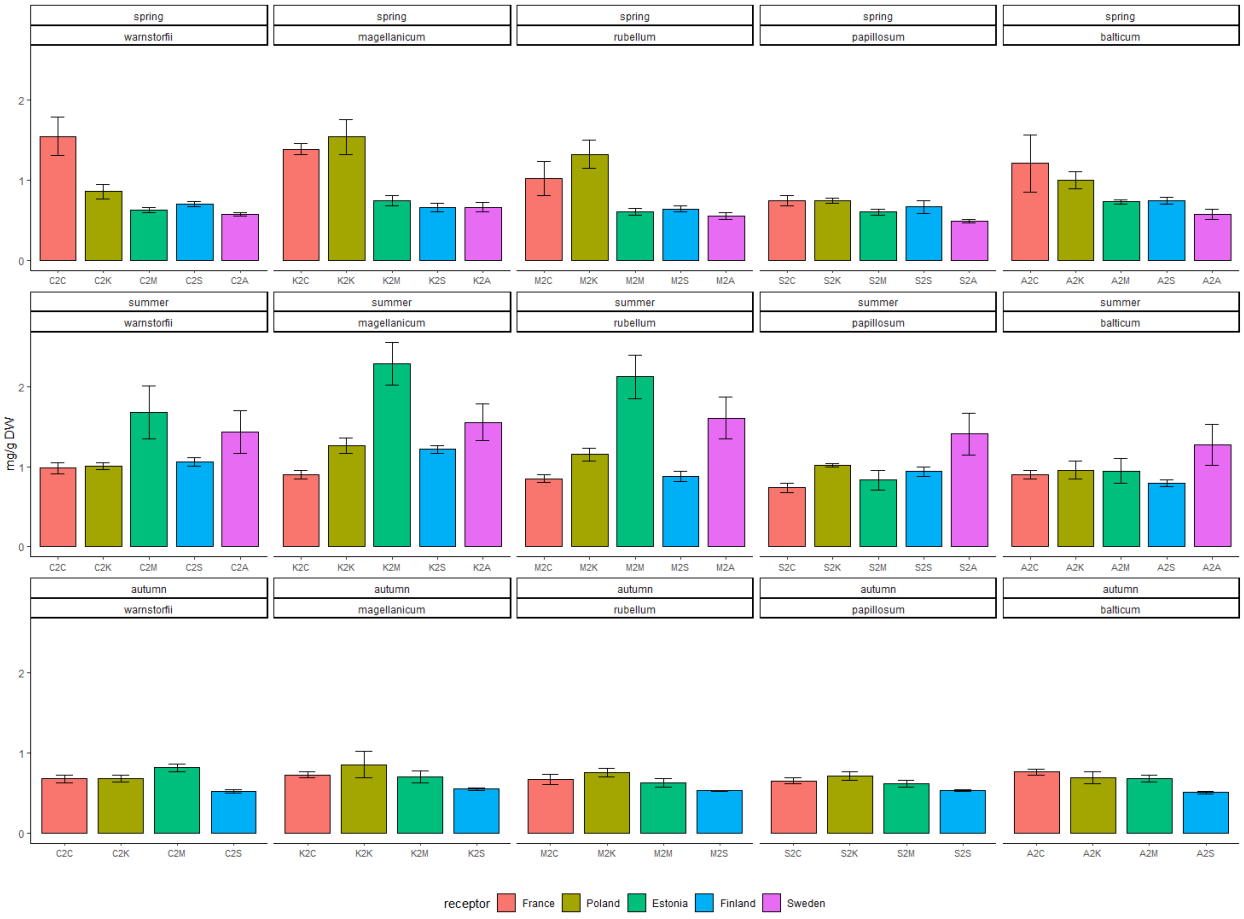


Figure S16. Barplot of total tannins content in the *Sphagnum* collected in five sites along the gradient over three seasons. Data represents means and standard errors (SE).

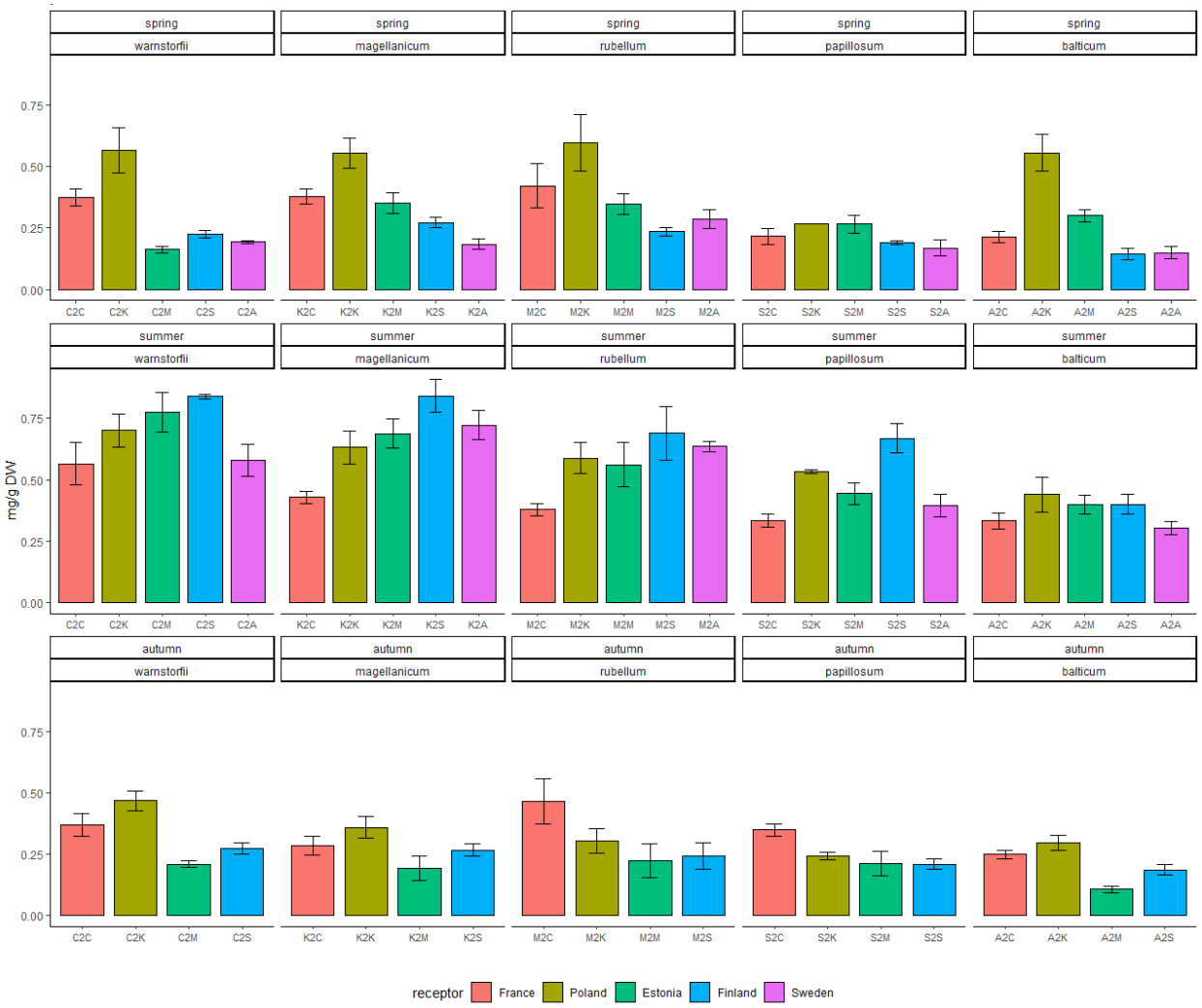


Figure S17. Barplot of total phenols content in the *Sphagnum* collected in five sites along the gradient over three seasons. Data represents means and standard errors (SE).

Figure S18. Barplot of total flavonoids content in the *Sphagnum* collected in five sites along the gradient over three seasons. Data represents means and standard errors (SE).

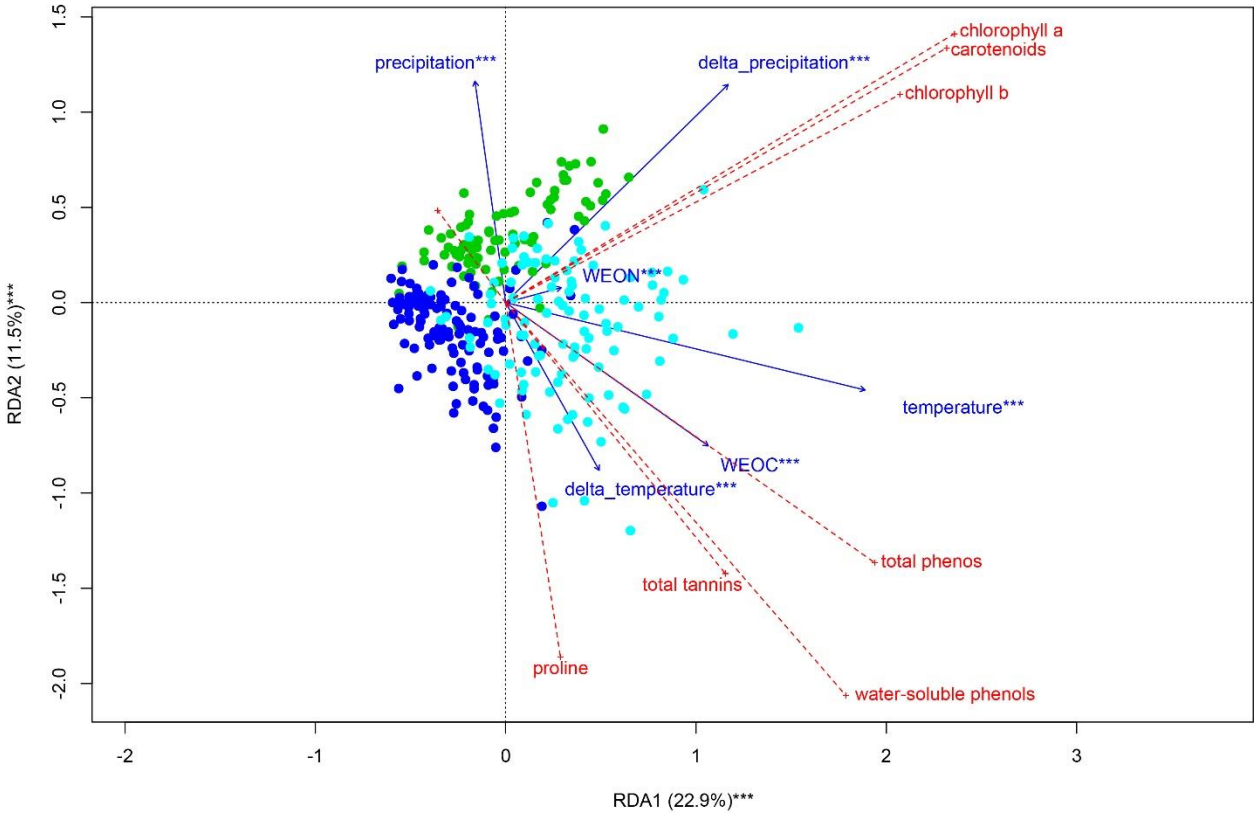
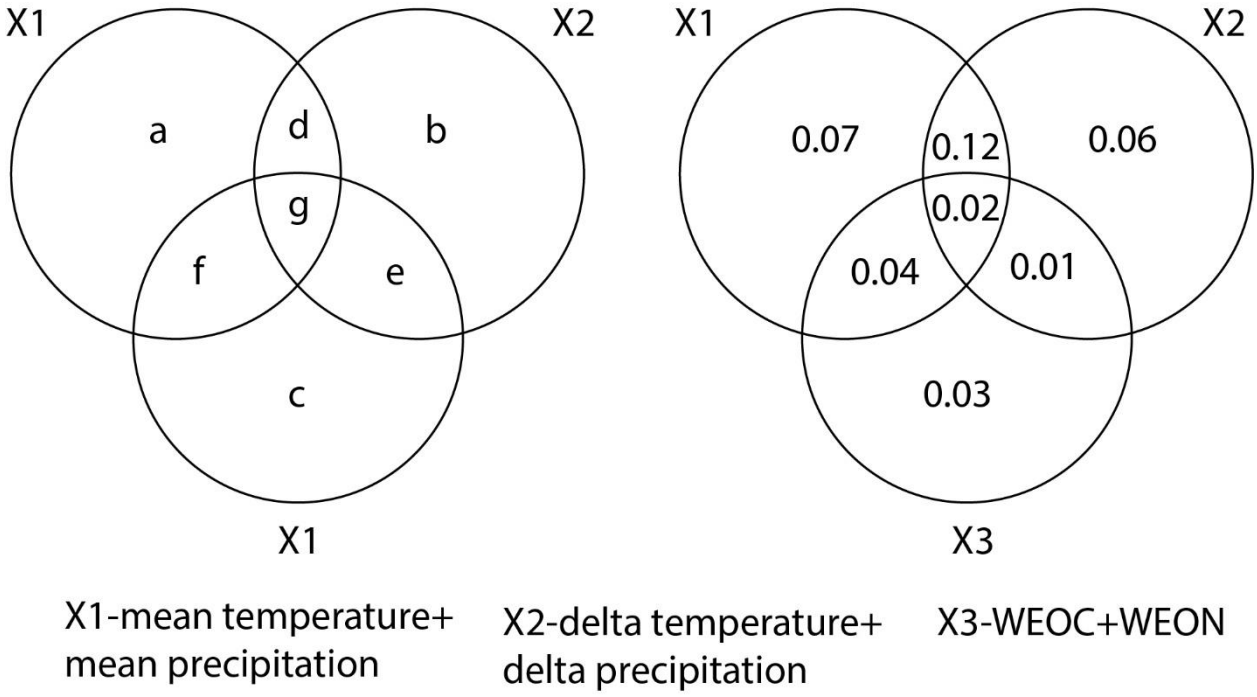


Figure S19. Redundancy Analysis (RDA) of metabolites in *Sphagnum* collected over three seasons in relation to local (WEOC and WEON) and regional (temperature, precipitation, delta temperature and delta) environmental factors. Adjusted R^2=34%. Colors represents the season: blue - spring; light blue – summer, green – autumn.



	Df	R.square	Adj.R.square	Testable
[a+d+f+g] = X1	2	0.2549305	0.25004480	TRUE
[b+d+e+g] = X2	2	0.2163397	0.21120091	TRUE
[c+e+f+g] = X3	2	0.1028410	0.09695801	TRUE
[a+b+d+e+f+g] = X1+X2	4	0.3275273	0.31864980	TRUE
[a+c+d+e+f+g] = X1+X3	4	0.2936602	0.28433560	TRUE
[b+c+d+e+f+g] = X2+X3	4	0.2879085	0.27850793	TRUE
[a+b+c+d+e+f+g] = All	6	0.3582979	0.34550653	TRUE

Figure S20. Variance partitioning with proportion of explained variance of all *Sphagnum* metabolites in *Sphagnum* five species. Values below 0 are not shown.

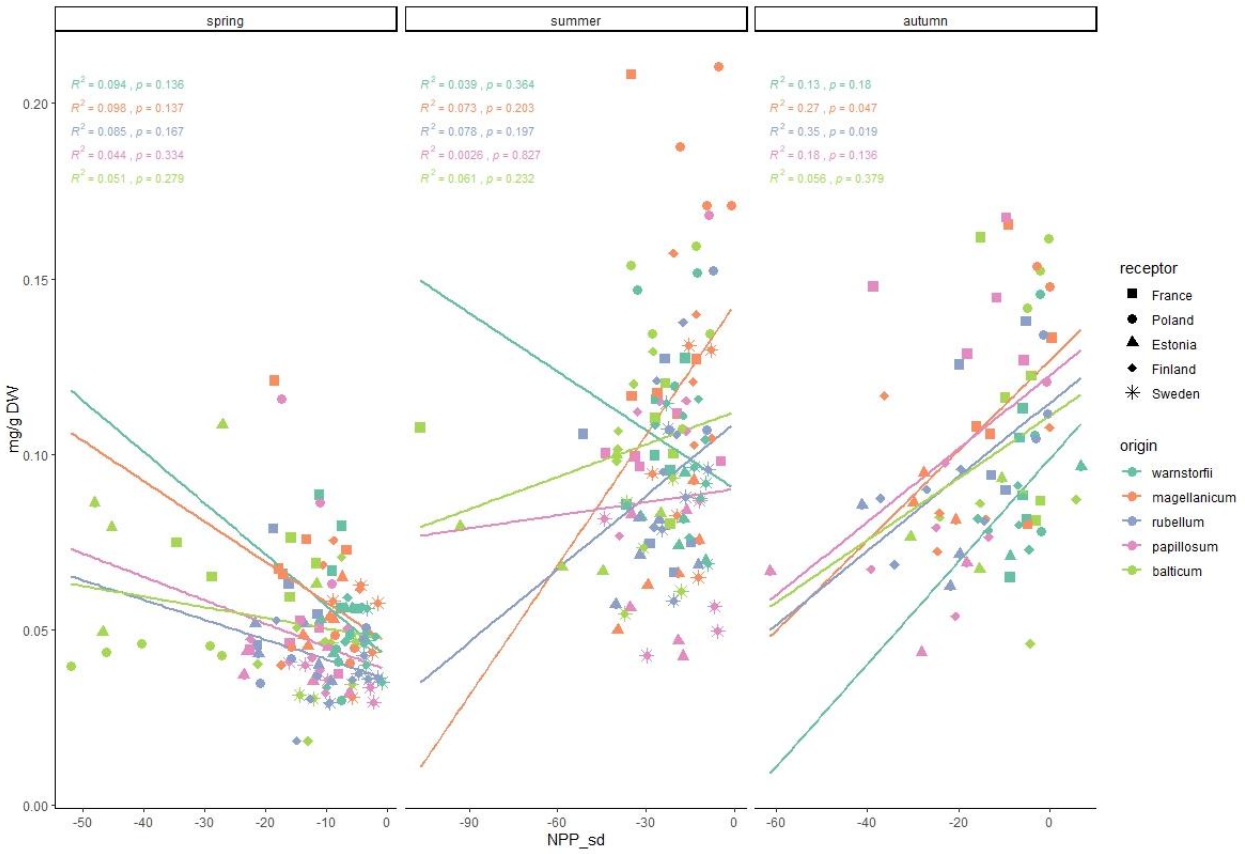


Figure S21. Correlation between *Sphagnum* carotenoids and GEP of boxes transplanted to five receptor sites along the gradient over three seasons. Receptor sites represent as shapes and transplanted species represented as colors. Both species and receptor sites are ordered according to south-north gradient (from warmer to colder).

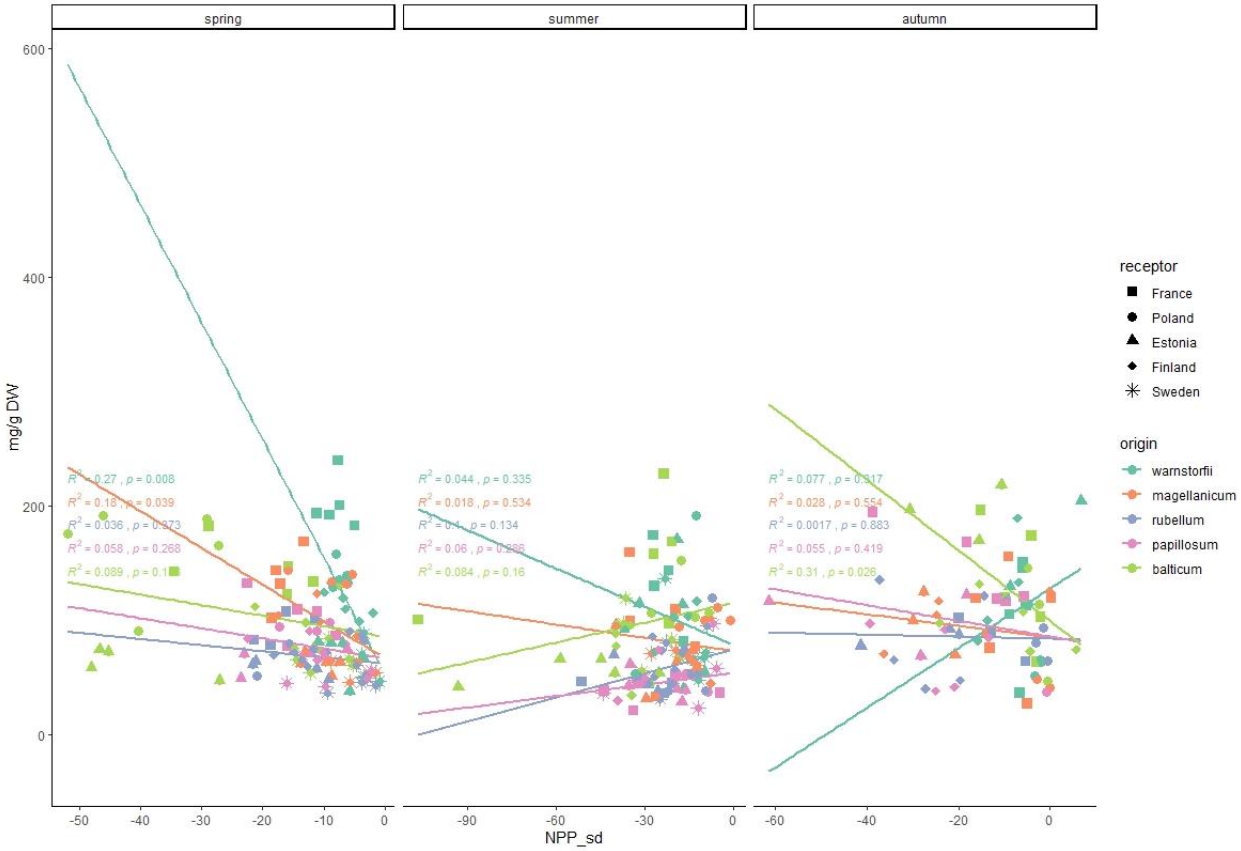


Figure S22. Correlation between *Sphagnum* total carbohydrates and GEP of boxes transplanted to five receptor sites along the gradient over three seasons. Receptor sites represent as shapes and transplanted species represented as colors. Both species and receptor sites are ordered according to south-north gradient (from warmer to colder).

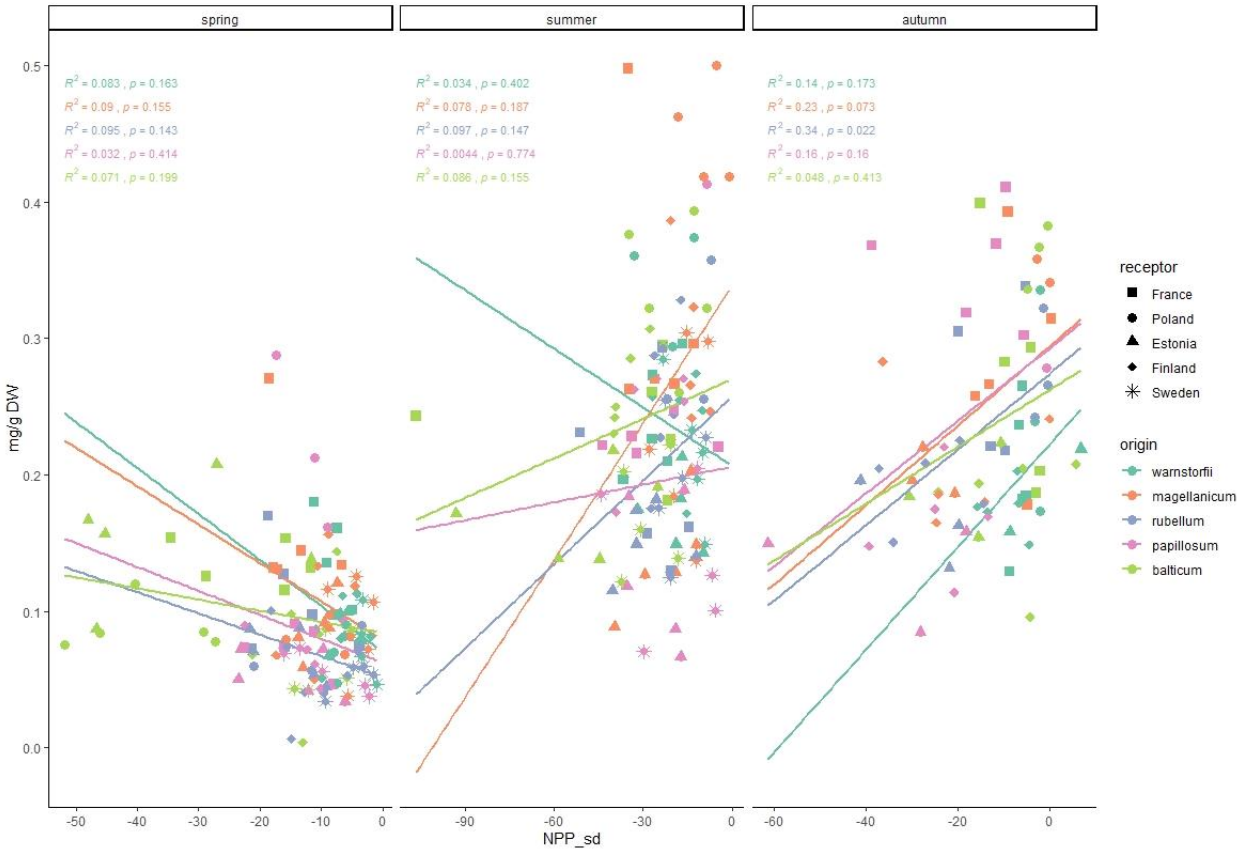


Figure S23. Correlation between *Sphagnum* chlorophyll a and GEP of boxes transplanted to five receptor sites along the gradient over three seasons. Receptor sites represent as shapes and transplanted species represented as colors. Both species and receptor sites are ordered according to south-north gradient (from warmer to colder).

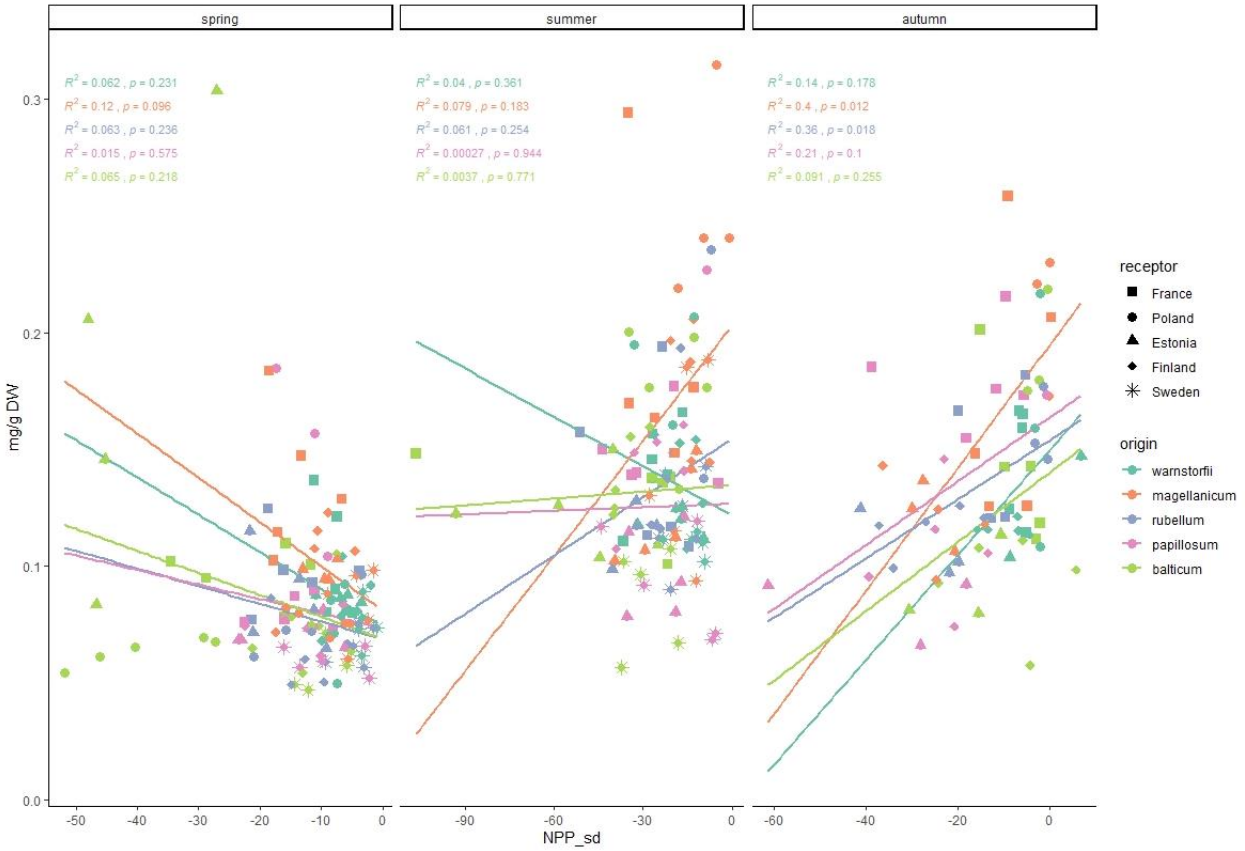


Figure S24. Correlation between *Sphagnum* chlorophyll b and GEP of boxes transplanted to five receptor sites along the gradient over three seasons. Receptor sites represent as shapes and transplanted species represented as colors. Both species and receptor sites are ordered according to south-north gradient (from warmer to colder).

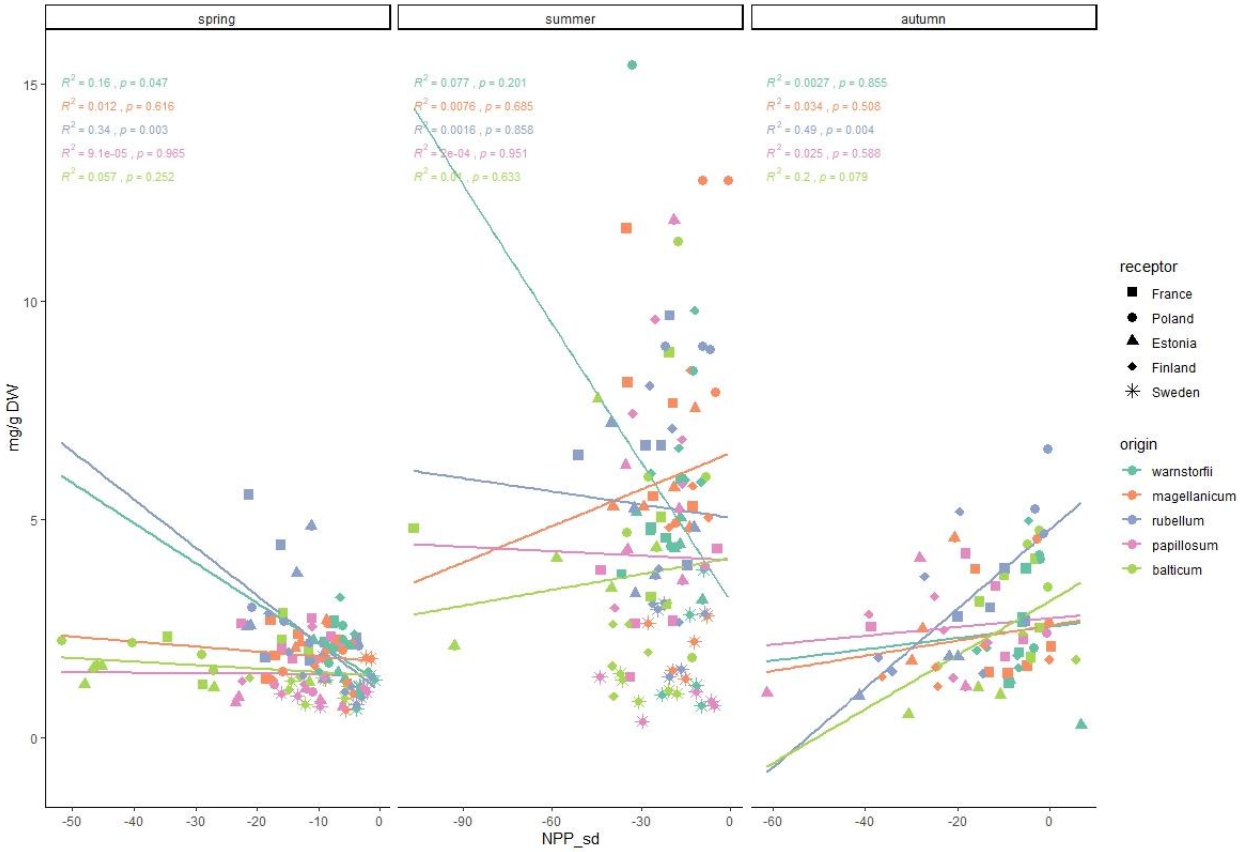


Figure S25. Correlation between *Sphagnum* total flavonoids and GEP of boxes transplanted to five receptor sites along the gradient over three seasons. Receptor sites represent as shapes and transplanted species represented as colors. Both species and receptor sites are ordered according to south-north gradient (from warmer to colder).

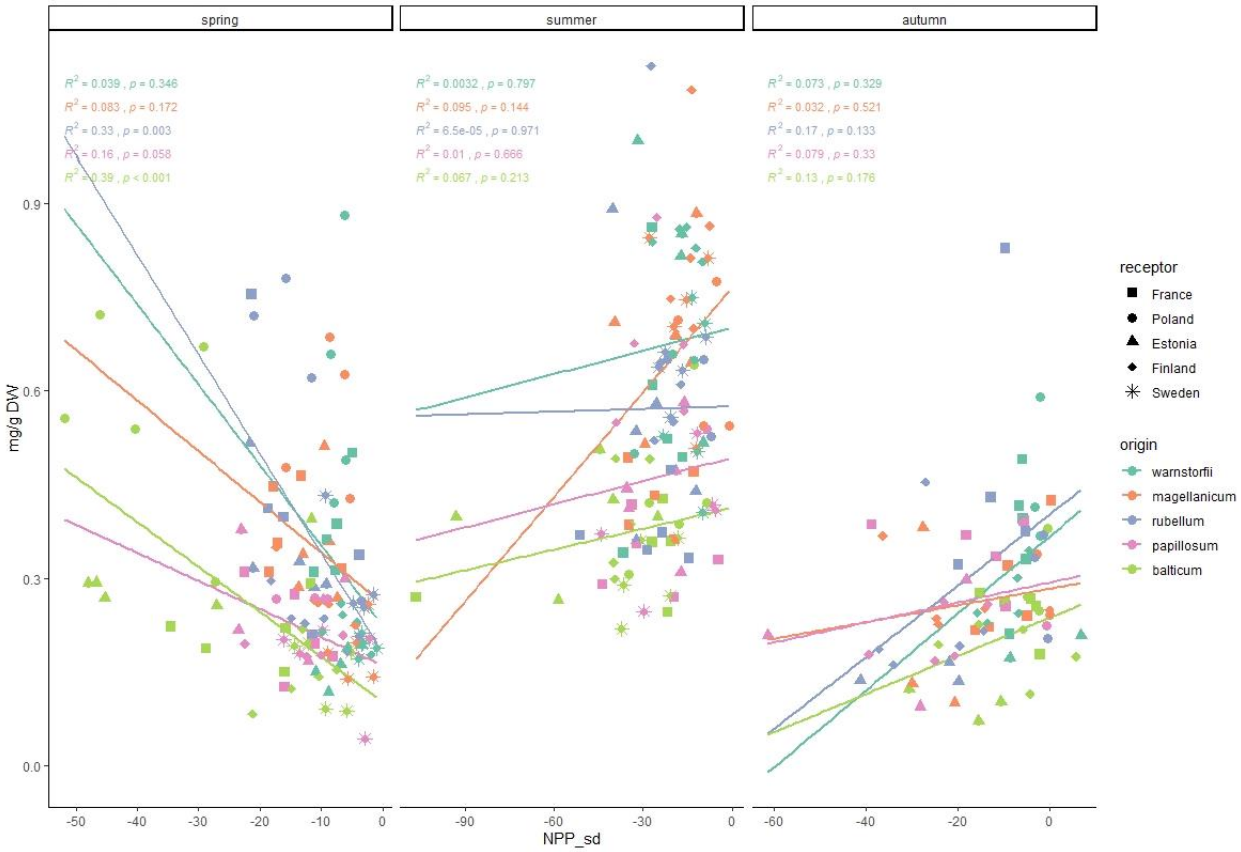


Figure S26. Correlation between *Sphagnum* total phenols and GEP of boxes transplanted to five receptor sites along the gradient over three seasons. Receptor sites represent as shapes and transplanted species represented as colors. Both species and receptor sites are ordered according to south-north gradient (from warmer to colder).

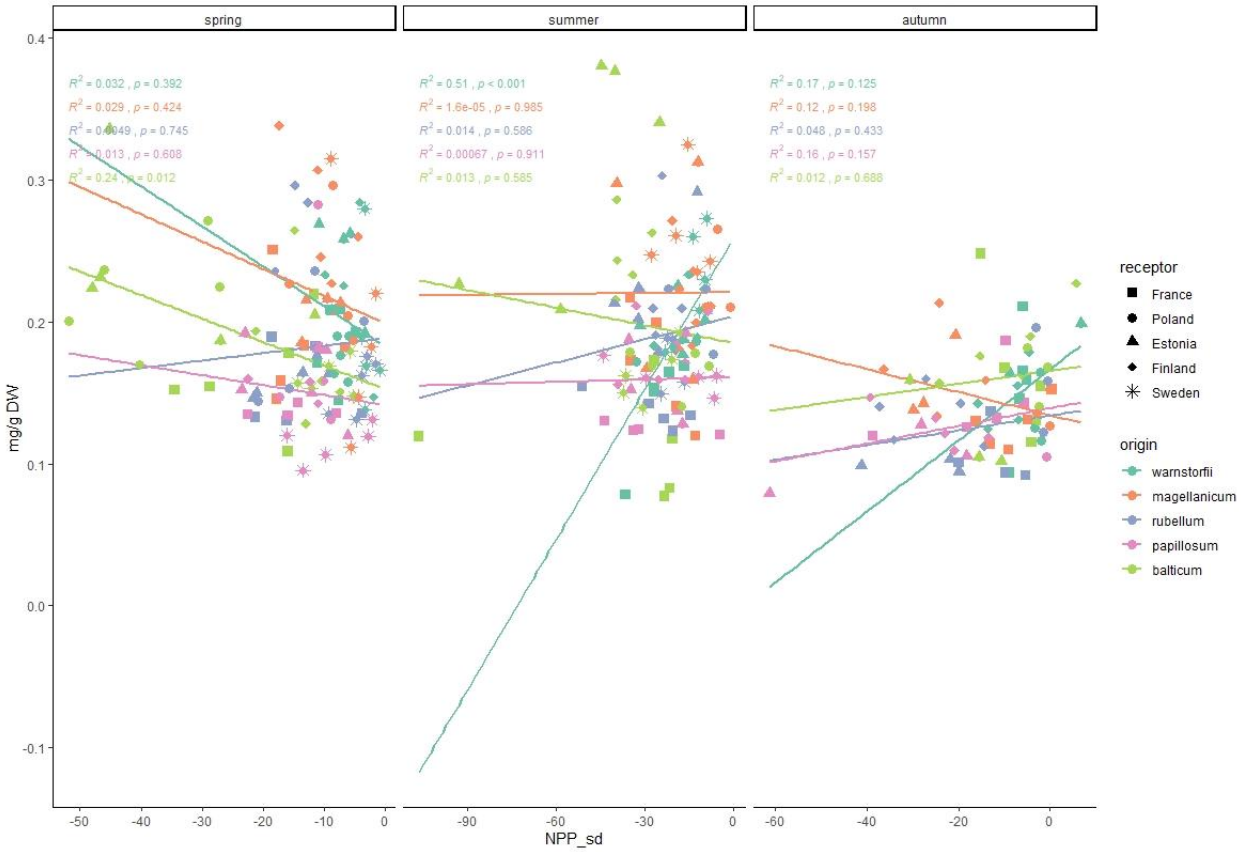


Figure S27. Correlation between *Sphagnum* proline and GEP of boxes transplanted to five receptor sites along the gradient over three seasons. Receptor sites represent as shapes and transplanted species represented as colors. Both species and receptor sites are ordered according to south-north gradient (from warmer to colder).

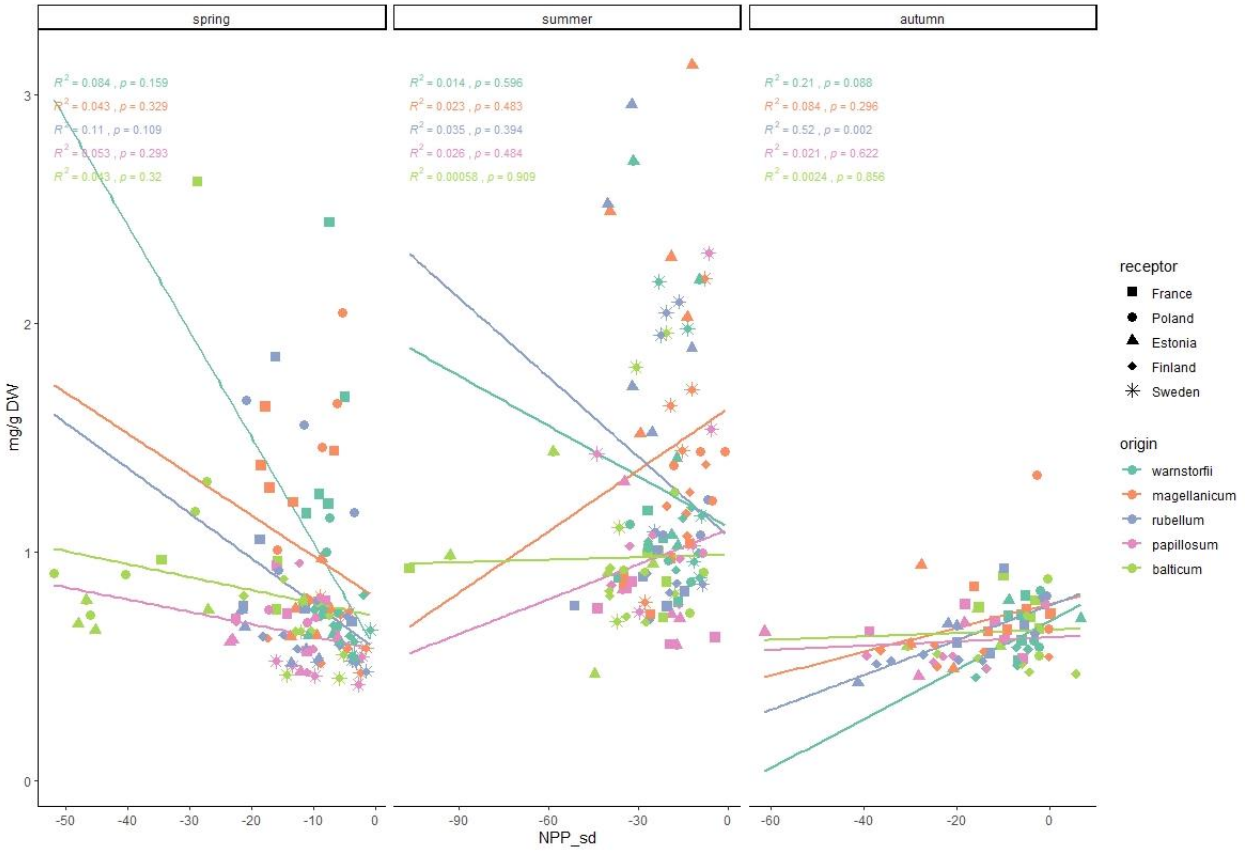


Figure S28. Correlation between *Sphagnum* total tannins and GEP of boxes transplanted to five receptor sites along the gradient over three seasons. Receptor sites represent as shapes and transplanted species represented as colors. Both species and receptor sites are ordered according to south-north gradient (from warmer to colder).

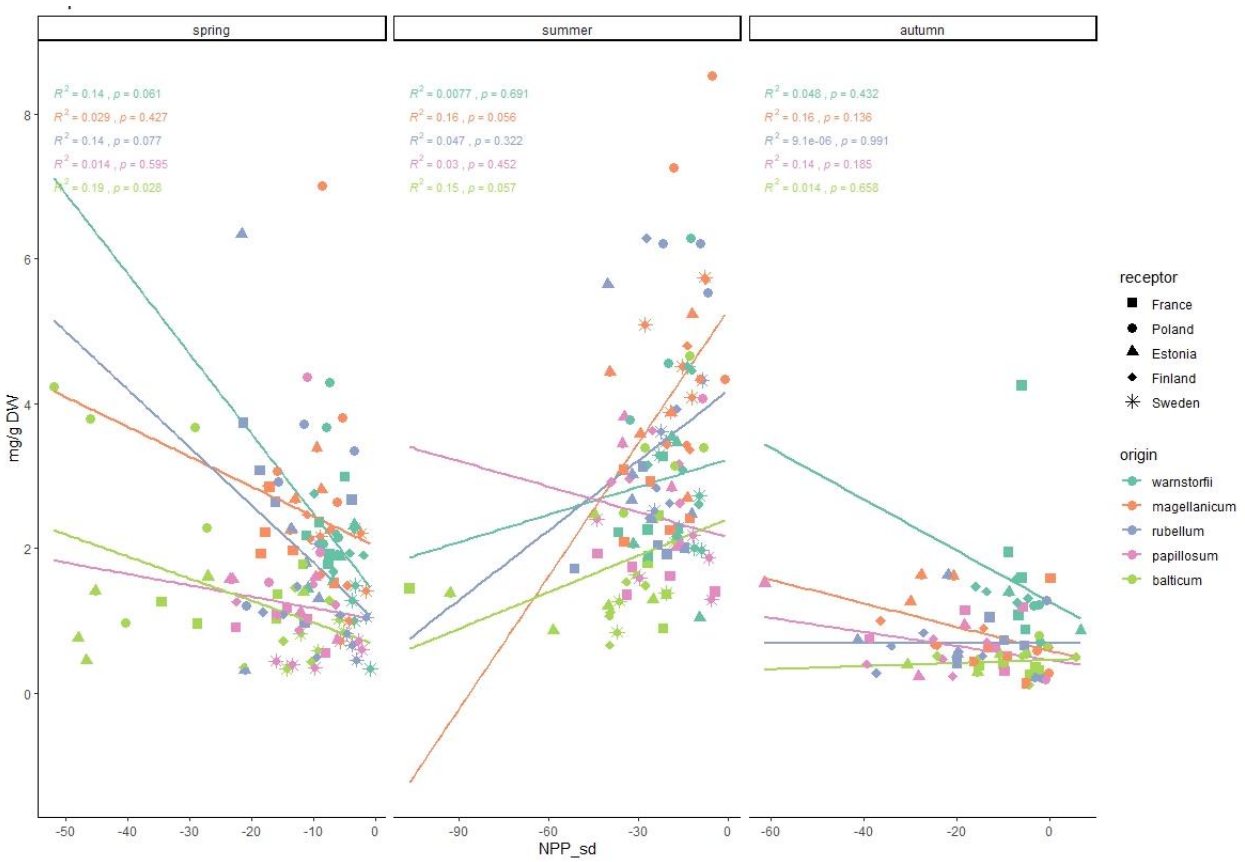


Figure S29. Correlation between water-soluble phenols and GEP of boxes transplanted to five receptor sites along the gradient over three seasons. Receptor sites represent as shapes and transplanted species represented as colors. Both species and receptor sites are ordered according to south-north gradient (from warmer to colder).

Supplementary tables

Table S1. Climatic data for the five study sites 30 days before sampling. Cumulative temperature and precipitation were calculated as summed values per every season of 2019.Temperature and precipitation seasonality calculated on averaged data over the period 1960-2018 (Fick and Hijmans, 2017).

country	season	mean temperature, °C	precipitation, mm	PAR, µmol photons/m²/day	cumulative temperature	cumulative precipitation	temperature seasonality*	precipitation seasonality**
France	spring	4.8	92	7847	151	92	54.5	1.5
Poland	spring	6.0	11	6890	192	32	78.5	2.7
Estonia	spring	8.0	40	9484	252	40	84.7	3.1
Finland	spring	6.8	31	7868	214	31	86.0	3.1
Sweden	spring	1.3	129	8391	42	128.6	75.2	3.8
France	summer	15.2	37	8635	957	286	54.5	1.5
Poland	summer	19.8	60	13320	1306	172	78.5	2.7
Estonia	summer	15.8	69	10523	1280	231	84.7	3.1
Finland	summer	14.3	53	9433	1149	145	86.0	3.1
Sweden	summer	11.1	29	9555	670	229.6	75.2	3.8
France	autumn	2.9	210	201	3668	1213	54.5	1.5
Poland	autumn	8.9	68	2646	3367	614	78.5	2.7
Estonia	autumn	7.9	105	4256	2082	585	84.7	3.1
Finland	autumn	7.4	73	3068	1512	396	86.0	3.1
Sweden	autumn	5.3	64	2980	1349	346.6	75.2	3.8

From (O'Donnell and Ignizio, 2012):

* "The amount of temperature variation over a given year (or averaged years) based on the standard deviation (variation) of monthly temperature averages. Expressed as degrees Celsius"

**"This is a measure of the variation in monthly precipitation totals over the course of the year. This index is the ratio of the standard deviation of the monthly total precipitation to the mean monthly total precipitation (also known as the coefficient of variation) and is expressed as a percentage."

Table S2. Summary of pairwise comparison of *Sphagnum* metabolites among samples collected from the box (boxes that stayed at the site of their origin) and outside of the box (undisturbed control) over three seasons. *- significance difference

Season-metabolite-country	group1	group2	n1	n2	statistic	df	P	P. significance
autumn_carotenoids_Estonia	in the box	on the site	5	5	-1.320595043	7.961450049	0.223	ns
autumn_carotenoids_Finland	in the box	on the site	5	5	0.592062237	7.999917996	0.57	ns
autumn_carotenoids_France	in the box	on the site	5	5	1.040921372	6.585305013	0.335	ns
autumn_carotenoids_Poland	in the box	on the site	4	5	-0.169363099	6.403937285	0.871	ns
autumn_carotenoidsbo_Estonia	in the box	on the site	5	5	1.685135824	5.452236511	0.148	ns
autumn_carotenoidsbo_Finland	in the box	on the site	5	5	-1.317130589	7.988914702	0.224	ns
autumn_carotenoidsbo_France	in the box	on the site	5	5	0.841328486	5.623209229	0.434	ns
autumn_carotenoidsbo_Poland	in the box	on the site	4	5	-3.067682863	4.627860893	0.0308	*
autumn_chla_Estonia	in the box	on the site	5	5	-1.273594418	7.82086972	0.239	ns
autumn_chla_Finland	in the box	on the site	5	5	0.586100825	7.991690692	0.574	ns
autumn_chla_France	in the box	on the site	5	5	1.084109743	6.705965861	0.316	ns
autumn_chla_Poland	in the box	on the site	4	5	0.133920038	6.997149993	0.897	ns
autumn_chlb_Estonia	in the box	on the site	5	5	-1.728463168	7.376268295	0.125	ns
autumn_chlb_Finland	in the box	on the site	5	5	0.668146612	7.999171717	0.523	ns
autumn_chlb_France	in the box	on the site	5	5	1.023337147	5.077683132	0.352	ns
autumn_chlb_Poland	in the box	on the site	4	5	-1.124190125	4.063389523	0.323	ns
autumn_flavonoids_Estonia	in the box	on the site	5	5	2.600473328	5.683143052	0.0427	*

autumn_flavonoids_Finland	in the box	on the site	5	5	1.405634375	7.704668924	0.199	ns
autumn_flavonoids_France	in the box	on the site	5	5	-0.876832226	6.895069459	0.41	ns
autumn_flavonoids_Poland	in the box	on the site	4	5	0.324132355	6.080436847	0.757	ns
autumn_total phenols_Estonia	in the box	on the site	5	5	0.45658641	4.29635879	0.67	ns
autumn_total phenols_Finland	in the box	on the site	5	5	0.747697812	7.998714875	0.476	ns
autumn_total phenols_France	in the box	on the site	5	5	-1.084412561	6.603396026	0.316	ns
autumn_total phenols_Poland	in the box	on the site	4	5	0.709232711	5.588138821	0.507	ns
autumn_proline_Estonia	in the box	on the site	5	5	-0.902766786	6.693261235	0.398	ns
autumn_proline_Finland	in the box	on the site	5	5	0.991753169	7.433135364	0.352	ns
autumn_proline_France	in the box	on the site	5	5	-0.997642292	6.469317563	0.354	ns
autumn_proline_Poland	in the box	on the site	4	5	0.650870762	4.660323714	0.546	ns
autumn_tannins_Estonia	in the box	on the site	5	5	-2.924383182	6.146649336	0.0257	*
autumn_tannins_Finland	in the box	on the site	5	5	0.554678487	6.525505272	0.598	ns
autumn_tannins_France	in the box	on the site	5	5	-0.831472911	5.751664874	0.439	ns
autumn_tannins_Poland	in the box	on the site	4	5	0.993539197	3.132026096	0.391	ns
autumn_water-soluble phenols_Estonia	in the box	on the site	5	5	0.601964059	7.468700881	0.565	ns
autumn_water-soluble phenols_Finland	in the box	on the site	5	5	-1.432689611	7.262705306	0.194	ns
autumn_water-soluble phenols_France	in the box	on the site	5	5	1.322715439	5.313711585	0.24	ns

autumn_water-soluble phenols_Poland	in the box	on the site	4	5	-1.988617433	3.312558357	0.132	ns
spring_carotenoids_Estonia	in the box	on the site	5	5	0.608272207	7.990118447	0.56	ns
spring_carotenoids_Finland	in the box	on the site	5	5	0.372815977	7.920863254	0.719	ns
spring_carotenoids_France	in the box	on the site	5	5	1.251736508	7.085202607	0.25	ns
spring_carotenoids_Poland	in the box	on the site	4	3	-11.53636857	2.200383485	0.00521	**
spring_carotenoids_Sweden	in the box	on the site	5	5	-0.17757547	5.562725376	0.865	ns
spring_carotenoidsbo_Estonia	in the box	on the site	5	5	1.550181702	4.649816576	0.186	ns
spring_carotenoidsbo_Finland	in the box	on the site	5	5	0.236938813	5.898484171	0.821	ns
spring_carotenoidsbo_France	in the box	on the site	5	5	3.809473814	7.680978108	0.00557	**
spring_carotenoidsbo_Poland	in the box	on the site	4	3	-7.424563687	4.844296256	0.0008	***
spring_carotenoidsbo_Sweden	in the box	on the site	5	5	0.598339149	7.370399152	0.568	ns
spring_chla_Estonia	in the box	on the site	5	5	0.131688035	7.998923466	0.898	ns
spring_chla_Finland	in the box	on the site	5	5	0.389100563	7.821537344	0.708	ns
spring_chla_France	in the box	on the site	5	5	1.330406897	7.761087591	0.221	ns
spring_chla_Poland	in the box	on the site	4	3	-12.62354389	2.486689447	0.00256	**
spring_chla_Sweden	in the box	on the site	5	5	-0.913138263	6.819786449	0.392	ns
spring_chlb_Estonia	in the box	on the site	5	5	1.68296355	6.981476176	0.136	ns
spring_chlb_Finland	in the box	on the site	5	5	1.218985778	5.193268234	0.275	ns
spring_chlb_France	in the box	on the site	5	5	0.193115783	4.269771711	0.856	ns
spring_chlb_Poland	in the box	on the site	4	3	-15.1135555	2.209739168	0.00284	**

spring_chlb_Sweden	in the box	on the site	5	5	-0.512736538	6.288598667	0.626	ns
spring_flavonoids_Estonia	in the box	on the site	5	5	3.152803317	4.146260205	0.0328	*
spring_flavonoids_Finland	in the box	on the site	5	5	1.859707826	7.694274105	0.101	ns
spring_flavonoids_France	in the box	on the site	5	5	1.570163259	7.991364911	0.155	ns
spring_flavonoids_Poland	in the box	on the site	4	3	1.223417403	4.728659978	0.279	ns
spring_flavonoids_Sweden	in the box	on the site	5	5	-3.393442458	7.215366207	0.011	*
spring_total phenols_Estonia	in the box	on the site	5	5	1.827554152	4.30203878	0.137	ns
spring_total phenols_Finland	in the box	on the site	5	5	1.157216023	5.55821783	0.294	ns
spring_total phenols_France	in the box	on the site	5	5	3.771236861	5.134589725	0.0124	*
spring_total phenols_Poland	in the box	on the site	4	3	5.541122053	3.015594609	0.0114	*
spring_total phenols_Sweden	in the box	on the site	5	5	-0.644709666	7.085643877	0.539	ns
spring_proline_Estonia	in the box	on the site	5	5	-0.324236772	5.540432573	0.758	ns
spring_proline_Finland	in the box	on the site	5	5	1.484529459	7.983655783	0.176	ns
spring_proline_France	in the box	on the site	5	5	2.178185773	7.497968379	0.0633	ns
spring_proline_Poland	in the box	on the site	4	3	-0.546688282	4.424775985	0.611	ns
spring_proline_Sweden	in the box	on the site	5	5	-1.073552978	4.780748505	0.334	ns
spring_tannins_Estonia	in the box	on the site	5	5	-0.586606587	7.196715328	0.575	ns
spring_tannins_Finland	in the box	on the site	5	5	2.018151651	4.810591312	0.102	ns
spring_tannins_France	in the box	on the site	5	5	2.600887304	4.091473644	0.0587	ns
spring_tannins_Poland	in the box	on the site	4	3	1.179391327	4.219620029	0.3	ns
spring_tannins_Sweden	in the box	on the site	5	5	-1.802079938	7.416092272	0.112	ns

spring_water-soluble phenols_Estonia	in the box	on the site	5	5	0.572379616	4.08725922	0.597	ns
spring_water-soluble phenols_Finland	in the box	on the site	5	5	-0.79985946	4.659540751	0.463	ns
spring_water-soluble phenols_France	in the box	on the site	5	5	2.589524084	7.362337155	0.0344	*
spring_water-soluble phenols_Poland	in the box	on the site	4	3	0.111715875	4.970818758	0.915	ns
spring_water-soluble phenols_Sweden	in the box	on the site	5	5	1.607138063	7.056124755	0.152	ns
summer_carotenoids_Estonia	in the box	on the site	5	5	1.888307893	6.488592157	0.104	ns
summer_carotenoids_Finland	in the box	on the site	5	5	1.022952092	7.622669529	0.338	ns
summer_carotenoids_France	in the box	on the site	5	5	-1.071138107	7.940258362	0.316	ns
summer_carotenoids_Poland	in the box	on the site	4	5	-0.842503762	6.822589504	0.428	ns
summer_carotenoids_Sweden	in the box	on the site	5	5	-0.955771008	6.026941852	0.376	ns
summer_carotenoidsbo_Estonia	in the box	on the site	5	5	-0.954481943	6.55291863	0.374	ns
summer_carotenoidsbo_Finland	in the box	on the site	5	5	0.04150034	6.572369235	0.968	ns
summer_carotenoidsbo_France	in the box	on the site	5	5	3.369811885	6.916070083	0.0121	*
summer_carotenoidsbo_Poland	in the box	on the site	4	5	0.347389253	5.01902382	0.742	ns
summer_carotenoidsbo_Sweden	in the box	on the site	5	5	-0.331435162	7.97583943	0.749	ns
summer_chla_Estonia	in the box	on the site	5	5	1.807842554	6.296445235	0.118	ns
summer_chla_Finland	in the box	on the site	5	5	0.9579635	7.481824501	0.368	ns
summer_chla_France	in the box	on the site	5	5	-1.099394506	7.641232252	0.305	ns

summer_chla_Poland	in the box	on the site	4	5	-0.835583158	6.868163867	0.431	ns
summer_chla_Sweden	in the box	on the site	5	5	-1.044955361	6.597519974	0.333	ns
summer_chlb_Estonia	in the box	on the site	5	5	2.324491281	6.06695761	0.0586	ns
summer_chlb_Finland	in the box	on the site	5	5	0.92487837	7.481643053	0.384	ns
summer_chlb_France	in the box	on the site	5	5	-0.226091438	7.869560912	0.827	ns
summer_chlb_Poland	in the box	on the site	4	5	-1.149479338	6.430127166	0.291	ns
summer_chlb_Sweden	in the box	on the site	5	5	-0.919095471	5.53691412	0.396	ns
summer_flavonoids_Estonia	in the box	on the site	5	5	-0.221519456	5.780499908	0.832	ns
summer_flavonoids_Finland	in the box	on the site	5	5	1.954718801	6.91078492	0.0921	ns
summer_flavonoids_France	in the box	on the site	5	5	-3.263966002	5.329161028	0.0204	*
summer_flavonoids_Poland	in the box	on the site	4	5	1.609485394	3.476876507	0.193	ns
summer_flavonoids_Sweden	in the box	on the site	5	5	5.38880787	7.661356889	0.000757	***
summer_total phenols_Estonia	in the box	on the site	5	5	2.195199829	5.557969265	0.0741	ns
summer_total phenols_Finland	in the box	on the site	5	5	0.848741128	7.768690055	0.421	ns
summer_total phenols_France	in the box	on the site	5	5	0.851305626	7.946693056	0.42	ns
summer_total phenols_Poland	in the box	on the site	4	5	-0.52074373	3.865482203	0.631	ns
summer_total phenols_Sweden	in the box	on the site	5	5	-1.031820521	7.035902924	0.336	ns
summer_proline_Estonia	in the box	on the site	5	5	2.97594355	5.086001276	0.0303	*
summer_proline_Finland	in the box	on the site	5	5	1.732904752	7.973859503	0.121	ns
summer_proline_France	in the box	on the site	5	5	0.744733375	5.341133847	0.488	ns
summer_proline_Poland	in the box	on the site	4	5	0.627201892	6.831684554	0.551	ns

summer_proline_Sweden	in the box	on the site	5	5	-0.975971051	4.355550756	0.38	ns
summer_tannins_Estonia	in the box	on the site	5	5	4.812906317	4.674491025	0.00576	**
summer_tannins_Finland	in the box	on the site	5	5	-1.695533853	4.962600941	0.151	ns
summer_tannins_France	in the box	on the site	5	5	3.384837372	5.51882568	0.0168	*
summer_tannins_Poland	in the box	on the site	4	5	1.153857204	6.273927566	0.291	ns
summer_tannins_Sweden	in the box	on the site	5	5	1.15257256	4.444766649	0.307	ns
summer_water-soluble phenols_Estonia	in the box	on the site	5	5	0.437520498	7.899310528	0.673	ns
summer_water-soluble phenols_Finland	in the box	on the site	5	5	1.073822545	5.905865651	0.325	ns
summer_water-soluble phenols_France	in the box	on the site	5	5	-0.755088646	4.603703009	0.487	ns
summer_water-soluble phenols_Poland	in the box	on the site	4	5	1.167862995	6.133167978	0.286	ns
summer_water-soluble phenols_Sweden	in the box	on the site	5	5	-0.370167531	7.820637198	0.721	ns

Table S3. Summary of pairwise comparison of *Sphagnum* gross ecosystem productivity (GEP) among measurements in the box (boxes that stayed at the site of their origin) and outside of the box (undisturbed control) over three seasons.

Season-metabolite-country	group1	group2	n1	n2	statistic	df	P	P significance
autumn	in the box	on the site	19	25	0.0839	42.0	0.929	ns
spring	in the box	on the site	24	23	-1.34	26.6	0.192	ns
summer	in the box	on the site	24	25	-0.541	43.6	0.591	ns

Table S4. Summary of linear effect mixed models testing the receptor site effect (fixed effect) on transplanted box pH. F and P-values based on one-way ANOVA

origin	Df	F	p
All species	2,39	1.04	0.36
balticum	2,6	1.35	0.32
papillosum	2,3	8.47	0.06
rubellum	2,6	1.47	0.3
magellanicum	2,6	0.35	0.71
warnstorfii	2,6	0.26	0.78

Table S5. Summary of linear effect mixed models testing the receptor site effect (fixed effect) on climate parameters. F and P-values based on one-way ANOVA

	Df	F	p
Temperature			
Country	4,277	71.4	<0.0001
Season	1,180	0.44	0.5
Country*season	4,277	8.7	<0.0001
Spring	4,151	16	<0.0001
Summer	4,150	23.5	<0.0001
Autumn	4,151	10.3	<0.0001
PAR			
Country	4,277	9.9	<0.0001
Season	1,180	85	<0.0001
Country*season	4,277	1.6	0.17
Spring	4,151	2.6	0.04
Summer	4,150	7.8	<0.0001
Autumn	4,151	32.3	<0.0001

Table S6. Summary of linear effect mixed models (LME) and linear models (LM) testing the effect of receptor site, box origin and season (fixed effects) on *Sphagnum* water content, WEOM and WEOC

	LME			LM		
	Df	F	p	Df	F	p
Sphagnum water content						
All seasons	4 species and 4 receptor sites			no balticum in autumn		
Receptor	3,127	1.42	0.24	4,243	3.5	0.04
Origin	3,12	8.35	0.003	4,243	11.7	9.4E-09
Season	2,32	98.06	2.24E-14	2	112	3.3E-35
Receptor*origin	9,127	1.34	0.22	1	1.3	0.2
Receptor*season	6,127	10.82	1.05E-09	7	10.7	<0.0001
Origin*season	6,32	0.82	0.56	8	1.2	0.3
Receptor*origin*season	18,127	0.86	0.63	27	0.7	0.9
Spring	5 species 5 sites			5 species 5 sites		
Receptor	4,75	2.3	0.07	4,95	2.0	0.1
Origin	4,16	7.0	0.002	4,95	6.1	0.0002
Receptor*origin	16,75	1.0	0.46	16,95	0.8	0.67
Summer	5 species 5 sites			5 species 5 sites		
Receptor	4,62	20.4	<0.0001	4,82	20.4	1.1E-11
Origin	4,16	2.7	0.07	4,82	2.7	0.04
Receptor*origin	16,62	1.0	0.42	16,82	1.0	0.42
Autumn	4 species and 4 sites			no balticum in autumn		
Receptor	3,41	8.2	0.0002	3,66	7.0	0.0003
Origin	3,12	1.9	0.2	4,66	3.4	0.01
Receptor*origin	3,12	0.7	0.7	11,66	0.8	0.6
WEOC						
All seasons	4 species and 4 receptor sites			no balticum in autumn		
Receptor	3,162	17.1	<0.0001	4,261	24.0	<2.2E-16
Origin	4,16	10.6	0.0002	4,261	15.6	1.9E-11

Season	2,40	144.5	<0.0001	2,261	176.4	<2.2E-15
Receptor*origin	2,162	1.6	0.1	16,261	1.7	0.054
Receptor*season	6,162	10.4	<0.0001	7,261	10.1	3.3E-11
Origin*season	8,40	3.0	0.01	8,261	3.7	0.0004
Receptor*origin*season	24,162	0.5	0.98	28,261	0.6	0.97
Spring	5 species 5 sites			5 species 5 sites		
Receptor	4,76	21.9	<0.0001	4,96	21.9	7.5E-13
Origin	4,16	3.5	0.03	4,9	3.5	0.01
Receptor*origin	16,76	1.0	0.4	16,96	1.0	0.4
Summer	5 species 5 sites			5 species 5 sites		
Receptor	4,72	9.1	<0.0001	4,92	8.9	4.2E-0.6
Origin	4,16	13.4	0.0001	4,92	13.1	1.8E-08
Receptor*origin	16,72	0.7	0.8	16,92	0.7	0.8
Autumn	4 species and 4 sites			no balticum in autumn		
Receptor	3,53	1.4	0.3	3,73	1.3	0.3
Origin	4,16	1.1	0.4	4,73	1.1	0.4
Receptor*origin	12,53	1.3	0.2	11,73	1.2	0.2
WEON						
All seasons	4 species and 4 receptor sites			no balticum in autumn		
Receptor	3,162	3.2	0.03	4,261	3.5	0.008
Origin	4,16	1.5	0.2	4,261	2.5	0.05
Season	2,40	16.3	<0.0001	2,261	18.5	3.1E-08
Receptor*origin	2,162	0.9	0.6	16,261	0.8	0.7
Receptor*season	6,162	15.3	<0.0001	7,261	12.3	1.2E-13
Origin*season	8,40	0.6	0.8	8,261	0.7	0.4
Receptor*origin*season	24,162	0.8	0.7	28,261	0.7	0.9
Spring	5 species 5 sites			5 species 5 sites		
Receptor	4,76	12.7	<0.0001	4,96	12.7	2.4E-08
Origin	4,16	0.4	0.8	4,96	0.4	0.8
Receptor*origin	16,76	0.7	0.8	16,96	0.7	0.8

Summer	5 species 5 sites			5 species 5 sites		
Receptor	4,72	12.0	<0.0001	4,92	11.7	1.1E-11
Origin	4,16	2.1	0.12	4,92	2.0	0.09
Receptor*origin	16,72	0.4	0.9	16,92	0.4	0.9
Autumn	4 species and 4 sites			no balticum in autumn		
Receptor	3,53	1.3	0.3	3,73	1.3	0.3
Origin	4,16	1.1	0.4	4,73	1.1	0.4
Receptor*origin	12,53	1.3	0.3	11,73	1.3	0.2

Table S7. Summary of linear effect mixed models (LME) and linear models (LM) testing the effect of receptor site, box origin and season (fixed effects) on *Sphagnum* metabolites

At the origin site			
LME at the site of origin			
	season	origin	season:origin
water-soluble phenols.numDF	2	4	8
water-soluble phenols.denDF	38	15	38
water-soluble phenols.F.value	69.46662462`	9.036092699	6.795627785
water-soluble phenols.p.value	2.02949E-13	0.000636891	1.63804E-05
chla.numDF	2	4	8
chla.denDF	38	15	38
chla.F.value	95.37204889	21.15670439	7.217156458
chla.p.value	1.55431E-15	5.01622E-06	8.85924E-06
chlb.numDF	2	4	8
chlb.denDF	38	15	38
chlb.F.value	58.69481865	16.05259597	7.613047878
chlb.p.value	2.39253E-12	2.69051E-05	5.05513E-06
carotenoids.numDF	2	4	8
carotenoids.denDF	38	15	38
carotenoids.F.value	80.74293876	19.13700488	7.900898238
carotenoids.p.value	2.07612E-14	9.33082E-06	3.39363E-06
proline.numDF	2	4	8
proline.denDF	38	15	38
proline.F.value	13.5856836	2.509585498	2.288016222
proline.p.value	3.53841E-05	0.085891506	0.041559231
carotenoidsbo.numDF	2	4	8
carotenoidsbo.denDF	38	15	38
carotenoidsbo.F.value	5.245561911	17.27820375	8.256053378
carotenoidsbo.p.value	0.00973432	1.73494E-05	2.09749E-06
tannins.numDF	2	4	8
tannins.denDF	38	15	38
tannins.F.value	53.05458838	9.4806724	14.77675488
tannins.p.value	1.00172E-11	0.000498655	1.51582E-09
total phenols.numDF	2	4	8
total phenols.denDF	38	15	38
total phenols.F.value	81.26218925	6.276420775	5.244998542
total phenols.p.value	1.88738E-14	0.003565554	0.000185641
flavonoids.numDF	2	4	8
flavonoids.denDF	38	15	38
flavonoids.F.value	23.2592454	11.76632424	21.85146088
flavonoids.p.value	2.53399E-07	0.000158334	5.36349E-12
LM at the site of origin			
	season	origin	season:origin
water-soluble phenols.Df	2	4	8
water-soluble phenols.Sum.Sq	6.724506634	5.028586368	2.631320832
water-soluble phenols.Mean.Sq	3.362253317	1.257146592	0.328915104
water-soluble phenols.F.value	42.75368946	15.98560547	4.182413664

water-soluble phenols.Pr. F.	4.5506E-12	7.8506E-09	0.000548103
chla.Df	2	4	8
chla.Sum.Sq	0.234032767	0.12711431	0.070840508
chla.Mean.Sq	0.117016384	0.031778578	0.008855063
chla.F.value	88.7395163	24.09932281	6.715248132
chla.Pr. F.	3.12226E-18	1.05516E-11	3.64197E-06
chlb.Df	2	4	8
chlb.Sum.Sq	0.045708997	0.047877765	0.023714855
chlb.Mean.Sq	0.022854498	0.011969441	0.002964357
chlb.F.value	44.97733275	23.55569288	5.833812857
chlb.Pr. F.	1.89543E-12	1.57224E-11	1.92984E-05
carotenoids.Df	2	4	8
carotenoids.Sum.Sq	0.037007356	0.025885059	0.014485049
carotenoids.Mean.Sq	0.018503678	0.006471265	0.001810631
carotenoids.F.value	69.69451026	24.37416058	6.819781912
carotenoids.Pr. F.	4.88195E-16	8.64283E-12	3.0046E-06
proline.Df	2	4	8
proline.Sum.Sq	0.029508334	0.010901724	0.01987844
proline.Mean.Sq	0.014754167	0.002725431	0.002484805
proline.F.value	13.5856836	2.509585499	2.288016222
proline.Pr. F.	1.49709E-05	0.051740787	0.033641765
carotenoidsbo.Df	2	4	8
carotenoidsbo.Sum.Sq	0.823649347	5.425989245	5.185406701
carotenoidsbo.Mean.Sq	0.411824673	1.356497311	0.648175838
carotenoidsbo.F.value	5.245561907	17.27820377	8.256053371
carotenoidsbo.Pr. F.	0.00810781	2.46259E-09	2.38491E-07
tannins.Df	2	4	8
tannins.Sum.Sq	1.0785116	0.603776836	1.201547465
tannins.Mean.Sq	0.5392558	0.150944209	0.150193433
tannins.F.value	43.63024945	12.21263359	12.15188961
tannins.Pr. F.	3.21168E-12	3.08693E-07	6.02596E-10
total phenols.Df	2	4	8
total phenols.Sum.Sq	0.554947698	0.309149056	0.143274499
total phenols.Mean.Sq	0.277473849	0.077287264	0.017909312
total phenols.F.value	42.99032884	11.97447941	2.774774026
total phenols.Pr. F.	4.14029E-12	3.9548E-07	0.011560345
flavonoids.Df	2	4	8
flavonoids.Sum.Sq	2.357186613	3.526553643	8.858063999
flavonoids.Mean.Sq	1.178593307	0.881638411	1.107258
flavonoids.F.value	20.0585371	15.00464721	18.84447803
flavonoids.Pr. F.	2.5381E-07	1.95337E-08	1.84247E-13

Reciprocal transplantation			
LM model on 5 species and 4 receptor sites			
	season	receptor	season:receptor
water-soluble phenols.Df	2	4	7
water-soluble phenols.F.value	159.8367332	16.42768436	8.297689519

water-soluble phenols.Pr. F.	9.93317E-49	3.04343E-12	2.63752E-09
chla.Df	2	4	7
chla.F.value	301.40927	51.34203156	15.37250687
chla.Pr. F.	4.68922E-74	2.63082E-33	2.52362E-17
chlb.Df	2	4	7
chlb.F.value	116.4055846	34.62766419	13.00345642
chlb.Pr. F.	1.24178E-38	5.46773E-24	1.02231E-14
carotenoids.Df	2	4	7
carotenoids.F.value	248.4330678	50.29954813	17.69136183
carotenoids.Pr. F.	1.24522E-65	9.2566E-33	8.48737E-20
proline.Df	2	4	7
proline.F.value	41.23758087	12.21587198	4.720050458
proline.Pr. F.	1.20715E-16	3.00304E-09	4.66602E-05
carotenoidsbo.Df	2	4	7
carotenoidsbo.F.value	17.71221547	12.54513575	11.9366538
carotenoidsbo.Pr. F.	5.10424E-08	1.73681E-09	1.62305E-13
tannins.Df	2	4	7
tannins.F.value	95.21658335	8.80683779	20.25449478
tannins.Pr. F.	4.12425E-33	9.39916E-07	1.92343E-22
total phenols.Df	2	4	7
total phenols.F.value	148.0471601	16.68428116	14.57351637
total phenols.Pr. F.	3.93384E-46	2.01545E-12	1.872E-16
flavonoids.Df	2	4	7
flavonoids.F.value	127.1564819	49.90375902	10.14121858
flavonoids.Pr. F.	2.84022E-41	1.49626E-32	1.84932E-11

LME on 4 species and 4 receptor sites

	season	receptor	season:receptor
water-soluble phenols.numDF	2	3	6
water-soluble phenols.denDF	38	154	154
water-soluble phenols.F.value	148.689075	11.43223829	12.29475264
water-soluble phenols.p.value	0	8.24555E-07	2.78456E-11
chla.numDF	2	3	6
chla.denDF	38	154	154
chla.F.value	218.7761542	54.0149034	13.04880488
chla.p.value	0	0	6.61138E-12
chlb.numDF	2	3	6
chlb.denDF	38	154	154
chlb.F.value	124.8998352	44.78333945	11.17363213
chlb.p.value	0	0	2.46921E-10
carotenoids.numDF	2	3	6
carotenoids.denDF	38	154	154
carotenoids.F.value	187.0469445	52.6006827	14.73945545
carotenoids.p.value	0	0	2.86549E-13
proline.numDF	2	3	6
proline.denDF	38	154	154
proline.F.value	49.45291382	15.33919062	3.286634492
proline.p.value	2.65382E-11	8.80274E-09	0.004527593
carotenoidsbo.numDF	2	3	6

carotenoidsbo.denDF	38	154	154
carotenoidsbo.F.value	14.97826329	5.936065587	11.83189401
carotenoidsbo.p.value	1.5977E-05	0.000739017	6.81134E-11
tannins.numDF	2	3	6
tannins.denDF	38	154	154
tannins.F.value	79.54742947	12.45128388	21.75659236
tannins.p.value	2.62013E-14	2.46458E-07	0
total phenols.numDF	2	3	6
total phenols.denDF	38	154	154
total phenols.F.value	110.154028	13.76983269	22.14929148
total phenols.p.value	2.22045E-16	5.29539E-08	0
flavonoids.numDF	2	3	6
flavonoids.denDF	38	154	154
flavonoids.F.value	139.0279635	11.93420883	4.898368535
flavonoids.p.value	0	4.53895E-07	0.000130504

LME on spring data

	origin	**receptor**	**origin:receptor**
water-soluble phenols.numDF	4	4	16
water-soluble phenols.denDF	16	76	76
water-soluble phenols.F.value	9.193466222	22.05940461	1.236618375
water-soluble phenols.p.value	0.000469327	4.10849E-12	0.261257779
chla.numDF	4	4	16
chla.denDF	16	76	76
chla.F.value	4.838647867	12.3999108	6.458403306
chla.p.value	0.009465382	8.19687E-08	7.45689E-09
chlb.numDF	4	4	16
chlb.denDF	16	76	76
chlb.F.value	2.714360896	9.102063142	5.396349771
chlb.p.value	0.067174304	4.62057E-06	1.92456E-07
carotenoids.numDF	4	4	16
carotenoids.denDF	16	76	76
carotenoids.F.value	5.087595555	15.36761719	5.528401557
carotenoids.p.value	0.007719103	2.97875E-09	1.26853E-07
proline.numDF	4	4	16
proline.denDF	16	76	76
proline.F.value	9.645035159	8.889276059	2.319384341
proline.p.value	0.000362927	6.07698E-06	0.007710575
carotenoidsbo.numDF	4	4	16
carotenoidsbo.denDF	16	76	76
carotenoidsbo.F.value	24.00560449	100.0274547	3.12269121
carotenoidsbo.p.value	1.36081E-06	0	0.000433814
tannins.numDF	4	4	16
tannins.denDF	16	76	76
tannins.F.value	6.125783223	36.04785443	2.670936885
tannins.p.value	0.003462942	0	0.002195084
total phenols.numDF	4	4	16
total phenols.denDF	16	76	76
total phenols.F.value	6.794198395	46.58754352	2.808961097

total phenols.p.value	0.002146179	0	0.001337034
flavonoids.numDF	4	4	16
flavonoids.denDF	16	76	76
flavonoids.F.value	7.969676894	19.22021896	2.249752019
flavonoids.p.value	0.000983987	5.8735E-11	0.009866044
LM on spring data			
	origin	**receptor**	**origin:receptor**
water-soluble phenols.Df	4	4	16
water-soluble phenols.Sum.Sq	3.326606508	5.718047114	1.264881381
water-soluble phenols.Mean.Sq	0.831651627	1.429511778	0.079055086
water-soluble phenols.F.value	11.89856985	20.45224851	1.13105348
water-soluble phenols.Pr. F.	6.83234E-08	3.27011E-12	0.338556094
chla.Df	4	4	16
chla.Sum.Sq	0.017809575	0.035437461	0.074357575
chla.Mean.Sq	0.004452394	0.008859365	0.004647348
chla.F.value	5.790780875	11.52248553	6.044338711
chla.Pr. F.	0.000322346	1.10993E-07	5.61846E-09
chlb.Df	4	4	16
chlb.Sum.Sq	0.005992719	0.016249364	0.038808281
chlb.Mean.Sq	0.00149818	0.004062341	0.002425518
chlb.F.value	3.192919764	8.657658275	5.169261344
chlb.Pr. F.	0.016525996	5.20438E-06	1.22308E-07
carotenoids.Df	4	4	16
carotenoids.Sum.Sq	0.003086049	0.007198816	0.010466478
carotenoids.Mean.Sq	0.000771512	0.001799704	0.000654155
carotenoids.F.value	6.11878056	14.27325775	5.188031228
carotenoids.Pr. F.	0.000198341	3.52887E-09	1.14308E-07
proline.Df	4	4	16
proline.Sum.Sq	0.041497121	0.038226047	0.03985561
proline.Mean.Sq	0.01037428	0.009556512	0.002490976
proline.F.value	9.618971252	8.860740979	2.309617824
proline.Pr. F.	1.38803E-06	3.92629E-06	0.006444039
carotenoidsbo.Df	4	4	16
carotenoidsbo.Sum.Sq	3.463830347	12.72637694	1.601025375
carotenoidsbo.Mean.Sq	0.865957587	3.181594234	0.100064086
carotenoidsbo.F.value	26.499168	97.35996475	3.06206108
carotenoidsbo.Pr. F.	8.13945E-15	6.47439E-33	0.000352305
tannins.Df	4	4	16
tannins.Sum.Sq	0.348993282	1.833620919	0.542337021
tannins.Mean.Sq	0.087248321	0.45840523	0.033896064
tannins.F.value	6.682548771	35.1103068	2.596177188
tannins.Pr. F.	8.67594E-05	4.78949E-18	0.002150398
total phenols.Df	4	4	16
total phenols.Sum.Sq	0.180598812	0.783695499	0.193118315
total phenols.Mean.Sq	0.045149703	0.195923875	0.012069895
total phenols.F.value	9.505046134	41.24646108	2.540989163

total phenols.Pr. F.	1.62073E-06	4.44179E-20	0.002660223
flavonoids.Df	4	4	16
flavonoids.Sum.Sq	1.086267049	2.619716055	1.226564899
flavonoids.Mean.Sq	0.271566762	0.654929014	0.076660306
flavonoids.F.value	7.969676898	19.22021896	2.249752018
flavonoids.Pr. F.	1.36617E-05	1.22E-11	0.008081691
LME on summer data			
	origin	**receptor**	**origin:receptor**
water-soluble phenols.numDF	4	4	16
water-soluble phenols.denDF	16	72	72
water-soluble phenols.F.value	28.82128072	29.56475013	1.795119899
water-soluble phenols.p.value	3.90555E-07	1.4988E-14	0.048528895
chla.numDF	4	4	16
chla.denDF	16	72	72
chla.F.value	6.555593963	44.87478566	1.36111608
chla.p.value	0.002537925	0	0.186293566
chlb.numDF	4	4	16
chlb.denDF	16	72	72
chlb.F.value	8.993064325	31.53951056	0.910365048
chlb.p.value	0.000527443	3.55271E-15	0.56073434
carotenoids.numDF	4	4	16
carotenoids.denDF	16	72	72
carotenoids.F.value	7.148348454	41.3386746	1.260705749
carotenoids.p.value	0.001683562	0	0.246352856
proline.numDF	4	4	16
proline.denDF	16	72	72
proline.F.value	6.134522746	19.61253954	3.823087392
proline.p.value	0.003440729	5.94126E-11	4.29226E-05
carotenoidsbo.numDF	4	4	16
carotenoidsbo.denDF	16	72	72
carotenoidsbo.F.value	17.6185116	3.559155235	1.727828788
carotenoidsbo.p.value	1.03295E-05	0.010486365	0.060444763
tannins.numDF	4	4	16
tannins.denDF	16	72	72
tannins.F.value	7.884030148	16.1811334	2.530463211
tannins.p.value	0.001038997	1.69741E-09	0.003884439
total phenols.numDF	4	4	16
total phenols.denDF	16	72	72
total phenols.F.value	16.05246891	21.15560208	2.010023423
total phenols.p.value	1.85616E-05	1.44522E-11	0.023645221
flavonoids.numDF	4	4	16
flavonoids.denDF	16	72	72
flavonoids.F.value	7.300937408	49.64984785	3.184484678
flavonoids.p.value	0.00151962	0	0.000389595
LM on summer data			
	origin	**receptor**	**origin:receptor**
water-soluble phenols.Df	4	4	16

water-soluble phenols.Sum.Sq	5.686639756	4.784183653	1.161108823
water-soluble phenols.Mean.Sq	1.421659939	1.196045913	0.072569301
water-soluble phenols.F.value	33.63887632	28.30046726	1.717112292
water-soluble phenols.Pr. F.	2.8074E-17	2.48379E-15	0.056878845
chla.Df	4	4	16
chla.Sum.Sq	0.045653173	0.308573377	0.038196567
chla.Mean.Sq	0.011413293	0.077143344	0.002387285
chla.F.value	6.4335398	43.48480032	1.345684875
chla.Pr. F.	0.000130698	1.93564E-20	0.18751015
chlb.Df	4	4	16
chlb.Sum.Sq	0.021109731	0.074033781	0.008547725
chlb.Mean.Sq	0.005277433	0.018508445	0.000534233
chlb.F.value	8.993064753	31.53951028	0.910365041
chlb.Pr. F.	3.55527E-06	1.55486E-16	0.559866563
carotenoids.Df	4	4	16
carotenoids.Sum.Sq	0.00946169	0.05406676	0.006756191
carotenoids.Mean.Sq	0.002365422	0.01351669	0.000422262
carotenoids.F.value	7.020039167	40.11448182	1.253178066
carotenoids.Pr. F.	5.6086E-05	2.06102E-19	0.244770452
proline.Df	4	4	16
proline.Sum.Sq	0.029504913	0.07164587	0.056096275
proline.Mean.Sq	0.007376228	0.017911468	0.003506017
proline.F.value	7.556893025	18.35016996	3.591889431
proline.Pr. F.	2.6124E-05	4.09464E-11	5.00198E-05
carotenoidsbo.Df	4	4	16
carotenoidsbo.Sum.Sq	9.257448003	1.870117831	3.631472314
carotenoidsbo.Mean.Sq	2.314362001	0.467529458	0.22696702
carotenoidsbo.F.value	17.61851238	3.559155195	1.727828768
carotenoidsbo.Pr. F.	9.10788E-11	0.009567626	0.054830194
tannins.Df	4	4	16
tannins.Sum.Sq	0.77446303	1.489392981	0.930675293
tannins.Mean.Sq	0.193615757	0.372348245	0.058167206
tannins.F.value	8.299735373	15.96146896	2.493456225
tannins.Pr. F.	9.22808E-06	5.86011E-10	0.003341811
total phenols.Df	4	4	16
total phenols.Sum.Sq	0.722104957	0.410847925	0.157466882
total phenols.Mean.Sq	0.180526239	0.102711981	0.00984168
total phenols.F.value	29.1169551	16.56634603	1.587357936
total phenols.Pr. F.	1.21604E-15	2.94529E-10	0.087909612
flavonoids.Df	4	4	16
flavonoids.Sum.Sq	3.436441008	16.35081495	4.112474242
flavonoids.Mean.Sq	0.859110252	4.087703737	0.25702964
flavonoids.F.value	9.061517006	43.1153008	2.711035574
flavonoids.Pr. F.	3.2387E-06	2.49413E-20	0.001458197
LME on autumn data			
	origin	**receptor**	**origin:receptor**

water-soluble phenols.numDF	4	3	12
water-soluble phenols.denDF	16	53	53
water-soluble phenols.F.value	13.76286458	4.465651335	1.654930286
water-soluble phenols.p.value	4.76011E-05	0.007201356	0.104532847
chla.numDF	4	3	12
chla.denDF	16	53	53
chla.F.value	2.789732517	44.07169089	2.263110771
chla.p.value	0.062203129	1.9984E-14	0.021107733
chlb.numDF	4	3	12
chlb.denDF	16	53	53
chlb.F.value	5.363765387	46.62915371	1.339012446
chlb.p.value	0.006190276	6.88338E-15	0.225302639
carotenoids.numDF	4	3	12
carotenoids.denDF	16	53	53
carotenoids.F.value	2.904842424	47.08351501	2.194135129
carotenoids.p.value	0.05537208	5.77316E-15	0.025407436
proline.numDF	4	3	12
proline.denDF	16	53	53
proline.F.value	5.992985807	1.777872584	3.525104704
proline.p.value	0.003821004	0.162578731	0.00071757
carotenoidsbo.numDF	4	3	12
carotenoidsbo.denDF	16	53	53
carotenoidsbo.F.value	3.126703189	10.05066655	1.687244449
carotenoidsbo.p.value	0.044415259	2.39791E-05	0.096304702
tannins.numDF	4	3	12
tannins.denDF	16	53	53
tannins.F.value	1.633171223	16.00699618	1.172801804
tannins.p.value	0.214541387	1.56146E-07	0.326160731
total phenols.numDF	4	3	12
total phenols.denDF	16	53	53
total phenols.F.value	4.442451229	19.86568443	1.560764169
total phenols.p.value	0.013229349	9.26197E-09	0.132330326
flavonoids.numDF	4	3	12
flavonoids.denDF	16	53	53
flavonoids.F.value	1.728419655	30.67134179	2.092903974
flavonoids.p.value	0.192948572	1.23537E-11	0.03331549
LM on autumn data			
	origin	**receptor**	**origin:receptor**
water-soluble phenols.Df	4	3	12
water-soluble phenols.Sum.Sq	2.419428594	0.588775925	0.872780284
water-soluble phenols.Mean.Sq	0.604857148	0.196258642	0.07273169
water-soluble phenols.F.value	13.76286467	4.465651321	1.654930281
water-soluble phenols.Pr. F.	2.06185E-08	0.006181187	0.095343757
chla.Df	4	3	12
chla.Sum.Sq	0.018797057	0.222714391	0.045746131

chla.Mean.Sq	0.004699264	0.07423813	0.003812178
chla.F.value	2.78973252	44.07169088	2.263110771
chla.Pr. F.	0.032472427	2.2981E-16	0.016810994
chlb.Df	4	3	12
chlb.Sum.Sq	0.012525918	0.075196737	0.008795221
chlb.Mean.Sq	0.003131479	0.025065579	0.000732935
chlb.F.value	5.606305303	44.87504671	1.312177853
chlb.Pr. F.	0.000543045	1.50529E-16	0.230444047
carotenoids.Df	4	3	12
carotenoids.Sum.Sq	0.003620358	0.044010785	0.008203772
carotenoids.Mean.Sq	0.00090509	0.014670262	0.000683648
carotenoids.F.value	2.904842428	47.08351498	2.194135128
carotenoids.Pr. F.	0.027393761	4.82118E-17	0.020595753
proline.Df	4	3	12
proline.Sum.Sq	0.017908958	0.002559694	0.020994781
proline.Mean.Sq	0.00447724	0.000853231	0.001749565
proline.F.value	8.101135109	1.543840129	3.165670098
proline.Pr. F.	1.83668E-05	0.210428843	0.001127422
carotenoidsbo.Df	4	3	12
carotenoidsbo.Sum.Sq	1.670054236	4.026243579	2.703604621
carotenoidsbo.Mean.Sq	0.417513559	1.342081193	0.225300385
carotenoidsbo.F.value	3.126703197	10.05066654	1.687244448
carotenoidsbo.Pr. F.	0.01973609	1.26969E-05	0.087317552
tannins.Df	4	3	12
tannins.Sum.Sq	0.028745337	0.213399414	0.06259005
tannins.Mean.Sq	0.007186334	0.071133138	0.005215838
tannins.F.value	1.601741769	15.8546644	1.162543306
tannins.Pr. F.	0.183017775	4.91505E-08	0.325980161
total phenols.Df	4	3	12
total phenols.Sum.Sq	0.105431033	0.270353249	0.077670216
total phenols.Mean.Sq	0.026357758	0.09011775	0.006472518
total phenols.F.value	5.487272916	18.76110567	1.347476992
total phenols.Pr. F.	0.00064229	4.02488E-09	0.211498399
flavonoids.Df	4	3	12
flavonoids.Sum.Sq	0.534068734	6.966058385	1.939366136
flavonoids.Mean.Sq	0.133517184	2.322019462	0.161613845
flavonoids.F.value	1.715662357	29.83736831	2.076697412
flavonoids.Pr. F.	0.155728676	1.06445E-12	0.029023814

Table S8. Summary of linear effect mixed models (LME) and linear models (LM) testing the effect of receptor site, box origin and season (fixed effects) on PCA axes on *Sphagnum* metabolites

LME on PCA axes							
	season	**receptor**	**origin**	**season:receptor**	**season:origin**	**receptor:origin**	**season:receptor:origin**
PC1.numDF	2	3	3	6	6	9	18
PC1.denDF	32	127	12	127	32	127	127
PC1.F.value	329.1530625	74.97053437	18.80736251	18.19907536	2.281609482	0.929161438	2.115657981
PC1.p.value	0	0	7.86604E-05	3.55271E-15	0.06034799	0.502336751	0.008581442
PC2.numDF	2	3	3	6	6	9	18
PC2.denDF	32	127	12	127	32	127	127
PC2.F.value	235.9223318	34.54114112	8.031931066	22.526299	3.70416515	2.749249699	1.784634357
PC2.p.value	0	2.22045E-16	0.003346539	0	0.006578794	0.005729519	0.03386398
LM on PCA axes							
	origin	**receptor**	**season**	**origin:receptor**	**origin:season**	**receptor:season**	**origin:receptor:season**
PC1.Df	4	4	2	16	8	7	28
PC1.Sum.Sq	92.89426482	218.3579823	577.1115895	15.52784741	27.20716311	84.88168131	36.92149417
PC1.Mean.Sq	23.2235662	54.58949558	288.5557947	0.970490463	3.400895389	12.12595447	1.318624792
PC1.F.value	35.73497719	83.99891567	444.0116841	1.493330277	5.233085998	18.65866347	2.029017699
PC1.Pr. F.	8.33681E-24	9.53222E-46	9.96942E-85	0.101800744	4.38486E-06	4.077E-20	0.002302546
PC2.Df	4	4	2	16	8	7	28
PC2.Sum.Sq	42.82449078	69.02778521	273.5358272	16.62856897	19.83669578	103.018513	20.35858024
PC2.Mean.Sq	10.70612269	17.2569463	136.7679136	1.03928556	2.479586972	14.71693042	0.727092151
PC2.F.value	22.1610589	35.72088743	283.1017238	2.151261402	5.132602579	30.46320048	1.505038981
PC2.Pr. F.	9.13926E-16	8.48789E-24	4.1993E-66	0.006982789	5.9162E-06	1.19604E-30	0.054049875

Table S9. Summary random regression mixed models (RRMMsTwo separate models: (1) PC1 and (2) PC2 on metabolites as response variable and cumulated temperature (1) and precipitation (2) as fixed variables.

	R^2	t-value	P
PC1			
Temperature	0.26	2.69	0.007
PC2			
Precipitation	0.48	1.54	0.0003

Table S10. Summary of linear effect mixed models (LME) and linear models (LM) testing the effect of receptor site, box origin and season (fixed effects) on gross ecosystem productivity

	LME			LM		
	Df	F	p	Df	F	p
All seasons						
Receptor	1,191	267.99	<0.0001	4,251	14.4	<0.0001
Origin	2,40	35.9	<0.0001	4,251	16.6	<0.0001
Season	4,191	17.91	<0.0001	2,251	47.5	<0.0001
Receptor*origin	16,191	2.06	0.0023	16,251	1.74	0.04
Receptor*season	8,191	7.45	<0.0001	8,251	5.9	<0.0001
Origin*season	8,40	4.13	0.0011	8,251	5.4	<0.0001
Receptor*origin*season	32,191	1,24	0.19	32,251	1	0.47
Spring						
Receptor	4,76	21.2	<0.0001	4,301	9.4	<0.0001
Origin	4,16	13.94	<0.0001	4,301	10.6	<0.0001
Receptor*origin	16,76	5.45	<0.0001	16,301	1.1	0.4
Summer						
Receptor	4,73	6.7	0.0001	4,301	9.4	<0.0001
Origin	4,16	4.7	0.01	4,301	10.6	<0.0001
Receptor*origin	16,73	0.86	0.61	16,301	1.1	0.4
Autumn						

Receptor	4,42	15.8	<0.0001	4,301	9.4	<0.0001
Origin	4,16	5.74	0.005	4,301	10.6	<0.0001
Receptor*origin	16,42	1.29	0.25	16,301	1.1	0.4
Summary of linear effect mixed models (LME) and linear models (LM) testing the effect of cumulative temperature and cumulative precipitation (fixed effects) on gross ecosystem productivity						
Sum.temp.	1,248	2.7	0.1	1,322	1.8	0.17
Sum. prec.	1,248	0.11	0.73	1,322	3.15	0.08
Sum. temp.* Sum. prec.	1,248	9.37	0.0024	1,322	18.9	<0.0001
Spring						
Sum.temp.	1,93	25.6	<0.0001	1,117	13.6	0.0004
Sum. prec.	1,93	0.4	0.6	1,117	0.31	0.57
Sum. temp.* Sum. prec.	1,93	5.6	0.02	1,117	2.8	0.1
Summer						
Sum.temp.	1,90	0.55	0.45	1,114	0.27	0.61
Sum. prec.	1,90	11.83	0.0009	1,114	7.7	0.006
Sum. temp.* Sum. prec.	1,90	3.87	0.052	1,114	2.65	0.1
Autumn						
Sum.temp.	1,59	6.7	0.01	1,83	6.7	0.01
Sum. prec.	1,59	7	0.01	1,83	7.1	0.009
Sum. temp.* Sum. prec.	1,59	23.3	<0.0001	1,83	22.9	<0.0001

Summary of linear effect mixed models (LME) and linear models (LM) testing the effect of delta temperature and delta precipitation (fixed effects) on gross ecosystem productivity						
Delta temp.	1,258	3.9	0.049	1,282	2	0.15
Delta prec.	1,258	14.4	0.0002	1,282	10.1	0.002
Delta temp.* Delta prec.	1,258	5.3	0.02	1,282	5.8	0.02
Summary of linear effect mixed models (LME) and linear models (LM) testing the effect of delta temperature, delta precipitation, WEOC and WEON (fixed effects) on gross ecosystem productivity						
Delta prec.	1,246	4.6	0.03	1,270	2.2	0.14
Delta temp.	1,246	16.6	0.0001	1,270	11.1	0.0009
WEOC	1,246	2.4	0.12	1,270	0.56	0.45
WEON	1,246	1.1	0.3	1,270	0.54	0.46
Delta temp.* Delta prec.	1,246	5.2	0.02	1,270	6.2	0.01
Delta prec.* WEOC	1,246	0.99	0.32	1,270	0.4	0.5
Delta temp.* WEOC	1,246	18.5	<0.0001	1,270	17.2	<0.0001
Delta prec.* WEON	1,246	0.6	0.44	1,270	0.15	0.7
Delta temp.* WEON	1,246	18.6	<0.0001	1,270	13.84	0.0002
WEOC*WEON	1,246	0.16	0.7	1,270	0.14	0.7
Delta temp.* Delta prec* WEOC	1,246	0.56	0.45	1,270	0.04	0.84
Delta temp.* Delta prec* WEON	1,246	3.17	0.07	1,270	1.3	0.25
Delta prec.* WEOC*WEON	1,246	0.02	0.89	1,270	0.0017	0.967
Delta temp.* WEOC*WEON	1,246	3.97	0.047	1,270	5.8	0.02

Delta temp.* Delta prec.* WEOC*WEON				1,246	0.89	0.34	1,270	0.27	0.61

Table S11. Summary of linear effect mixed models testing the correlation betwwen gross ecosystem productivity (fixed effect) and PC1 and PC2 on metabolites. F and P-values based on one-way ANOVA

	Df	F	P
PC1	1,232	5.27	0.02
PC2	1,232	0.15	0.69

Chapter 6. General discussion

General discussion

6.1. General synthesis

Understanding how climate change will affect peatland ecosystems is a critical issue, given their importance to the global carbon cycle (Dixon and Turner, 1991; Mcguire et al., 2009). In peatlands, *Sphagnum* mosses are conspicuous components of peatlands, where they make a significant contribution to aboveground biomass and soil carbon sequestration due to their unique morphological and biochemical (metabolites) traits (Page and Baird, 2016; Rydin and Jeglum, 2013; Turetsky, 2003). For example, *Sphagnum* metabolites actively shape peatland habitat by producing recalcitrant litter. *Sphagnum* also compete with vascular plants, drive microbial structure and activities, and possibly control carbon and nutrients cycling. However, the effect of climate change on *Sphagnum* metabolites *per se* remains largely unknown, as most of studies to date are concentrated on the effect of climate changes on vegetation communities and ecosystem functions (*e.g.*Binet et al., 2017; Bragazza et al., 2016; Dieleman et al., 2016b; Jassey et al., 2013; Jassey and Signarbieux, 2019; Robroek et al., 2009), overlooking potential mechanisms behind these changes that could serve as early warning indicators. Long-term climate change is anticipated to significantly change peat-forming areas, with plausible carbon loss due to modifications of peatland processes linked to *Sphagnum* and their traits (Delarue et al., 2011; Dorrepaal et al., 2009a; Fenner and Freeman, 2011; Jassey et al., 2011a, 2011c). Other models suggest that peatland may expand and remain carbon sink in the future (Gallego-Sala et al., 2018), making their response to climate change uncertain. Despite the importance of peatlands in carbon storage, important peatland-specific processes that regulate carbon accumulation are not widely used in current climate models (Frolking et al., 2013; Limpens et al., 2008) and the direction of cycle feedback to climate remains uncertain (Frolking et al., 2011). Therefore, there is an urgent need to understand how *Sphagnum* traits, especially metabolites, dynamically respond to climate changes in order to erase uncertainties in the response of peatlands under climate changes.

The aim of my PhD work was to explore the potential of *Sphagnum* metabolites to provide deeper mechanistic understanding of the *Sphagnum* functional trait space, and to predict microbial community composition and functioning across environmental gradients. I further examined how seasonal patterns of *Sphagnum* metabolites respond to climate changes and the consequence for peatland C uptake (Fig 6-1).

My findings showed that *Sphagnum* species growing in different local (vegetation composition, nutrients content) and regional (temperature, precipitation) environmental

conditions possess a suite of diverse biochemical traits that support *Sphagnum* form and function, as well as its resistance to environmental changes. Additionally, it was found that the volume of the *Sphagnum* trait space was four times larger when biochemical traits were added to the usual suite of morphological-anatomical traits, than when they were excluded. *Sphagnum* interspecific trait variations was shown to play a key role in driving microbial community composition and microbial traits in addition to local and regional environmental conditions. The addition of *Sphagnum* traits to local and regional environmental variables in a structural equation model (SEM) increased our ability to better predict microbial community structure and functions variability across environmental gradients. Additionally, the metabolites were shown to be better predictors of microbial community structure and traits, compared to anatomical and morphological traits. Finally, using reciprocal transplantation and seasonal monitoring, showed that *Sphagnum* species, transplanted to new sites, had similar responses of metabolites concentrations and gross ecosystem productivity over all seasons, with the maximum values in warmer sites. *Sphagnum* metabolites were very plastic in response to temperature and precipitation and the variation in phenotype (graphically represented as reaction norms) had similar slopes and curvatures. More interestingly, my data showed important linkages between *Sphagnum* metabolites and C-related processes, which were the most prominent in spring and autumn. See Fig. 6-1 for the synthesis of the main results.

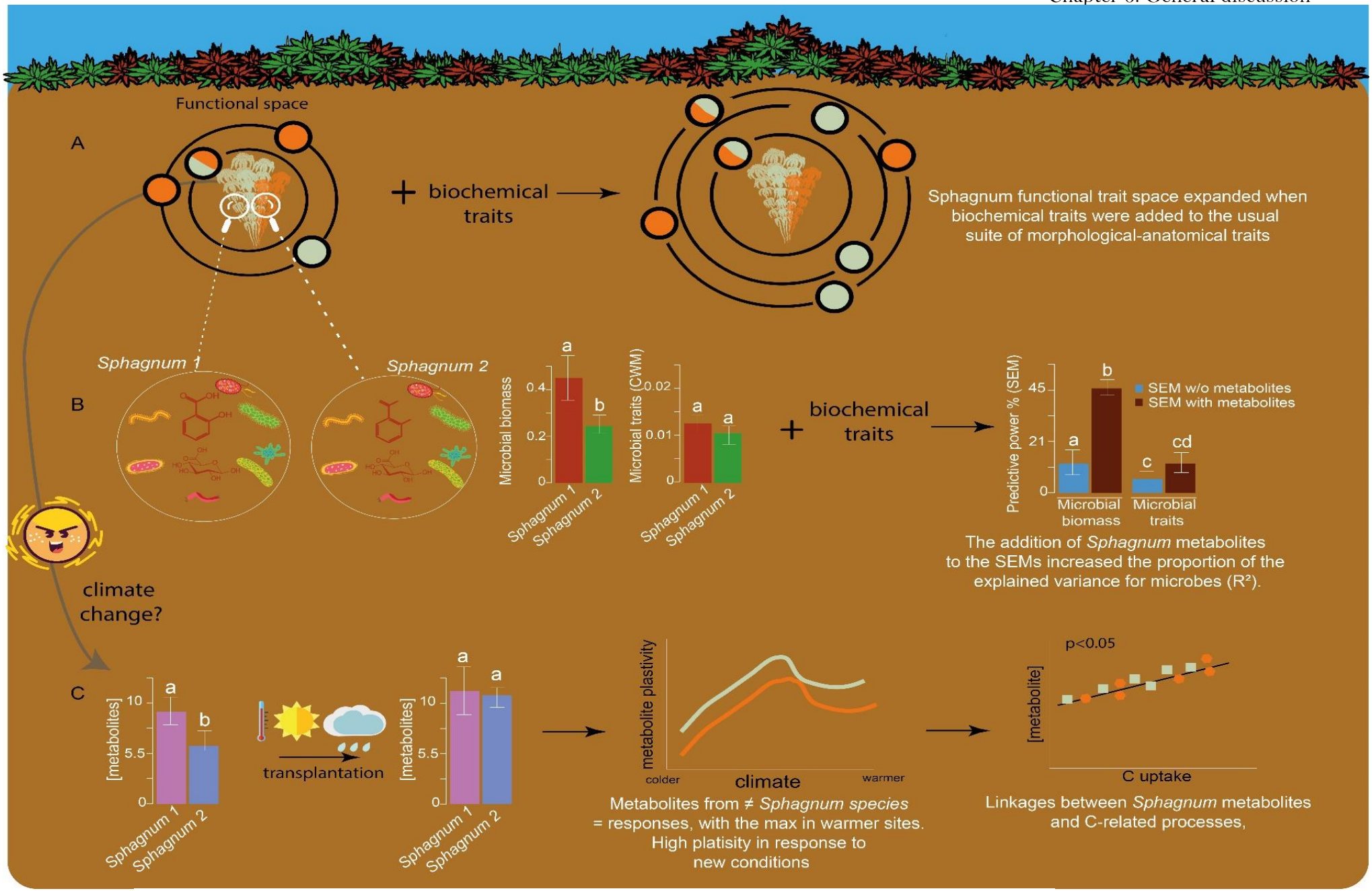


Figure 6- 1. Synthesis of the main results highlighted in my thesis. (A)- Chapter 3, (B)- Chapter 4, (C)-Chapter 5.

6.2. The role of *Sphagnum* biochemical traits in *Sphagnum* trait functional space

The trait-based approach is widely used to link the organismal functioning to ecological processes and it could allow to mechanistically predict the response of plant to changing conditions (Garnier and Navas, 2012a). However, most of research to date is focused on vascular plants, while non-vascular plants traits (*e.g.* moss traits) contributions to ecosystem processes remain scarce (since 2000, only 25% of studies were related to non-vascular plants) (St. Martin and Mallik, 2017). In this thesis, we evaluated classes of metabolites using UV-spectrometry (carbohydrates, phenols, flavonoids, tannins, proline and pigments) to characterize the overall differences/similarities between *Sphagnum* mosses collected in different environments. Moss traits differ from those of vascular plant, as mosses lack roots, cuticle lignin in their tissues, and stomata that regulate water loss (Rice, 2009). Vascular plants are known to be a source of a huge variety of metabolites (*i.e.* biochemical traits) and many of them have been explicitly characterized (*e.g.* Defossez et al., 2021; Obata and Fernie, 2012; Skoneczny et al., 2018; Turner et al., 2016), whereas those of mosses are less investigated. Even though moss and vascular plant cells have similar classes of metabolites, their structure and side chain compositions.

To set the place of *Sphagnum* metabolites in the plant kingdom, I pooled results on classes of *Sphagnum* metabolites (from Chapter 3) with those obtained from other mosses and vascular plants with medicinal properties (*e.g.* antimicrobial) found in the literature. *Sphagnum* metabolites showed a closed proximity to those produced by other mosses and medicinal herbs (see names on Fig. 6-2), while some *Sphagnum* species were slightly separated from other plants, suggesting that plant cells (both vascular and non-vascular) produce similar classes of metabolites, but the structure and side chain composition differ (Cannell et al., 2020; Roberts et al., 2012). To check this assumption, more precise analytical techniques than UV-spectrometry should be applied. For example, Fudyma et al. (2019) by using metabolomic analysis by FTICR-MS showed that *Sphagnum fallax* metabolite signatures were similar to those of medicinal plants like mullein, CBD, creosote and chia and the drivers of that similarities were proteins, lignin and amino sugars. Some of the compound found in both *Sphagnum* and herb are known to have antimicrobial properties (*e.g.* tetrahydrocannabinolic acid, quercetin glycoside). However, *Sphagnum fallax* was still driven by their unique features as each *Sphagnum fallax* replicate plotted away from many of the other plant clusters. In addition, Lang et al. (2009) using FTIR-ATR on bryophytes, lichens and vascular plants showed that *Sphagnum* species were grouped with other mosses and some liverworts and

vascular plants. This similarity in chemical composition was reflected in low degradability, and mass losses were negatively correlated with structural carbohydrates and aromatic compounds. Thus, taken together, plant metabolic pathways followed a "descent with modification" pattern, when closely related species have more similar sets of metabolic reactions (*i.e.* chemical reaction of catabolism and anabolism) (Cannell et al., 2020; Chae et al., 2014). For example, mosses were found to possess a set of carbohydrate-related reactions not related with any known pathway comparing with other plants.

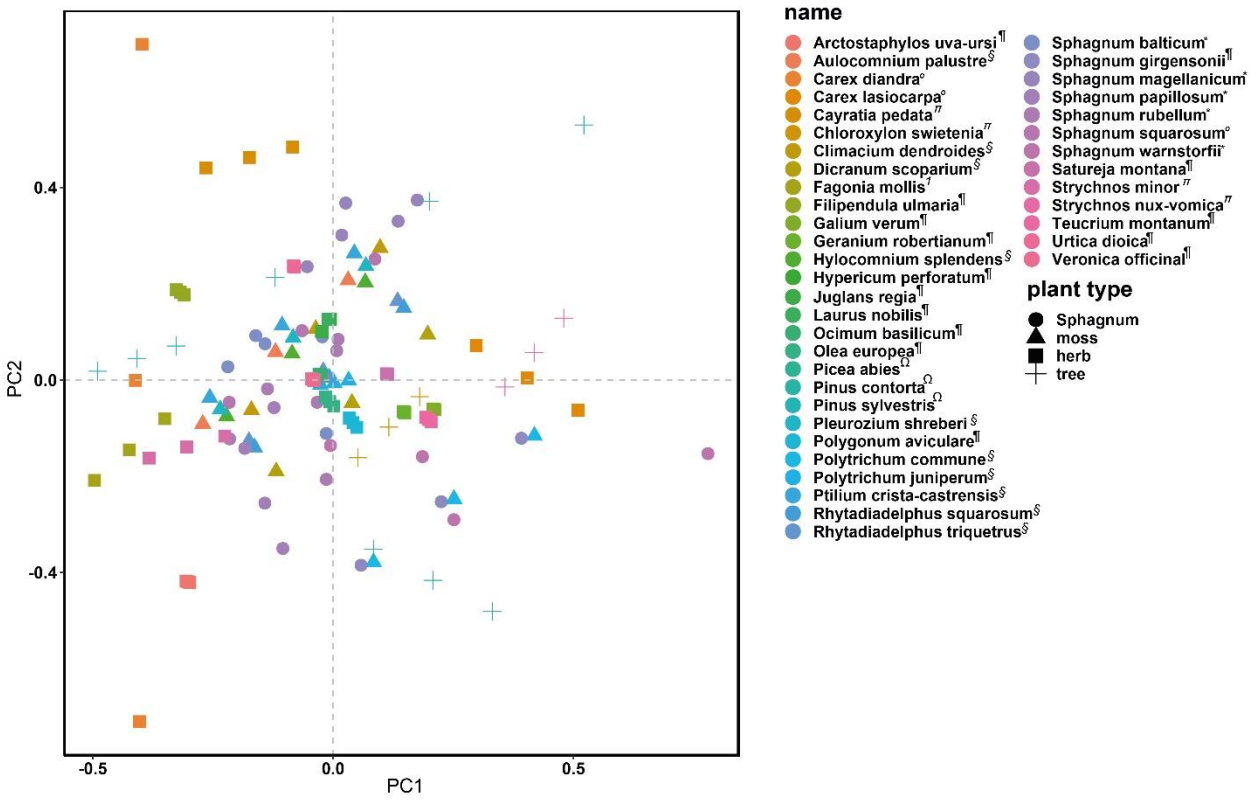


Figure 6-2. Principal component analysis on metabolites (phenols, flavonoids, carbohydrates, proline), showing the distribution of the plants in the ordination space. Colour respresent species, while shape — the plant group. References: ¶-(Mekinić et al., 2019); §-(Klavina et al., 2015); °-(Scheffer et al., 2001); π-(Enkhtaivan et al., 2015); *1*-(El-Zayat et al., 2020); Ω-(Stolter et al., 2009); *-(Sytiuk et al., 2022).

Five *Sphagnum* species from three different families showed the prominent differences in anatomical and morphological traits and metabolites, which were different not only between families, but also between species within the same family (Chapter 3). For example, *S. rubellum and S. balticum* are driven by holocellulose, soluble Klason lignin, number of hyaline cells, dry bulk density and shoot density; *S. warnstorfii* and *S. magellanicum* by phenols, tannins, carbohydrates, proteins, flavonoids, sphagnan, pigments, cation exchange capacities,

capitulum volume, capitulum water-holding capacities and the surface of hyaline cells; and *S. papillosum* is driven by enzyme activities like APX, SOD and CAT, and width of chlorocyste (Fig. 6-3; pooled data from the literature and from Chapter 3). Similar findings for traits were reported in Bengtsson et al. (2018, 2016) for 15 *Sphagnum* species and some studies on moss (Bengtsson et al., 2020a; Chiapusio et al., 2018; Dorrepaal et al., 2005; Gong et al., 2020b), suggesting a high interspecific variability in their inherited anatomical, morphological and biochemical traits. Interspecific traits variability is a consequence of *Sphagnum* co-existing in the community with increasing number plants, and thus new species potentially expand the traits distribution for the community (Clark, 2016; Michel et al., 2012). Thus, interspecific variability may not only control local conditions like moisture retention and biomass production, but also increase resistance of the community to ongoing climate changes as environmental changes more likely affect ecosystem at the community level (structure, density) than at the individual species level (Brooker, 2006; Suding et al., 2008).

Sphagnum anatomical and morphological traits are increasingly used to explain how *Sphagnum* species interact with environmental conditions (Bengtsson et al., 2020b; Jassey and Signarbieux, 2019; Laine et al., 2021). Meanwhile, biochemical traits were mostly used to show trade-off in resource partitioning for indication of litter decomposability (and in response to water table height and/or light intensity) (Bengtsson et al., 2018; Freeman et al., 2001b; Mazziotta et al., 2019; Turetsky et al., 2008), but less is known on how *Sphagnum* biochemical traits interact with its environment (local and regional changes) and their relationship with anatomical and morphological traits. The findings in Chapter 3 addressed this gap, and the hypervolume of the *Sphagnum* trait space showed a four-fold increase, when biochemical traits were included than when they were excluded for four *Sphagnum* species. These findings confirm that *Sphagnum* metabolites may capture key differences in foliar chemistry and responses to environmental variability that are complementary to anatomical and morphological traits. The combination of anatomical, morphological and biochemical traits can significantly improve predictions of ecosystem processes (Walker et al., 2019), as 'classical' anatomical traits *per se*, which are widely used by ecologists (Díaz et al., 2016) have low explanatory power of ecological processes (Plas et al., 2020).

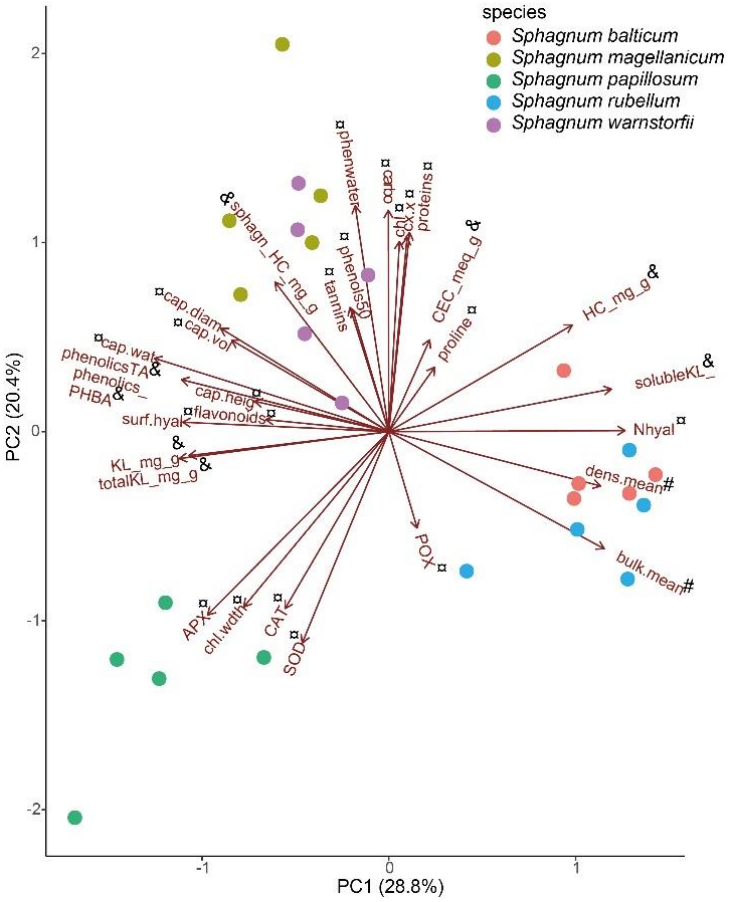


Figure 6-3. Principle component analysis on *Sphagnum* metabolites, anatomical and morphological traits. References: #-(Bengtsson et al., 2016); &-(Bengtsson et al., 2018); ¤- (Sytiuk et al., 2022). Traits abbreviations: HC_mg_g- Holocellulose, solubleKL- soluble Klason lignin, Nhyal-number of hyaline cells, dens.mean-shoot density, bulk.mean- dry bulk density, POX- peroxidase activity, SOD- superoxide dismutase, CAT- catalase activity,chl.wdth-width of chlorocystes, APX- ascorbate peroxidase activity, totalKL_mg_g- total Klason lignin, KL_mg_g- Klason lignin, surf.hyal-area of hyaline cells, cap.heig-capitulum height, phenolics_PHBA-4-hydroxybenzoic phenols, phenolicsTA-tannic acid phenols, cap.wat-capitulum water-holding capacities, cap.volume-capitulum volume, cap.diam-capitulum diameter, phenols50-total phenols, phenwat-water-soluble phenols, carbo—carbohydrates, chla—chlorophyll a, chlb—chlorophyll b, CEC_meq_g-cation exchange

Dissimilar environmental pressure on plants for growth, survival and reproduction in different areas has resulted in high diversity of form and function (*i.e.* functional diversity) occurring both across and within habitats. My findings confirmed that *Sphagnum* species growing in different local environmental (vegetation composition, nutrients content) and regional (temperature, precipitation) conditions possess a suite of diverse traits that supports *Sphagnum* form and function as well as its resistance to environmental changes. More particularly, we found that *Sphagnum* traits can be grouped into four clusters related to growth (proteins, total carbohydrates, carotenoids and total chlorophyll), biomass (capitulum diameter, volume and height), defense (total tannins, total phenols, POX, water-soluble

phenols and proline) and water stress tolerance (flavonoids, APX, CAT, SOD, capitulum water-holding capacity, area of hyaline cell and the width of cholocyste) when considering environmental conditions. The given results show that among four clusters, only one cluster of water stress tolerance combined anatomical, morphological and biochemical (metabolites) traits. This suggests that an interplay between biochemical (metabolites and enzyme activities) and phenotypical (morphological and anatomical) traits support plant performance and mediates the effect of environment on ecosystem processes (Falster et al., 2011; Guo et al., 2017; Mazziotta et al., 2018). My SEM analysis revealed that water stress tolerance and growth clusters were significant descriptors of *Sphagnum* form and function. However, when environmental effects were filtered, it was found that clusters containing most of biochemical traits (defense and water stress tolerance clusters) were disbanded, whilst the biomass cluster with classical morphological traits remained. This release of metabolites-containing clusters can be related to the fact that plant metabolites are the ultimate expression agents of genetic changes and the first responders to environmental changes (Handakumbura et al., 2019; Peñuelas and Sardans, 2009), thus these traits may better describe aspects of *Sphagnum* physiology not captured by classical functional traits like capitulum diameter, volume and height. Metabolites provide an effective way to assess variation among *Sphagnum* phenotypes associated to environmental tolerance (Bakhtiari et al., 2020; Callis-Duehl et al., 2017; Chiapusio et al., 2018; Defossez et al., 2021).

6.3. *Sphagnum* biochemical traits and microbes

Recent studies showed that microbial communities associated to *Sphagnum* mosses differs along with *Sphagnum* phylogeny and environmental factors as pH and nutrients availability (Bragina et al., 2013b; Opelt et al., 2007a; Tveit et al., 2020). However, other studies showed that microbial composition did not significantly vary between different *Sphagnum* species (Bragina et al., 2012b; Putkinen et al., 2012). My results also suggested that microbial community structure, and additionally, trait composition did not vary with *Sphagnum* phylogenetic distance. These findings may suggest that certain microbial taxa and traits are strongly related with particular *Sphagnum* traits, while other microbial taxa and traits are more generalist and mostly influenced by environmental conditions. Additionally, my results corroborated the findings that local and regional conditions are important drivers microbial communities and traits (Andersen et al., 2010; Bragina et al., 2013b; Elliott et al., 2015; Jassey et al., 2014; Tveit et al., 2020; Urbanová and Bárta, 2016). However, only considering

environmental factors as drivers of microbial communities cannot fully explain the variation observed within microbial communities (De Gruyter et al., 2020).

Using structural equation modelling (SEM), I found that the addition of *Sphagnum* traits to environmental conditions (temperature, precipitation, *Sphagnum* water content, water extractable organic matter), significantly increased a proportion of the explained variance (R^2). The most remarkable R^2 increases were for the biomass of decomposers (+42%) and phototrophs (+19%), as well as for growth yield microbial traits (+10%). *Sphagnum* anatomical and morphological traits were rather poor predictors and played auxiliary role, while *Sphagnum* metabolites were observed to be important drivers for microbial community structure and traits. This corroborates and expands the findings from (Jassey et al., 2011b) who showed that in addition to climatic variables, *Sphagnum* phenols explained big portion of the testate amoeba diversity. These findings for microbial composition and traits reflect the extension of *Sphagnum* functional trait space when metabolites were considered. Nevertheless, I found a little number of correlations between anatomical and morphological traits and microbial composition and traits: biomass of cyanobacteria (primary producers), nematodes (large consumers), and microbial traits related to growth yield (*i.e.* respiration, size and volume) and resource acquisition (*i.e.* some extracellular enzymes) were positively correlated to *Sphagnum* species with high capitulum size, and, hence, high water- holding capacities and width of chlorocystes. *Sphagnum* species with high water- holding capacity are better protected from desiccation (Jassey and Signarbieux, 2019) and subsequently their inhabitants and the hunting space for large consumers is less limited, comparing for those living in smaller *Sphagnum* species. Similarly to *Sphagnum*, in vascular plants the increased root surface area improved opportunities for mycorrhizal fungi colonization in grasslands (Sweeney et al., 2020). However, a small number of correlations could be related to a small number of *Sphagnum* anatomical and morphological traits were used in this study comparing to *Sphagnum* metabolites. Important to mentioned that there is almost no research has been performed on the effect of *Sphagnum* anatomical and morphological traits variation on microbial structure and traits.

Comparative effects between *Sphagnum* anatomical and morphological traits and metabolites provide evidence that *Sphagnum* metabolites play a central role in structuring microbial communities and their traits. In my work, I showed diverse effects of *Sphagnum* metabolites on microbial community and traits — most of them being unreported before: the biomass of cyanobacteria, fungi and bacteria, as well as a number of resource acquisition traits, such as extracellular enzymes, were positively correlated to many metabolites, including total

carbohydrates, proteins, *Sphagnum* pigments, total phenols and/ or tannins, while the biomass of microalgae and nematodes, and most of microbial growth yield traits (*i.e.* microbial pigments, respiration, biomass, volume and size) were negatively correlated. Hamard et al. (2019) assumed that chemical composition of *Sphagnum* leachates from different species does not significantly differ in term of compounds, but rather their proportions, and therefore specific compounds/proportions in leachates may have specific effect (positive or negative) on certain microorganisms. Similar assumptions were shown for vascular plants that beneficial interactions between microbes and plants often involve specific metabolites (Hiruma, 2019).

Among 11 classes of *Sphagnum* metabolites, I found that four of them had most of the correlations with microbial structure and traits (Table 6-1): (1) pigments+proteins, (2) carbohydrates (*i.e.* glucose), (3) water-soluble phenols and (4) lipids (symmetric and antisymmetric lipids). For the first time *Sphagnum* pigments and proteins were found to be positively correlated with cyanobacteria and decomposers biomass and microbial growth traits. However, these compounds rather evidence about *Sphagnum* performance and relation to growth, than about potential direct effect on microbes. More likely this positive correlation shows that the activity of these microorganisms benefits the growth of *Sphagnum* (*e.g.* fungi provide shelter for cyanobacteria, while it fixes N fixation for *Sphagnum* and fungi). We caution not to use these metabolites as absolute markers of beneficial *Sphagnum*-microbial interactions, but as auxiliary markers of the overall *Sphagnum* performance. Besides, *Sphagnum* releases easy degradable carbohydrates (*i.e.* glucose) that more likely boosted nutrient mineralization by decomposers' enzymes, which directly and positively feeds back to *Sphagnum* growth, but restraining other microbial activities.

Water-soluble phenols have the biggest portion of correlations, most of them were negatively correlated with microbes and microbial traits. My research supports previous findings that phenols (1) are released into the surroundings to interact with *Sphagnum* associated microbial communities and (2) have antimicrobial and inhibitory properties of *Sphagnum* phenols and their important role in driving the microbial community structure and functioning (*e.g.* Fudyma et al., 2019; Hamard et al., 2019; Jassey et al., 2013, 2011a; Mellegård et al., 2009; Opelt et al., 2007b), which ultimately affecting *Sphagnum* fitness, peatland primary productivity and the peatland C cycle. In parallel, I found less correlations with more complex compounds like polysaccharides, other aromatics, lignin like phenolics, which were negatively correlated with resource acquisition traits, but positively with growth traits. The compounds may be a structural component of the cell wall (like sphagnan), occurrences of which bear resistance of organic matter to degradation. Once being hydrolyzed

and released into the environment, sphagnan acidifies the surrounding water (Soudzilovskaia et al., 2010; Verhoeven and Liefveld, 1997), and it can also participate in inhibition of microbial activities (Stalheim et al., 2009).

Such compounds like tannins, flavonoids and proline had only few correlations in this study, however these compounds have rarely or even never (like proline) been studied in *Sphagnum*-microbial interactions (Table 6-1). The negative correlation between microbial growth traits and hydrolysable tannins shows a potential in inhibition of microbial growth and consumers biomass in addition to its known properties to deactivate microbial enzymes by forming tannin-protein-complexes (*e.g.* Verhoeven and Liefveld, 1997; Zak et al., 2019), suggesting its importance in microbial structure shaping. In my work, flavonoids, in addition to their potential antimicrobial effect (Basile et al., 1999b; Fudyma et al., 2019; Opelt et al., 2007b), showed to be beneficial for consumers and their traits suggesting their selective activity on specific microorganisms without affecting others. Positive correlation between proline and N-degrading enzymes could suggest that proline is a source of nitrogen for microorganisms. However, the role of proline in *Sphagnum*-microbial interactions remains unknown, as proline is produced by all living cells for osmoregulation and cell protection, thus during extraction it could be extracted simultaneously from microbial and *Sphagnum* cells. Finally, *Sphagnum* lipids showed many diverse correlations with microbial activities, suggesting that they are either insoluble component of a cell wall, or a soluble solute which serves as energy source as well they play role in humification processes and development of peat composition (Klavina, 2018; Limpens et al., 2017), with its antimicrobial potential (Xie and Lou, 2009). Alternatively, some lipids extracted from *Sphagnum* can be related to fungal metabolites like ergosterol (Fudyma et al., 2019) or phototrophs that can be an important the source of lipids (Griffiths and Harrison, 2009; Huang et al., 2012), which could possess antimicrobial properties (Leflaive and Ten-Hage, 2007).

Table 6- 1. Overview of the interactions between *Sphagnum* metabolites and microbial structure and traits. ↘-negative correlation, ↗-positive correlation, ↘↗-9-16 correlations, ↘↗-4-6 correlations, ↘↗-3 correlations. The total number of microbial groups and traits used in the study was 29 (for the full list see Fig. 4-6, Chapter 4). Chlorophyll (a+b), carotenoids and proteins were merged in pigments+proteins group, symmetric and antisymmetric lipids were referred as lipids

	Pigments +proteins	Carbohydrates	Total phenols	Total flavonoids	Total tannins	Proline	Water-soluble phenols	Poly-saccharides	Other aromatics	Lignin-like phenolics	Lipids
Phototrophs											
Microalgae	↘	↘					↘				
Cyanobacteria	↗	↗			↗		↗				
Decomposers											
Fungi	↗		↗				↗				
Methanotrophic bacteria											
Other bacteria	↗										
Consumers											
Testate amoebae							↘				
Rotifers	↗								↘	↘	
Nematodes	↘	↘		↗							
Flagellates						↗					
Ciliates					↘						
Microbial traits											
Growth yield	↘	↘	↘		↘		↘		↗	↗	↗
Resource acquisition	↗	↗		↗		↗		↘	↘	↘	↘
Stress tolerance	↘			↗			↘				

Aforementioned interactions between *Sphagnum* metabolites and microbes and their activities not only confirmed previous knowledges but also brought new insights to this topic, as these interactions are important for the overall nutrients cycling. The used UV-spectrometry analytical method in this study is relatively cheap and easy to perform. Nevertheless, this method also has its limitations as it gives general information about concentration of metabolites classes only, without providing the exact chemical formula and overlapping compounds from different classes. The utilization of metabolomics can provide more information about the interactions and their directions. In particular, more attention should be given to how to extract and quantify *Sphagnum* metabolites to be able to distinguish the effects of strictly *Sphagnum*- derived metabolites (case of proline and lipids) from microbial metabolites on microbial community composition and functioning or alternatively, apply positive and/or negative controls. The next step to study these interactions is to frame an experiment under controlled (or semi-) conditions and measuring additional parameters like evaluation of antiproliferative and antimicrobial activities of *Sphagnum*-extracted leachates, microbial respiration, detection of genes that specify antibiotic production and/or total-community DNA isolation.

6.4. The response of *Sphagnum* metabolites dynamic to climate changes and the consequences for peatland C uptake

Reciprocal transplantation along a latitudinal gradient allowed me to evaluate the effect of climate seasonality and warming on *Sphagnum* biochemical traits and to relate shifts in traits to ecosystem processes such as ecosystem C uptake. The results of seasonal monitoring along the latitudinal gradient showed that most of *Sphagnum* metabolites and gross ecosystem productivity (GEP) showed seasonal variability with the peak in summer, despite species and receptor site. The peak of *Sphagnum* metabolites concentration in summer was also reported in other works on *Sphagnum* mosses (Chiapusio et al., 2018; Klavina et al., 2018) and for other mosses (Mandi et al., 2022; Peters et al., 2019, 2018). These enhanced processes in summer can be related to more intense biological activity like photosynthesis of *Sphagnum* during summer (Lambers et al., 2008; Loisel et al., 2012; Rousk et al., 2017; Thakur and Kapila, 2017). Photosynthesis plays a key pole in plant performance in its environment, and it launches primary metabolism. Higher concentrations of metabolites in summer could also help to cope with high temperature and light irradiation, and drought (Xie and Lou, 2009), and biotic stresses as increased herbivory pressure and competition with other plants (Chiapusio et al.,

2013; Glime, 2006; Whitehead et al., 2018). In parallel, GEP showed seasonal variability, with the maximum C uptake in summer, as it was shown in other studies on peatlands (Bubier et al., 1998; Gavazov et al., 2018; Jassey and Signarbieux, 2019; Korrensalo et al., 2017; Lafleur et al., 2001; Tian et al., 2020; Walker et al., 2017). *Sphagnum* productivity is variable globally and highly related to water availability, temperature (Gunnarsson, 2005) and integral photosynthetically active radiation during the growing season. Seasonal variability of water availability may play a significant role in seasonal response of photosynthetic C fluxes (Adkinson and Humphreys, 2011). *Sphagnum* photosynthesis, like in vascular plants, is positively correlated with temperature (Williams and Flanagan, 1998), until optimum is reached, then it follows by decline (Hanson et al., 1999; Maseyk et al., 1999).

I found that upon transplantation to warmer sites, *Sphagnum* metabolite concentrations were the highest for all species and over all seasons, suggesting that warming stimulates *Sphagnum* physiological processes, similarly to summer conditions. Specifically, temperature was positively correlated with chlorophyll a, b and carotenoids, total and water-soluble phenols, tannins and flavonoids, while precipitation was negatively correlated with total and water-soluble phenols, tannins and proline over the seasons. Even though my findings on *Sphagnum* metabolites under warming differ from other findings for *Sphagnum* phenols and pigments (Dorrepaal et al., 2005; Jassey et al., 2013, 2011a; V. E. J. Jassey et al., 2016; Rastogi et al., 2020; Reczuga et al., 2018b), we can hypotheses that environmental filtering rather than taxonomy or phylogeny is a major driver of metabolite dynamic within *Sphagnum* mosses. Using random regression models (RRMM), we were able to assess the variation in phenotype in response to transplantation along the gradient of each *Sphagnum* species and the average response of five species by using reaction norms. It was found that the reaction norms of *Sphagnum* metabolites (PC1) in response to temperature were positive parabolic curves, with the maximum at +7.9°C (autumn, Estonia). On the contrary, the response of *Sphagnum* metabolites (PC2) to cumulative precipitation was negative parabolic curve with the maximum reaction norm at 11 and 31 mm (spring, Poland and Finland). The diverse direction of reaction norms to temperature and precipitation could be related to *Sphagnum* either possess broad physiological optima or (2) not genetically specialized ecotypes (Såstad et al., 1999) or (3) to the compromises between temperature and precipitation In addition, reaction norms of five species close to each other and changing over the time, suggesting that plasticity more likely moves species to new adaptation optima. Additionally, Limpens et al. (2017) showed that a response of the most of *Sphagnum* metabolites from

different species is driven by either environment or microtopography, but not by *Sphagnum* phylogeny.

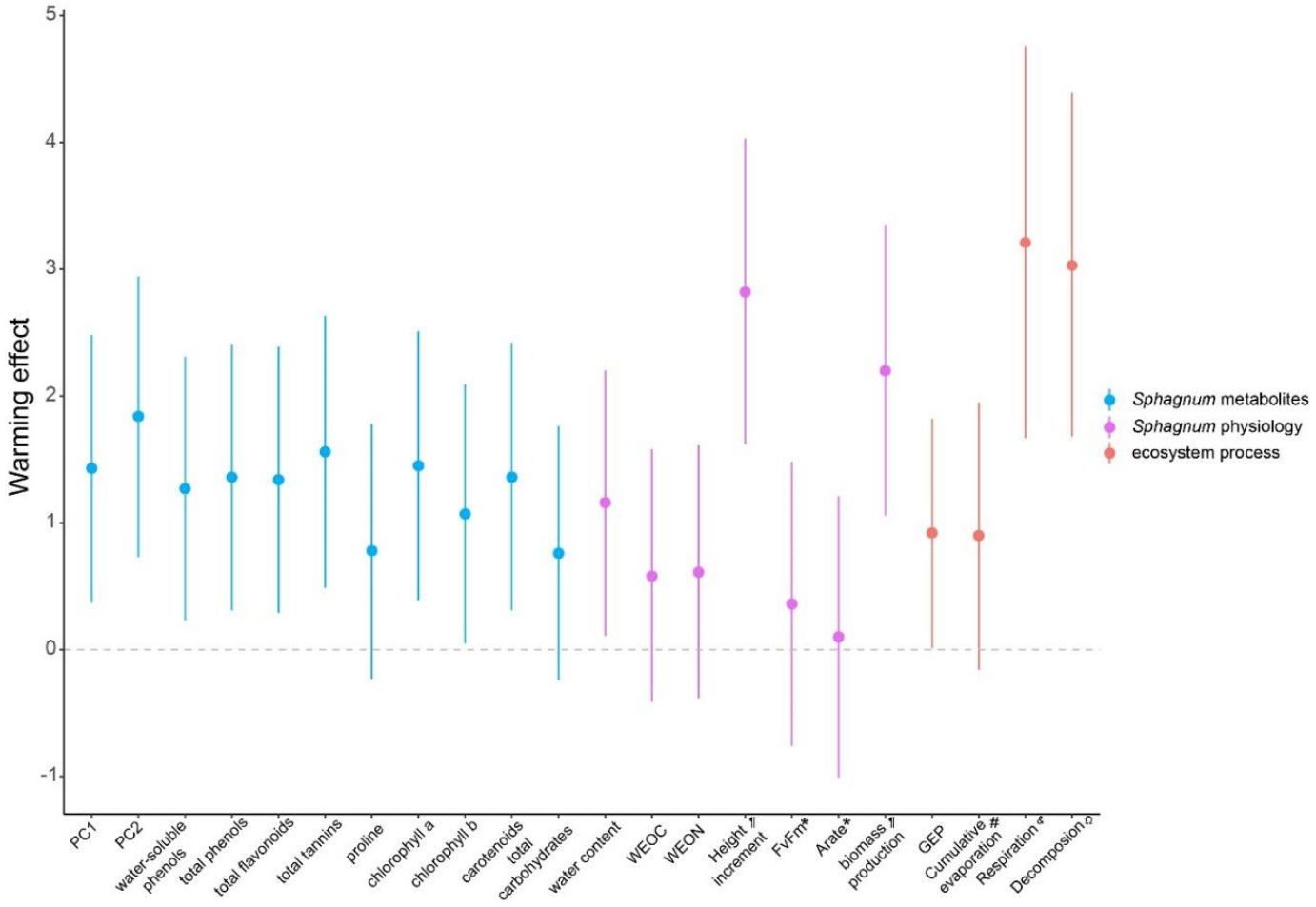


Figure 6-4. Warming effect on *Sphagnum* metabolites, *Sphagnum* physiology and ecosystem processes. Data: (Breeuwer et al., 2008); * (Jassey and Signarbieux, 2019); # (Robroek et al., 2007); & (Tian et al., 2020); Ω (Dieleman et al., 2016b). Data without symbols are taken from Chapter 5.

Compiling my findings and the results from other works (*e.g.* Fig. 6-4) allowed me to assume that (1) warming has mostly positive effects on *Sphagnum* physiology and performance related to C cycling as well as C uptake, (2) *Sphagnum* metabolites significantly respond to climatic change most of the time and (3) these compounds could be used as early warning indicators of climate change. These responses may be due to short-term observations, as Dorrepaal et al. (2003) cautioned that long-term warming will have negative effect on *Sphagnum* productivity. However, dynamics in reaction norms of *Sphagnum* species may

suggest that shifts in phenotypes across the gradient mirror a set of phenotypes that maximizes fitness in different environments (Henn et al., 2018). This points on traits liability – ability to change during lifetime (Via, 1994) and that biochemical traits (metabolites) act as primary mechanism of adaptation to environmental changes (Metlen et al., 2009). Indeed, changes among *Sphagnum* anatomical and morphological traits can take weeks or years to become apparent (Jassey and Signarbieux, 2019; Oke et al., 2020), whereas changes in *Sphagnum* metabolite concentrations occur more quickly after an environmental stimulus (Bakhtiari et al., 2020; Callis-Duehl et al., 2017; Defossez et al., 2021; Jassey et al., 2011c). With the regard of these findings, the utilization of metabolites and linking them with carbon-related processes may serve as early warnings of shifts in peatlands functioning. Moor et al., (2015) reported that changes in community-weighted mean traits led to ambiguous consequences for carbon sequestration. To verify this assumption, I linked *Sphagnum* metabolites and carbon uptake and thus I found that C uptake increased with increasing carbohydrates, proline, flavonoids and phenols concentrations in spring, while in autumn C accumulation increased along the decreasing concentration of carotenoids, chlorophyll a and b, tannins and increasing of carbohydrates. The most prominent correlation between *Sphagnum* metabolites and C uptake was observed in warmer sites at the beginning and the end of the growing season, suggesting that warming-induced adaptation of *Sphagnum* metabolites to new conditions may support C uptake. The linkages between *Sphagnum* metabolites and C-related processes suggest that climate-induced shifts in *Sphagnum* metabolites can feedback to ecosystem processes of carbon assimilation. Thus, my findings show important linkages between *Sphagnum* metabolism and C-related processes are season dependent although the exact mechanisms behind these linkages remain unclear and require further studies. To expand the potential of this findings, the inclusion of several parameters can be beneficial: to test *Sphagnum* performance markers (like growth, biomass production, photosynthetic capacity) exhibit similar plastic response as metabolites; check the genetic basis of the variability in five species; use the metabolomics to see if any specific compounds dictate the direction of metabolites-C uptake linkages.

I already went into that direction and performed metabolomics on five *Sphagnum* species collected from Sweden, Estonia and France. The first step of compounds identification after one year of transplantation experiment has been recently performed using UHPLC-HRMS (with the help of Stéphan Greff at SCECM IMBE, Marseille). The results show that transplantation of the same species to different sites with different environmental conditions reshape the chemical composition (Fig. 6-5) compared to the site of origin, subsequently it

can create a cascade effect to the ecological processes. Although these results are still very preliminary, they show the potential of metabolome to improve mechanistic and predictive power in *Sphagnum* ecology in the frame of climate changes.

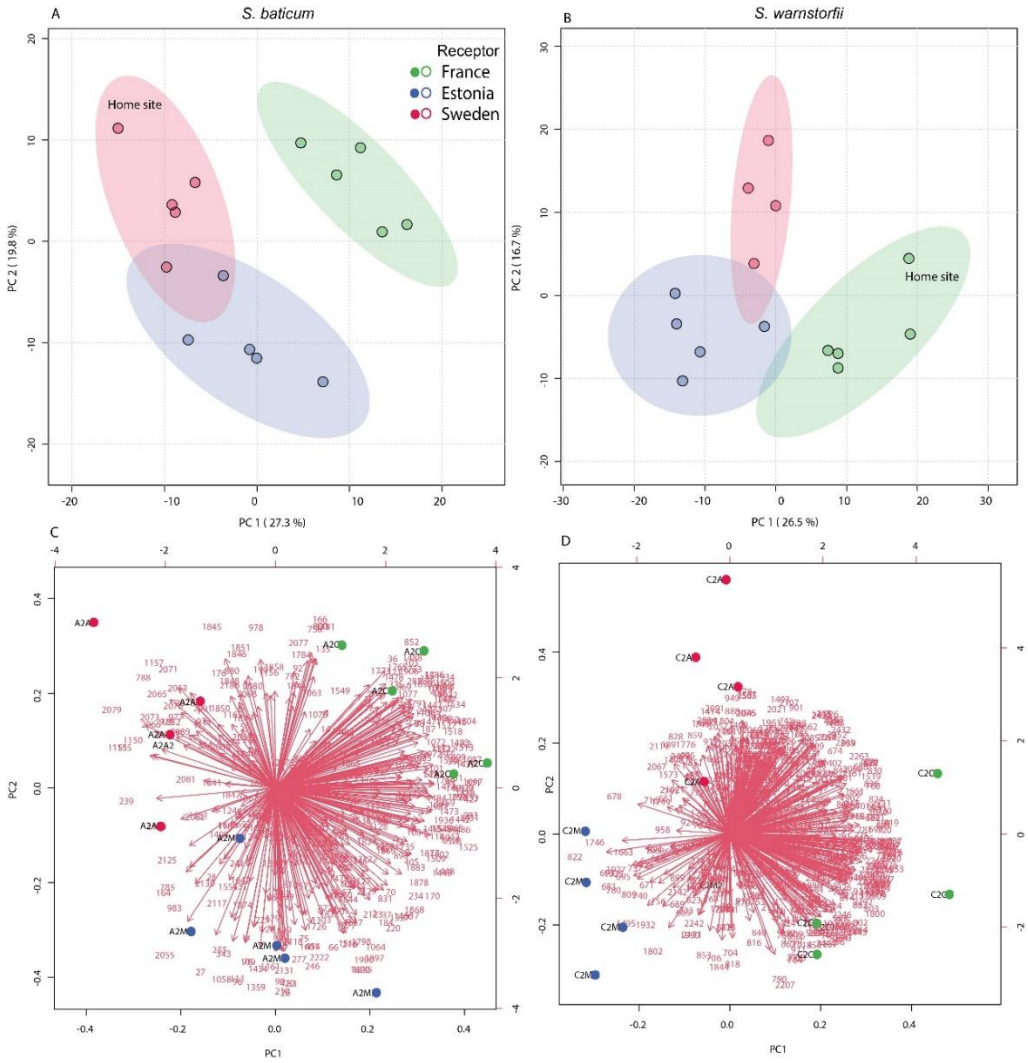


Figure 6-5. Principal component analysis plot derived from FTICR-HRMS data (positive mode), showing the distribution of the metabolites in *Sphagnum balticum* (A, C) and *S. warnstorfii* (B, D) transplanted to three sites alone the latitudinal gradient. A and B represent the scores plots, C and D represent the loading to axes 1 and 2.

Conclusion and perspectives

(English version)

The results of my thesis supported previous findings about a high interspecific variability in their inherited anatomical, morphological and biochemical (metabolites) traits in *Sphagnum* mosses (Bengtsson et al., 2020a, 2018, 2016; Chiapusio et al., 2018; Dorrepaal et al., 2005; Gong et al., 2020b). In this thesis I described new traits to be measured in *Sphagnum* (like enzyme activities, proline, flavonoids) in relation to *Sphagnum* growing environment. Using joint species distribution modelling (JSDM) approach, I found anatomical, morphological and biochemical traits had relatively poor shared responses to environmental conditions. Also, it was showed that *Sphagnum* biochemical were regulated by external forces, such as climate, nutrient availability and plant cover, that were not well represented by anatomical and morphological traits. Additionally, for the first time a significant expansion of *Sphagnum* functional traits was reported, when *Sphagnum* biochemical traits were taken into consideration. When environmental parameters were filtered from the JSDM, the clusters with metabolites were disbanded, while the cluster with anatomical/morphological traits remained. This suggests that these biochemical traits may describe aspects of *Sphagnum* physiology not captured by classical functional. Thus, the interplay between biochemical (metabolites and enzyme activities) and phenotypical (morphological and anatomical) traits may regulate the effect of the environmental stability on the ecosystem processes (Falster et al., 2011; Guo et al., 2017; Mazziotta et al., 2019). Overall, this study provided evidence that measurements of the metabolites and antioxidant enzyme activities, once properly incorporated with classical morphological and anatomical traits expand our understanding of the coupling between physiology and fitness in *Sphagnum* trait-based studies. Even though my study reports new linkages among anatomical, morphological and biochemical traits, some limitations have to be acknowledged and considered for further experiments. To expand the influence of these findings and erase potential confounding effect (one single species per site), more *Sphagnum* species can be included for the analysis and besides the equal numbers of anatomical, morphological and biochemical traits should be measured. Seasonal monitoring could help to see whether the interplay between traits is a constant phenomenon or changes over the time.

I found that *Sphagnum* phylogeny does not drive *Sphagnum* microbial structure and microbial traits, indicating that certain microbial taxa and traits are strongly related with particular *Sphagnum* traits, while other microbial taxa and traits are more generalist and mostly influenced by environmental conditions. Indeed, I identified that regional and local variables were as important drivers of microbial community and traits, similarly to what

reported (Elliott et al., 2015; Jassey et al., 2014; Urbanová and Bárta, 2016). *Sphagnum* interspecific trait variations were shown to play a key role in driving microbial community composition and microbial traits in addition to local and regional environmental conditions. Interestingly, anatomical and morphological traits were poor predictors of microbial communities and traits, compared with biochemical traits. Findings of Leff et al. (2018) showed similar trends for plant leaf and root traits of vascular plants, suggesting that plant traits are poor predictors of microbial communities and microbial processes. However, *Sphagnum* metabolites were shown to be better predictors of microbial community structure and traits. The exact mechanisms by which *Sphagnum* mosses shape their microbiome are yet unknown, but differences in the metabolite cocktails that *Sphagnum* release into their surrounding are likely to be an important factor, as Hamard et al.(2019) showed for *Sphagnum* and Hiruma (2019) for vascular plants. Further studies are clearly needed to assess fundamental chemical and structural data of *Sphagnum* metabolites using more advanced analytical techniques. Identified compounds can be possibly used as biomarkers of antimicrobial activities in peatlands and evaluate changes in carbon cycling.

Using reciprocal transplantation along a latitudinal gradient together with seasonal monitoring allowed to evaluate the effect of climate seasonality and warming (temperature and precipitation) on *Sphagnum* biochemical traits and relate the shifts in traits to ecosystem process of carbon uptake. *Sphagnum* metabolites from five species showed similar response to seasonal variability, with the maximum concentrations in summer. This increase in metabolites in summer could be related to more intense biological activity of *Sphagnum* during summer (Lambers et al., 2008; Rousk et al., 2017; Thakur and Kapila, 2017) to help coping with abiotic stress as high temperature and light irradiation, and drought (Xie and Lou, 2009), and biotic stresses as increased herbivory pressure and competition with other plants (Chiapusio et al., 2013; Glime, 2006; Whitehead et al., 2018). Similarly to *Sphagnum* metabolites, gross ecosystem productivity (GEP) showed seasonal variability, with the maximum C uptake in summer, as it was shown in other studies on peatlands (Bubier et al., 1998; Gavazov et al., 2018; Jassey and Signarbieux, 2019; Korrensalo et al., 2017; Lafleur et al., 2001; Tian et al., 2020; Walker et al., 2017). Upon transplantation to warmer sites, *Sphagnum* metabolite concentrations and gross ecosystem were higher for all species and over all seasons, suggesting that warming stimulates *Sphagnum* physiological processes, similarly to summer conditions. I found that *Sphagnum* metabolites plastic response to climate change were similar for all species. *Sphagnum* metabolites in response to temperature were positive parabolic curve, while to cumulative precipitation was negative parabolic curve. Interestingly

to mention, that the reaction norms were closer to each other, but the distance was changing over the time, as mentioned in (Sultan, 2000). This could suggest that species originating from similar environments can possess similar responses to new climate conditions. More likely, species metabolome, when moved to new conditions, tends to switch towards local optima, suggesting the advantage to adopt similar phenotype, but only if transplanted species had dissimilar phenotype from the members of a new community (Muscarella and Uriarte, 2016). Nevertheless, additional studies are required with longer period of observation and including genetic analysis to detect the genetic variation under new environmental conditions. Finally, I quantified a shift in a suite of primary and secondary metabolites alongside local rates of gross ecosystem productivity. I reported linkages between *Sphagnum* metabolites and C-related processes, assuming that climate-induced shifts in *Sphagnum* metabolites can feedback to ecosystem processes of carbon assimilation. Indeed, Moor et al., (2015) reported that changes in community-weighted mean traits led to ambiguous consequences for carbon sequestration. *Sphagnum* metabolism and C-related processes are season dependent although the exact mechanisms behind these linkages remain unclear and require further studies.

In a nutshell, trait-based approach used in this thesis has a potential for understanding and predicting *Sphagnum* functional space, associated microbial community structure and microbial traits, carbon-related ecosystem processes as well as response to climate change. Nevertheless, nowadays there is a scarce number of studies that links directly *Sphagnum* traits and ecosystem functioning. To solve this issue, the application of more precise analytical equipment can help to erase uncertainties, *e.g.* by linking a specific compound to a certain microorganism or the response of metabolite profiling to a reciprocal transplantation. Additionally, long-term experiments (several years) can help, where traits and ecosystem processes are assessed simultaneously with considering the causal inferences about the parameters affecting traits and ecosystem functioning and the feedbacks between them.

(Version française)

Mes résultats confirment la grande variabilité interspécifique dans les traits anatomiques, morphologiques et biochimiques hérités chez la sphaigne (Bengtsson et al., 2020a, 2018, 2016; Chiapusio et al., 2018; Dorrepaal et al., 2005; Gong et al., 2020). Dans cette thèse, j'ai décrit de nouveaux traits fonctionnels à mesurer dans les sphaignes, comme les activités enzymatiques, la proline, ou les flavonoïdes. En utilisant une approche de modélisation conjointe de la distribution des espèces (JSDM), j'ai trouvé que les traits anatomiques, morphologiques et biochimiques (métabolites) avaient des réponses partagées relativement faibles aux conditions environnementales. De plus, il a été démontré que la biochimie des sphaignes était régulée par des forces externes, telles que le climat, la disponibilité des nutriments et la couverture végétale, qui n'étaient pas bien représentées par les traits anatomiques et morphologiques. En outre, pour la première fois, j'ai montré une expansion significative de l'espace fonctionnels des sphaignes lorsque leurs traits biochimiques étaient pris en considération. De plus, lorsque les paramètres environnementaux ont été filtrés du modèle JSDM, les clusters avec les métabolites ont été dissous, tandis que le cluster avec les traits anatomiques/morphologiques est resté. Cela suggère que ces traits biochimiques peuvent décrire des aspects de la physiologie des sphaignes qui ne sont pas pris en compte par les fonctions classiques. Ainsi, l'interaction entre les traits biochimiques (métabolites et activités enzymatiques) et phénotypiques (morphologiques et anatomiques) peut réguler l'effet de la stabilité environnementale sur les processus de l'écosystème (Falster et al., 2011; Guo et al., 2017; Mazziotta et al., 2019). Dans l'ensemble, cette étude a fourni des preuves que les mesures des métabolites et des activités enzymatiques antioxydantes, une fois correctement incorporées aux traits morphologiques et anatomiques classiques, élargissent notre compréhension du couplage entre la physiologie et la forme physique dans les études basées sur les traits de vie des sphaignes. Même si notre étude rapporte de nouveaux liens entre les traits anatomiques, morphologiques et biochimiques, certaines limites doivent être reconnues et prises en compte pour des expériences ultérieures. Afin d'étendre l'influence de ces résultats et d'effacer l'effet confondant potentiel dans cette étude (une seule espèce par site), d'autres espèces de sphaigne devront être incluses à l'avenir dans l'analyse et un nombre égal de traits anatomiques, morphologiques et biochimiques devront être mesurés. Un suivi saisonnier pourrait également permettre de voir si l'interaction entre ces différentes caractéristiques fonctionnelles est un phénomène constant ou s'il change au fil du temps.

Nous avons constaté que la phylogénie de la sphaigne ne déterminait pas la structure microbienne et les traits microbiens de la sphaigne, ce qui indique que certains taxons et traits

microbiens sont fortement liés à des caractéristiques particulières de la sphaigne, tandis que d'autres taxons et traits microbiens sont plus généralistes et principalement influencés par les conditions environnementales. En effet, nous avons identifié que les variables régionales et locales étaient des moteurs importants de la communauté microbienne et des traits, de manière similaire à ce qui a été rapporté (Elliott et al., 2015; Jassey et al., 2014; Urbanová et Bárta, 2016). Il a été démontré que les variations des traits interspécifiques des sphaignes jouaient un rôle clé dans la composition de la communauté microbienne et les traits microbiens, en plus des conditions environnementales locales et régionales. Il est intéressant de noter que les traits anatomiques et morphologiques étaient de mauvais prédicteurs des communautés et des traits microbiens, par rapport aux traits biochimiques. Les conclusions de Leff et al. (2018) ont montré des tendances similaires pour les traits des feuilles et des racines des plantes vasculaires, suggérant que les traits des plantes sont de mauvais prédicteurs des communautés microbiennes et des processus microbiens. Cependant, les métabolites des sphaignes se sont avérés être de meilleurs prédicteurs de la structure et des traits des communautés microbiennes. Les mécanismes exacts par lesquels les sphaignes façonnent leur microbiome sont encore inconnus, mais les différences dans les cocktails de métabolites que les sphaignes libèrent dans leur environnement sont probablement un facteur important, comme Hamard et al. (2019) l'ont montré pour les sphaignes et Hiruma (2019) pour les plantes vasculaires. D'autres études sont clairement nécessaires pour évaluer les données chimiques et structurelles fondamentales des métabolites de la sphaigne en utilisant des techniques analytiques plus avancées. Les composés identifiés peuvent éventuellement être utilisés comme biomarqueurs des activités antimicrobiennes dans les tourbières et évaluer les changements dans le cycle du carbone.

L'utilisation de la transplantation réciproque le long d'un gradient latitudinal ainsi que le survi saisonnier ont permis d'évaluer l'effet de la saisonnalité et du réchauffement climatique (température et précipitation) sur les caractéristiques biochimiques des sphaignes et de relier les changements de caractéristiques au processus d'absorption du carbone par l'écosystème. Les métabolites de cinq espèces de sphaignes ont montré une réponse similaire à la variabilité saisonnière, avec les concentrations maximales en été. Cette augmentation des métabolites en été pourrait être liée à une activité biologique plus intense de la sphaigne pendant l'été (Lambers et al., 2008; Rousk et al., 2017; Thakur et Kapila, 2017) pour aider à faire face aux stress abiotiques comme les températures élevées, l'irradiation lumineuse et la sécheresse (Xie et Lou, 2009), et aux stress biotiques comme la pression accrue de l'herbivorie et la compétition avec d'autres plantes (Chiapusio et al., 2013; Glime, 2006; Whitehead et al., 2018).

De façon similaire, la productivité brute de l'écosystème (PBE) a montré une variabilité saisonnière, avec l'absorption maximale de C en été, comme cela a été montré dans d'autres études sur les tourbières (Bubier et al., 1998; Gavazov et al., 2018; Jassey et Signarbieux, 2019; Korrensalo et al., 2017; Lafleur et al., 2001; Tian et al., 2020; Walker et al., 2017). Lors de la transplantation sur des sites plus chauds, les concentrations de métabolites de sphaignes et l'écosystème brut étaient plus élevés pour toutes les espèces et sur toutes les saisons, ce qui suggère que le réchauffement stimule les processus physiologiques des sphaignes de manière similaire aux conditions estivales. Nous avons constaté que les métabolites des sphaignes en réponse au changement climatique étaient similaires pour toutes les espèces. Les métabolites de toutes les espèces de sphaignes ont montré une courbe parabolique positive en réponse à l'augmentation de la température, tandis qu'en réponse aux précipitations cumulées, la courbe parabolique était négative. Il est intéressant de mentionner que les normes de réaction étaient plus proches les unes des autres entre les espèces, mais que la distance changeait au fil du temps, comme mentionné dans (Sultan, 2000). Cela pourrait suggérer que les espèces originaires d'environnements similaires peuvent avoir des réponses similaires aux nouvelles conditions climatiques. Il est plus probable que le métabolome des espèces, lorsqu'elles sont déplacées vers de nouvelles conditions, tende à s'orienter vers les optima locaux, ce qui suggère l'avantage d'adopter un phénotype similaire, mais seulement si les espèces transplantées ont un phénotype différent de celui des membres de la nouvelle communauté (Muscarella et Uriarte, 2016). Néanmoins, des études supplémentaires sont nécessaires avec une période d'observation plus longue et incluant une analyse génétique pour détecter la variation génétique dans les nouvelles conditions environnementales. Enfin, nous avons quantifié un changement dans une suite de métabolites primaires et secondaires parallèlement aux taux locaux de productivité brute de l'écosystème. Nous avons signalé des liens entre les métabolites de la sphaigne et les processus liés au carbone, en supposant que les changements induits par le climat dans les métabolites de la sphaigne peuvent rétroagir sur les processus d'assimilation du carbone de l'écosystème. En effet, Moor et al. (2015) ont signalé que les changements dans les traits moyens pondérés par la communauté ont eu des conséquences ambiguës sur la séquestration du carbone. Le métabolisme de la sphaigne et les processus liés au C dépendent de la saison, bien que les mécanismes exacts derrière ces liens ne soient pas clairs et nécessitent des études supplémentaires.

En bref, l'approche basée sur les traits biochimique des sphaignes utilisée dans cette thèse a montré un fort potentiel pour mieux comprendre et prédire l'espace fonctionnel des sphaignes, la structure des communautés microbiennes associées et les traits microbiens, et

les processus écosystémiques liés à l'assimilation du carbone, notamment dans un contexte de changements climatiques. Il existe aujourd'hui un nombre limité d'études qui établissent un lien direct entre les caractéristiques biochimiques des plantes et le fonctionnement des écosystèmes, et mes résultats montrent clairement le besoin de développer plus d'études dans ce sens. Pour résoudre ce problème, l'application d'équipements analytiques plus précis devra être envisagée afin d'effacer les incertitudes, par exemple en reliant un composé spécifique à un certain microorganisme ou la réponse du profilage des métabolites à une transplantation réciproque. En outre, les expériences à long terme (plusieurs années) peuvent être utiles, car elles permettent d'évaluer simultanément les caractéristiques et les processus de l'écosystème tout en tenant compte des inférences causales sur les paramètres qui influent sur les caractéristiques et le fonctionnement de l'écosystème et sur les rétroactions entre eux.

Bibliography list

Abascal, K., Ganora, L., Yarnell, E., 2005. The effect of freeze-drying and its implications for botanical medicine: A review. Phyther. Res. 19, 655–660. https://doi.org/10.1002/ptr.1651

Abbott, G.D., Swain, E.Y., Muhammad, A.B., Allton, K., Belyea, L.R., Laing, C.G., Cowie, G.L., 2013. Effect of water-table fluctuations on the degradation of Sphagnum phenols in surficial peats. Geochim. Cosmochim. Acta 106, 177–191. https://doi.org/10.1016/j.gca.2012.12.013

Achard, P., Genschik, P., 2009. Releasing the brakes of plant growth: How GAs shutdown della proteins. J. Exp. Bot. 60, 1085–1092. https://doi.org/10.1093/jxb/ern301

Adkinson, A.C., Humphreys, E.R., 2011. The response of carbon dioxide exchange to manipulations of Sphagnum water content in an ombrotrophic bog. Ecohydrology 4, 733–743. https://doi.org/10.1002/eco.171

Adler, P.B., Fajardo, A., Kleinhesselink, A.R., Kraft, N.J.B., 2013. Trait-based tests of coexistence mechanisms. Ecol. Lett. 16, 1294–1306. https://doi.org/10.1111/ele.12157

Adler, P.B., Salguero-Gómez, R., Compagnoni, A., Hsu, J.S., Ray-Mukherjee, J., Mbeau-Ache, C., Franco, M., 2014. Functional traits explain variation in plant life history strategies. Proc. Natl. Acad. Sci. 111, 10019–10019. https://doi.org/10.1073/pnas.1410430111

Aebi, H., 1984. Catalase in Vitro. Methods Enzymol. 105, 121–126. https://doi.org/10.1016/S0076-6879(84)05016-3

Agati, G., Azzarello, E., Pollastri, S., Tattini, M., 2012. Flavonoids as antioxidants in plants: Location and functional significance. Plant Sci. 196, 67–76. https://doi.org/10.1016/j.plantsci.2012.07.014

Ågren, J., Schemske, D.W., 2012. Reciprocal transplants demonstrate strong adaptive differentiation of the model organism Arabidopsis thaliana in its native range. New Phytol. 194, 1112–1122. https://doi.org/10.1111/j.1469-8137.2012.04112.x

Ahanger, M.A., Gul, F., Ahmad, P., Akram, N.A., 2018. Environmental Stresses and Metabolomics—Deciphering the Role of Stress Responsive Metabolites, in: Ahmad, P., Ahanger, Mohammad Abass, Singh, V.P., Tripathi, D.K., Alam, P., Alyemeni, M.N. (Eds.), Plant Metabolites and Regulation Under Environmental Stress. Elsevier, pp. 53–67. https://doi.org/10.1016/B978-0-12-812689-9.00003-0

Aharoni, A., Galili, G., 2011. Metabolic engineering of the plant primary-secondary metabolism interface. Curr. Opin. Biotechnol. 22, 239–244. https://doi.org/10.1016/j.copbio.2010.11.004

Ahuja, I., de Vos, R.C.H., Bones, A.M., Hall, R.D., 2010. Plant molecular stress responses face climate change. Trends Plant Sci. 15, 664–674. https://doi.org/10.1016/j.tplants.2010.08.002

Ainsworth, E.A., Gillespie, K.M., 2007. Estimation of total phenolic content and other oxidation substrates in plant tissues using Folin-Ciocalteu reagent. Nat. Protoc. 2, 875–877. https://doi.org/10.1038/nprot.2007.102

Alexander, J.M., Diez, J.M., Levine, J.M., 2015. Novel competitors shape species' responses to climate change. Nature 525, 515–518. https://doi.org/10.1038/nature14952

Allen, M.R., Dube, P.O., Solecki, William, Aragón-Durand, Fernando, Cramer France, W., Humphreys, Stephen, Dasgupta, P., Millar, R., Dube, O., Solecki, W, Aragón-Durand, F, Cramer, W., Humphreys, S, Kainuma, M., Kala, J., Mahowald, N., Mulugetta, Y., Perez, R., Wairiu, M., Zickfeld, K., Zhai, P., Pörtner, H., Roberts, D., Skea, J., Shukla, P., Pirani, A., Moufouma-Okia, W., Péan, C., Pidcock, R., Connors, S., Matthews, J., Chen, Y., Zhou, X., Gomis, M., Lonnoy, E., Maycock, T., Tignor, M., Waterfield, T., 2018. Framing and Context, in: Masson-Delmotte, V., Zhai, P., Pörtner, H.-O., Roberts, D., Skea, J., Shukla, P.R., Pirani, A., Moufouma-Okia, W., C. Péan, R.P., Connors, S., Matthews, J.B.R., Y. Chen, X.Z., Gomis, M.I., Lonnoy, E., Maycock, T.,

Tignor, M., Waterfield, T. (Eds.), Global Warming of 1.5°C. An IPCC Special Report on the Impacts of Global Warming of 1.5°C above Pre-Industrial Levels and Related Global Greenhouse Gas Emission Pathways, in the Context of Strengthening the Global Response to the Threat of Climate Change,. Australia.

Alnsour, M., Ludwig-Müller, J., 2015. Potential effects of climate change on plant primary and secondary metabolism and its influence on plant ecological interactions. J. Endocytobiosis Cell Res. 26, 90–99.

Andersen, R., Grasset, L., Thormann, M.N., Rochefort, L., Francez, A.J., 2010. Changes in microbial community structure and function following Sphagnum peatland restoration. Soil Biol. Biochem. 42, 291–301. https://doi.org/10.1016/j.soilbio.2009.11.006

Anderson, R.L., Foster, D.R., Motzkin, G., Anderson, R.L., Foster, D.R., Motzkin, G., 2003. Integrating Lateral Expansion into Models of Peatland Development in Temperate New England. J. Ecol. 91, 68–76.

Arndt, D.S., Blunden, J., Dunn, R.J.H., 2020. State of the Climate in 2019. Bull. Am. Meteorol. Soc. 101, SI-S8. https://doi.org/10.1175/2020BAMSSTATEOFTHECLIMATE.1

Arnold, P.A., Kruuk, L.E.B., Nicotra, A.B., 2019. How to analyse plant phenotypic plasticity in response to a changing climate. New Phytol. 222, 1235–1241. https://doi.org/10.1111/nph.15656

Asakawa, Y., Ludwiczuk, A., 2018. Chemical Constituents of Bryophytes: Structures and Biological Activity. J. Nat. Prod. 81, 641–660. https://doi.org/10.1021/acs.jnatprod.6b01046

Averill, C., Bhatnagar, J.M., Dietze, M.C., Pearse, W.D., Kivlin, S.N., 2019. Global imprint of mycorrhizal fungi on whole-plant nutrient economics. Proc. Natl. Acad. Sci. U. S. A. 116, 23163–23168. https://doi.org/10.1073/pnas.1906655116

Ayres, E., Van Der Wal, R., Sommerkorn, M., Bardgett, R.D., 2006. Direct uptake of soil nitrogen by mosses. Biol. Lett. 2, 286–288. https://doi.org/10.1098/rsbl.2006.0455

Bakhtiari, M., Glauser, G., Defossez, E., Rasmann, S., 2021. Ecological convergence of secondary phytochemicals along elevational gradients, New Phytologist. https://doi.org/10.1111/nph.16966

Bakhtiari, M., Glauser, G., Defossez, E., Rasmann, S., 2020. Ecological convergence of secondary phytochemicals along elevational gradients. New Phytol. 229, 1755–1767. https://doi.org/10.1111/nph.16966

Ballance, S., Børsheim, K.Y., Inngjerdingen, K., Paulsen, B.S., Christensen, B.E., 2007. A re-examination and partial characterisation of polysaccharides released by mild acid hydrolysis from the chlorite-treated leaves of Sphagnum papillosum. Carbohydr. Polym. 67, 104–115. https://doi.org/10.1016/j.carbpol.2006.04.020

Ballance, S., Kristiansen, K.A., Holt, J., Christensen, B.E., 2008. Interactions of polysaccharides extracted by mild acid hydrolysis from the leaves of Sphagnum papillosum with either phenylhydrazine, o-phenylenediamine and its oxidation products or collagen. Carbohydr. Polym. 71, 550–558. https://doi.org/10.1016/j.carbpol.2007.06.025

Barber, C.B., Dobkin, D.P., Huhdanpaa, H.T., 1996. The Quickhull algorithm for convex hulls. ACM Trans. Math. Softw. 22, 469–483.

Barberán, A., Mcguire, K.L., Wolf, J.A., Jones, F.A., Wright, S.J., Turner, B.L., Essene, A., Hubbell, S.P., Faircloth, B.C., Fierer, N., 2015. Relating belowground microbial composition to the taxonomic, phylogenetic, and functional trait distributions of trees in a tropical forest. Ecol. Lett. 18, 1397–1405. https://doi.org/10.1111/ele.12536

Bardgett, R.D., Wardle, D.A., 2010. Aboveground-Belowground linkages, Oxford Series in Ecology and Evolution.

Barlow, R.G., Cummings, D.G., Gibb, S.W., 1997. Improved resolution of mono- and divinyl chlorophylls a and b and zeaxanthin and lutein in phytoplankton extracts using reverse phase C-8 HPLC. Mar. Ecol. Prog. Ser. 161, 303–307.

Basile, A., Giordano, S., López-Sáez, J.A., Cobianchi, R.C., 1999a. Antibacterial activity of pure flavonoids isolated from mosses. Phytochemistry 52, 1479–1482. https://doi.org/10.1016/S0031-9422(99)00286-1

Basile, A., Giordano, S., López-Sáez, J.A., Cobianchi, R.C., 1999b. Antibacterial activity of pure flavonoids isolated from mosses. Phytochemistry 52, 1479–1482. https://doi.org/10.1016/S0031-9422(99)00286-1

Bates, 1973. Rapid determination of free proline for w a t e r - s t r e s s studies 207, 205–207.

Baxter, R., Emes, M.J., Lee, J.A., 1992. Effects of an experimentally applied increase in ammonium on growth and amino-acid metabolism of Sphagnum cuspidatum Ehrh. ex. Hoffm. from differently polluted areas. New Phytol. 120, 265–274. https://doi.org/10.1111/j.1469-8137.1992.tb05663.x

Bekir, J., Mars, M., Souchard, J.P., Bouajila, J., 2013. Assessment of antioxidant, anti-inflammatory, anti-cholinesterase and cytotoxic activities of pomegranate (Punica granatum) leaves. Food Chem. Toxicol. 55, 470–475. https://doi.org/10.1016/j.fct.2013.01.036

Benchikh, Y., Zaoui, A., Derbal, R., Mostapha Bachir Bey, ·, Louaileche, H., 2019. Optimisation of extraction conditions of phenolic compounds and antioxidant activity of Ruta chalepensis L. using response surface methodology. J. Food Meas. Charact. 13, 883–891. https://doi.org/10.1007/s11694-018-0002-3

Bengtsson, F., Granath, G., Cronberg, N., Rydin, H., 2020a. Mechanisms behind species-specific water economy responses to water level drawdown in peat mosses. Ann. Bot. 219–230. https://doi.org/10.1093/aob/mcaa033

Bengtsson, F., Granath, G., Rydin, H., 2016. Photosynthesis, growth, and decay traits in Sphagnum - a multispecies comparison. Ecol. Evol. 6, 3325–3341. https://doi.org/10.1002/ece3.2119

Bengtsson, F., Rydin, H., Baltzer, J.L., Bragazza, L., Bu, Z.J., Caporn, S.J.M.M., Dorrepaal, E., Flatberg, K.I., Galanina, O., Gałka, M., Ganeva, A., Goia, I., Goncharova, N., Hájek, M., Haraguchi, A., Harris, L.I., Humphreys, E., Jiroušek, M., Kajukało, K., Karofeld, E., Koronatova, N.G., Kosykh, N.P., Laine, A.M., Lamentowicz, M., Lapshina, E., Limpens, J., Linkosalmi, M., Ma, J.Z., Mauritz, M., Mitchell, E.A.D.D., Munir, T.M., Natali, S.M., Natcheva, R., Payne, R.J., Philippov, D.A., Rice, S.K., Robinson, S., Robroek, B.J.M.M., Rochefort, L., Singer, D., Stenøien, H.K., Tuittila, E.S., Vellak, K., Waddington, J.M., Granath, G., 2020b. Environmental drivers of Sphagnum growth in peatlands across the Holarctic region. J. Ecol. 1–15. https://doi.org/10.1111/1365-2745.13499

Bengtsson, F., Rydin, H., Hájek, T., 2018. Biochemical determinants of litter quality in 15 species of Sphagnum. Plant Soil 425, 161–176. https://doi.org/10.1007/s11104-018-3579-8

Berini, J.L., Brockman, S.A., Hegeman, A.D., Reich, P.B., Muthukrishnan, R., Montgomery, R.A., Forester, J.D., 2018. Combinations of abiotic factors differentially alter production of plant secondary metabolites in five woody plant species in the boreal-temperate transition zone. Front. Plant Sci. 9. https://doi.org/10.3389/fpls.2018.01257

Biddanda, B.A., McMillan, A.C., Long, S.A., Snider, M.J., Weinke, A.D., 2015. Seeking sunlight: Rapid phototactic motility of filamentous mat-forming cyanobacteria optimize photosynthesis and enhance carbon burial in Lake Huron's submerged sinkholes. Front. Microbiol. 6, 1–13. https://doi.org/10.3389/fmicb.2015.00930

Binet, P., Rouifed, S., Jassey, V.E.J., Toussaint, M.L., Chiapusio, G., 2017. Experimental climate warming alters the relationship between fungal root symbiosis and Sphagnum litter phenolics in two peatland microhabitats. Soil Biol. Biochem. 105, 153–161.

https://doi.org/10.1016/j.soilbio.2016.11.020

Bjorkman, A.D., Myers-Smith, I.H., Elmendorf, S.C., Normand, S., Rüger, N., Beck, P.S.A., Blach-Overgaard, A., Blok, D., Cornelissen, J.H.C., Forbes, B.C., Georges, D., Goetz, S.J., Guay, K.C., Henry, G.H.R., HilleRisLambers, J., Hollister, R.D., Karger, D.N., Kattge, J., Manning, P., Prevéy, J.S., Rixen, C., Schaepman-Strub, G., Thomas, H.J.D., Vellend, M., Wilmking, M., Wipf, S., Carbognani, M., Hermanutz, L., Lévesque, E., Molau, U., Petraglia, A., Soudzilovskaia, N.A., Spasojevic, M.J., Tomaselli, M., Vowles, T., Alatalo, J.M., Alexander, H.D., Anadon-Rosell, A., Angers-Blondin, S., Beest, M. te, Berner, L., Björk, R.G., Buchwal, A., Buras, A., Christie, K., Cooper, E.J., Dullinger, S., Elberling, B., Eskelinen, A., Frei, E.R., Grau, O., Grogan, P., Hallinger, M., Harper, K.A., Heijmans, M.M.P.D., Hudson, J., Hülber, K., Iturrate-Garcia, M., Iversen, C.M., Jaroszynska, F., Johnstone, J.F., Jørgensen, R.H., Kaarlejärvi, E., Klady, R., Kuleza, S., Kulonen, A., Lamarque, L.J., Lantz, T., Little, C.J., Speed, J.D.M., Michelsen, A., Milbau, A., Nabe-Nielsen, J., Nielsen, S.S., Ninot, J.M., Oberbauer, S.F., Olofsson, J., Onipchenko, V.G., Rumpf, S.B., Semenchuk, P., Shetti, R., Collier, L.S., Street, L.E., Suding, K.N., Tape, K.D., Trant, A., Treier, U.A., Tremblay, J.P., Tremblay, M., Venn, S., Weijers, S., Zamin, T., Boulanger-Lapointe, N., Gould, W.A., Hik, D.S., Hofgaard, A., Jónsdóttir, I.S., Jorgenson, J., Klein, J., Magnusson, B., Tweedie, C., Wookey, P.A., Bahn, M., Blonder, B., van Bodegom, P.M., Bond-Lamberty, B., Campetella, G., Cerabolini, B.E.L., Chapin, F.S., Cornwell, W.K., Craine, J., Dainese, M., de Vries, F.T., Díaz, S., Enquist, B.J., Green, W., Milla, R., Niinemets, Ü., Onoda, Y., Ordoñez, J.C., Ozinga, W.A., Penuelas, J., Poorter, H., Poschlod, P., Reich, P.B., Sandel, B., Schamp, B., Sheremetev, S., Weiher, E., 2018. Plant functional trait change across a warming tundra biome. Nature 562, 57–62. https://doi.org/10.1038/s41586-018-0563-7

Björkman, O., 1981. Responses to Different Quantum Flux Densities, in: Physiological Plant Ecology I. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 57–107. https://doi.org/10.1007/978-3-642-68090-8_4

Bond-Lamberty, B., Gower, S.T., 2007. Estimation of stand-level leaf area for boreal bryophytes. Oecologia 151, 584–592. https://doi.org/10.1007/s00442-006-0619-5

Bonnett, S.A.F., Ostle, N., Freeman, C., 2006. Seasonal variations in decomposition processes in a valley-bottom riparian peatland. Sci. Total Environ. 370, 561–573. https://doi.org/10.1016/j.scitotenv.2006.08.032

Borowik, A., Wyszkowska, J., 2016. Soil moisture as a factor affecting the microbiological and biochemical activity of soil. Plant, Soil Environ. 62, 250–255. https://doi.org/10.17221/158/2016-PSE

Borrelli, G.M., Trono, D., 2016. Molecular approaches to genetically improve the accumulation of health-promoting secondary metabolites in staple crops-a case study: The lipoxygenase-b1 genes and regulation of the carotenoid content in pasta products. Int. J. Mol. Sci. 17. https://doi.org/10.3390/ijms17071177

Both, C., Van Asch, M., Bijlsma, R.G., Van Den Burg, A.B., Visser, M.E., 2009. Climate change and unequal phenological changes across four trophic levels: Constraints or adaptations? J. Anim. Ecol. 78, 73–83. https://doi.org/10.1111/j.1365-2656.2008.01458.x

Bradford, M., 1976. A Rapid and Sensitive Method for the Quantitation of Microgram Quantities of Protein Utilizing the Principle of Protein-Dye Binding. Anal. Biochem. 7, 248–54. https://doi.org/10.1016/j.cj.2017.04.003

Bradley, R.L., Titus, B.D., Preston, C.P., 2000. Changes to mineral N cycling and microbial communities in black spruce humus after additions of (NH4)2SO4 and condensed tannins extracted from Kalmia angustifolia and balsam fir. Soil Biol. Biochem. 32, 1227–1240. https://doi.org/10.1016/S0038-0717(00)00039-0

Bragazza, L., Buttler, A., Robroek, B.J.M., Albrecht, R., Zaccone, C., Jassey, V.E.J., Signarbieux, C., 2016. Persistent high temperature and low precipitation reduce peat carbon accumulation. Glob. Chang. Biol. 22, 4114–4123. https://doi.org/10.1111/gcb.13319

Bragazza, L., Freeman, C., 2007. High nitrogen availability reduces polyphenol content in Sphagnum peat. Sci. Total Environ. 377, 439–443. https://doi.org/10.1016/j.scitotenv.2007.02.016

Bragazza, L., Freeman, C., Jones, T., Rydin, H., Limpens, J., Fenner, N., Ellis, T., Gerdol, R., Hájek, M., Hájek, T., Iacumin, P., Kutnar, L., Tahvanainen, T., Toberman, H., 2006. Atmospheric nitrogen deposition promotes carbon loss from peat bogs. Proc. Natl. Acad. Sci. U. S. A. 103, 19386–19389. https://doi.org/10.1073/pnas.0606629104

Bragina, A., Berg, C., Cardinale, M., Shcherbakov, A., Chebotar, V., Berg, G., 2012a. Sphagnum mosses harbour highly specific bacterial diversity during their whole lifecycle. ISME J. 6, 802–813. https://doi.org/10.1038/ismej.2011.151

Bragina, A., Berg, C., Müller, H., Moser, D., Berg, G., 2013a. Insights into functional bacterial diversity and its effects on Alpine bog ecosystem functioning. Sci. Rep. 3, 1–8. https://doi.org/10.1038/srep01955

Bragina, A., Cardinale, M., Berg, C., Berg, G., 2013b. Vertical transmission explains the specific Burkholderia pattern in Sphagnum mosses at multi-geographic scale. Front. Microbiol. 4, 1–10. https://doi.org/10.3389/fmicb.2013.00394

Bragina, A., Maier, S., Berg, C., Müller, H., Chobot, V., Hadacek, F., Berg, G., 2012b. Similar diversity of Alphaproteobacteria and nitrogenase gene amplicons on two related Sphagnum mosses. Front. Microbiol. 2, 1–10. https://doi.org/10.3389/fmicb.2011.00275

Bragina, A., Müller, C., Berg, G., 2015. The moss microbiome : new insights into the microbial world of plants and its biotechnological potential. Rostocker Meeresbiologische Beiträge 26, 25–33.

Bragina, A., Oberauner-Wappis, L., Thallinger, G.G., Müller, H., Bragina, A., Zachow, C., Berg, G., Halwachs, B., Oberauner-Wappis, L., Zachow, C., Halwachs, B., Thallinger, G.G., Müller, H., Berg, G., 2014. The Sphagnum microbiome supports bog ecosystem functioning under extreme conditions. Mol. Ecol. 23, 4498–4510. https://doi.org/10.1111/mec.12885

Breeuwer, A., Heijmans, M.M.P.D., Gleichman, M., Robroek, B.J.M., Berendse, F., 2009. Response of Sphagnum species mixtures to increased temperature and nitrogen availability. Plant Ecol. 204, 97–111. https://doi.org/10.1007/s11258-009-9571-x

Breeuwer, A., Heijmans, M.M.P.D., Robroek, B.J.M., Berendse, F., 2008. The effect of temperature on growth and competition between Sphagnum species. Oecologia 156, 155–167. https://doi.org/10.1007/s00442-008-0963-8

Bridgham, S.D., Updegraff, K., Pastor, J., 2001. A Comparison of Nutrient Availability Indices Along an Ombrotrophic–Minerotrophic Gradient in Minnesota Wetlands. Soil Sci. Soc. Am. J. 65, 259–269. https://doi.org/10.2136/sssaj2001.651259x

Brock, T.C.M., Bregman, R., 1989. Periodicity in growth, productivity, nutrient content and decomposition of Sphagnum recurvum var. mucronatum in a fen woodland. Oecologia 80, 44–52. https://doi.org/10.1007/BF00789930

Brooker, R.W., 2006. Plant{\textendash}plant interactions and environmental change. New Phytol. 171, 271–284.

Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S.M., Botta-Dukát, Z., Chytrý, M., Field, R., Jansen, F., Kattge, J., Pillar, V.D., Schrodt, F., Mahecha, M.D., Peet, R.K., Sandel, B., van Bodegom, P., Altman, J., Alvarez-Dávila, E., Arfin Khan, M.A.S., Attorre, F., Aubin, I., Baraloto, C., Barroso, J.G., Bauters, M., Bergmeier, E., Biurrun, I., Bjorkman, A.D., Blonder, B., Čarni, A., Cayuela, L., Černý, T., Cornelissen, J.H.C., Craven, D., Dainese, M., Derroire, G., De Sanctis, M., Díaz, S., Doležal, J., Farfan-Rios, W., Feldpausch, T.R., Fenton, N.J., Garnier, E., Guerin, G.R., Gutiérrez, A.G., Haider, S., Hattab, T., Henry, G., Hérault, B., Higuchi, P., Hölzel, N., Homeier, J., Jentsch, A., Jürgens, N., Kącki, Z., Karger, D.N., Kessler, M., Kleyer, M., Knollová, I., Korolyuk, A.Y., Kühn, I., Laughlin, D.C., Lens, F., Loos, J., Louault, F., Lyubenova, M.I., Malhi, Y., Marcenò, C., Mencuccini, M., Müller, J. V., Munzinger, J., Myers-

Smith, I.H., Neill, D.A., Niinemets, Ü., Orwin, K.H., Ozinga, W.A., Penuelas, J., Pérez-Haase, A., Petřík, P., Phillips, O.L., Pärtel, M., Reich, P.B., Römermann, C., Rodrigues, A. V., Sabatini, F.M., Sardans, J., Schmidt, M., Seidler, G., Silva Espejo, J.E., Silveira, M., Smyth, A., Sporbert, M., Svenning, J.-C., Tang, Z., Thomas, R., Tsiripidis, I., Vassilev, K., Violle, C., Virtanen, R., Weiher, E., Welk, E., Wesche, K., Winter, M., Wirth, C., Jandt, U., 2018. Global trait–environment relationships of plant communities. Nat. Ecol. Evol. https://doi.org/10.1038/s41559-018-0699-8

Bryant, J.P., Chapin, F.S., Klein, D.R., 1983. Carbon/Nutrient Balance of Boreal Plants in Relation to Vertebrate Herbivory. Oikos 40, 357. https://doi.org/10.2307/3544308

Bubier, J.L., Crill, P.M., Moore, T.R., Savage, K., Varner, R.K., 1998. Seasonal patterns and controls on net ecosystem CO2 exchange in a boreal peatland complex. Global Biogeochem. Cycles 12, 703–714. https://doi.org/10.1029/98GB02426

Buermann, W., Forkel, M., O'Sullivan, M., Sitch, S., Friedlingstein, P., Haverd, V., Jain, A.K., Kato, E., Kautz, M., Lienert, S., Lombardozzi, D., Nabel, J.E.M.S., Tian, H., Wiltshire, A.J., Zhu, D., Smith, W.K., Richardson, A.D., 2018. Widespread seasonal compensation effects of spring warming on northern plant productivity. Nature 562, 110–114. https://doi.org/10.1038/s41586-018-0555-7

Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: Understanding AIC and BIC in model selection. Sociol. Methods Res. 33, 261–304. https://doi.org/10.1177/0049124104268644

Burns, J.H., Anacker, B.L., Strauss, S.Y., Burke, D.J., 2015. Soil microbial community variation correlates most strongly with plant species identity, followed by soil chemistry, spatial location and plant genus. AoB Plants 7, 1–10. https://doi.org/10.1093/aobpla/plv030

Buttler, A., Robroek, B.J.M., Laggoun-Défarge, F., Jassey, V.E.J., Pochelon, C., Bernard, G., Delarue, F., Gogo, S., Mariotte, P., Mitchell, E.A.D., Bragazza, L., 2015. Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. J. Veg. Sci. 26, 964–974. https://doi.org/10.1111/jvs.12296

Callis-Duehl, K., Vittoz, P., Defossez, E., Rasmann, S., 2017. Community-level relaxation of plant defenses against herbivores at high elevation. Plant Ecol. 218, 291–304. https://doi.org/10.1007/s11258-016-0688-4

Calow, P., 1987a. Towards a Definition of Functional Ecology. Funct. Ecol. 1, 57. https://doi.org/10.2307/2389358

Calow, P., 1987b. Towards a Definition of Functional Ecology. Funct. Ecol. 1, 57. https://doi.org/10.2307/2389358

Cannell, N., Emms, D.M., Hetherington, A.J., MacKay, J., Kelly, S., Dolan, L., Sweetlove, L.J., 2020. Multiple Metabolic Innovations and Losses Are Associated with Major Transitions in Land Plant Evolution. Curr. Biol. 30, 1783-1800.e11. https://doi.org/10.1016/j.cub.2020.02.086

Carrell, A.A., Kolton, M., Glass, J.B., Pelletier, D.A., Warren, M.J., Kostka, J.E., Iversen, C.M., Hanson, P.J., Weston, D.J., 2019. Experimental warming alters the community composition, diversity, and N $_2$ fixation activity of peat moss (*Sphagnum fallax*) microbiomes. Glob. Chang. Biol. gcb.14715. https://doi.org/10.1111/gcb.14715

Chae, L., Kim, T., Nilo-Poyanco, R., Rhee, S.Y., 2014. Genomic signatures of specialized metabolism in plants. Science (80-.). 344, 510–513. https://doi.org/10.1126/science.1252076

Chang, C.C., Yang, M.H., Wen, H.M., Chern, J.C., 2002. Estimation of total flavonoid content in propolis by two complementary colometric methods. J. Food Drug Anal. 10, 178–182. https://doi.org/10.38212/2224-6614.2748

Chapin, F.S., Oechel, W.C., Van Cleve, K., Lawrence, W., 1987. The role of mosses in the phosphorus cycling of an Alaskan black spruce forest. Oecologia 74, 310–315.

https://doi.org/10.1007/BF00379375

Charman, D.J., Beilman, D.W., Blaauw, M., Booth, R.K., Brewer, S., Chambers, F.M., Christen, J.A., Gallego-Sala, A., Harrison, S.P., Hughes, P.D.M., Jackson, S.T., Korhola, A., Mauquoy, D., Mitchell, F.J.G., Prentice, I.C., Van Der Linden, M., De Vleeschouwer, F., Yu, Z.C., Alm, J., Bauer, I.E., Corish, Y.M.C., Garneau, M., Hohl, V., Huang, Y., Karofeld, E., Le Roux, G., Loisel, J., Moschen, R., Nichols, J.E., Nieminen, T.M., MacDonald, G.M., Phadtare, N.R., Rausch, N., Sillasoo, U., Swindles, G.T., Tuittila, E.S., Ukonmaanaho, L., Väliranta, M., Van Bellen, S., Van Geel, B., Vitt, D.H., Zhao, Y., 2013. Climate-related changes in peatland carbon accumulation during the last millennium. Biogeosciences 10, 929–944. https://doi.org/10.5194/bg-10-929-2013

Chaves, J.O., de Souza, M.C., da Silva, L.C., Lachos-Perez, D., Torres-Mayanga, P.C., Machado, A.P. da F., Forster-Carneiro, T., Vázquez-Espinosa, M., González-de-Peredo, A.V., Barbero, G.F., Rostagno, M.A., 2020. Extraction of Flavonoids From Natural Sources Using Modern Techniques. Front. Chem. 8. https://doi.org/10.3389/fchem.2020.507887

Chelli, S., Marignani, M., Barni, E., Petraglia, A., Puglielli, G., Wellstein, C., Acosta, A.T.R., Bolpagni, R., Bragazza, L., Campetella, G., Chiarucci, A., Conti, L., Nascimbene, J., Orsenigo, S., Pierce, S., Ricotta, C., Tardella, F.M., Abeli, T., Aronne, G., Bacaro, G., Bagella, S., Benesperi, R., Bernareggi, G., Bonanomi, G., Bricca, A., Brusa, G., Buffa, G., Burrascano, S., Caccianiga, M., Calabrese, V., Canullo, R., Carbognani, M., Carboni, M., Carranza, M.L., Catorci, A., Ciccarelli, D., Citterio, S., Cutini, M., Dalle Fratte, M., De Micco, V., Del Vecchio, S., Di Martino, L., Di Musciano, M., Fantinato, E., Filigheddu, R., Frattaroli, A.R., Gentili, R., Gerdol, R., Giarrizzo, E., Giordani, P., Gratani, L., Incerti, G., Lussu, M., Mazzoleni, S., Mondoni, A., Montagnani, C., Montagnoli, A., Paura, B., Petruzzellis, F., Pisanu, S., Rossi, G., Sgarbi, E., Simonetti, E., Siniscalco, C., Slaviero, A., Stanisci, A., Stinca, A., Tomaselli, M., Cerabolini, B.E.L., 2019. Plant–environment interactions through a functional traits perspective: a review of Italian studies. Plant Biosyst. 153, 853–869. https://doi.org/10.1080/11263504.2018.1559250

Chen, Y. Da, Moles, A., Bu, Z.J., Zhang, M.M., Wang, Z.C., Zhao, H.Y., 2021. Induced defense and its cost in two bryophyte species. Am. J. Bot. 108, 777–787. https://doi.org/10.1002/ajb2.1654

Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science (80-.). 333, 1024–1026. https://doi.org/10.1126/science.1206432

Chevin, L.M., Lande, R., 2011. Adaptation to marginal habitats by evolution of increased phenotypic plasticity. J. Evol. Biol. 24, 1462–1476. https://doi.org/10.1111/j.1420-9101.2011.02279.x

Chiapusio, G., Jassey, V.E.J., Bellvert, F., Comte, G., Weston, L.A., Delarue, F., Buttler, A., Toussaint, M.L., Binet, P., 2018. Sphagnum Species Modulate their Phenolic Profiles and Mycorrhizal Colonization of Surrounding Andromeda polifolia along Peatland Microhabitats. J. Chem. Ecol. 44, 1146–1157. https://doi.org/10.1007/s10886-018-1023-4

Chiapusio, G., Jassey, V.E.J., Hussain, M.I., Binet, P., 2013. Chapter 3. Evidences of Bryophyte Allelochemical Interactions: The Case of Sphagnum, in: Cheema, Z.A., Farooq, M., Wahid, A. (Eds.), Allelopathy: Current Trends and Future Applications. pp. 39–54. https://doi.org/10.1007/978-3-642-30595-5

Chobot, V., Kubicová, L., Nabbout, S., Jahodář, L., Hadacek, F., 2008. Evaluation of antioxidant activity of some common mosses. Zeitschrift fur Naturforsch. - Sect. C J. Biosci. 63, 476–482. https://doi.org/10.1515/znc-2008-7-802

Chomel, M., Guittonny-Larchevêque, M., Fernandez, C., Gallet, C., DesRochers, A., Paré, D., Jackson, B.G., Baldy, V., 2016. Plant secondary metabolites: a key driver of litter decomposition and soil nutrient cycling. J. Ecol. 104, 1527–1541. https://doi.org/10.1111/1365-2745.12644

Choudhury, S., Panda, P., Sahoo, L., Panda, S.K., 2013. Reactive oxygen species signaling in plants under abiotic stress. Plant Signal. Behav. 8, e23681. https://doi.org/10.4161/psb.23681

Cipollini, D., Rigsby, C.M., Barto, E.K., 2012. Microbes as Targets and Mediators of Allelopathy in Plants. J. Chem. Ecol. 38, 714–727. https://doi.org/10.1007/s10886-012-0133-7

Clark, J.S., 2016. Why species tell more about traits than traits about species: Predictive analysis. Ecology 97, 1979–1993. https://doi.org/10.1002/ecy.1453

Clymo, R.S., 1987. Interactions of Sphagnum with water and air, in: Hutchinson, T., Meema, K. (Eds.), Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems. spri, Berlin, pp. 513–239.

Clymo, R.S., 1983. Peat, in: Gore, A.J.P. (Ed.), Mires: Swamp, Bog, Fen and Moor. Elsevier, Amsterdam, pp. 159–224. https://doi.org/10.2307/3898373

Clymo, R.S., 1963. Ion exchange in Sphagnum and its relation to bog ecology. Ann. Bot. 27, 309–324. https://doi.org/10.1093/oxfordjournals.aob.a083847

Clymo, R.S., Hayward, P.M., 1982. The Ecology of Sphagnum, in: Smith, A.J.E. (Ed.), Bryophyte Ecology. Springer, Dordrecht, pp. 229–289. https://doi.org/10.1007/978-94-009-5891-3_8

Coley, P.D., Bryant, J.P., Chapin, F.S., 1985. Resource availability defense. Science (80-.). 230, 895–899.

Cornelissen, J.H.C., Lang, S.I., Soudzilovskaia, N.A., During, H.J., 2007. Comparative cryptogam ecology: A review of bryophyte and lichen traits that drive biogeochemistry. Ann. Bot. 99, 987–1001. https://doi.org/10.1093/aob/mcm030

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., Van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T. V., Díaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieretti, M.V., Westoby, M., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecol. Lett. 11, 1065–1071. https://doi.org/10.1111/j.1461-0248.2008.01219.x

Crotty, F. V., Adl, S.M., Blackshaw, R.P., Murray, P.J., 2013. Measuring soil protist respiration and ingestion rates using stable isotopes. Soil Biol. Biochem. 57, 919–921. https://doi.org/10.1016/j.soilbio.2012.10.039

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

Crowther, T.W., van den Hoogen, J., Wan, J., Mayes, M.A., Keiser, A.D., Mo, L., Averill, C., Maynard, D.S., 2019. The global soil community and its influence on biogeochemistry. Science (80-.). 365, eaav0550. https://doi.org/10.1126/science.aav0550

Cruz De Carvalho, R., Catalá, M., Marques Da Silva, J., Branquinho, C., Barreno, E., 2012. The impact of dehydration rate on the production and cellular location of reactive oxygen species in an aquatic moss. Ann. Bot. 110, 1007–1016. https://doi.org/10.1093/aob/mcs180

Czapek, F., 1899. Zur Chemie der Zellmembranen bei den Laub-und Lebermoosen. Flora 86, 361–381.

Dahl, Å., Galán, C., Hajkova, L., Pauling, A., Sikoparija, B., Smith, M., Vokou, D., 2013. The Onset, Course and Intensity of the Pollen Season, Allergenic Pollen: Springer Netherlands, Dordrecht. https://doi.org/10.1007/978-94-007-4881-1

Das, K., Roychoudhury, A., 2014. Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants. Front. Environ. Sci. 2, 1–13. https://doi.org/10.3389/fenvs.2014.00053

Davey, M.L., Currah, R.S., 2006. Interactions between mosses (Bryophyta) and fungi. Can. J. Bot. 84, 1509–1519. https://doi.org/10.1139/B06-120

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173. https://doi.org/10.1038/nature04514

Davidson, N.C., Middleton, B.A., McInnes, R.J., Everard, M., Irvine, K., van Dam, A.A., Finlayson, C.M., 2018. Ecosystem services of peatlands: Implications for restoration, in: The Wetland Book. Springer Netherlands, Dordrecht, pp. 3–14. https://doi.org/10.1007/978-90-481-9659-3_356

Davies, K.J.A., 1986. Free radicals and protein degradation. J. Free Radicals Biol. Med. 2, 155–173.

De Deyn, G.B., Cornelissen, J.H.C., Bardgett, R.D., 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecol. Lett. 11, 516–531. https://doi.org/10.1111/j.1461-0248.2008.01164.x

De Gruyter, J., Weedon, J.T., Bazot, S., Dauwe, S., Fernandez-Garberí, P.-R., Geisen, S., De La Motte, L.G., Heinesch, B., Janssens, I.A., Leblans, N., Manise, T., Ogaya, R., Löfvenius, M.O., Peñuelas, J., Sigurdsson, B.D., Vincent, G., Verbruggen, E., 2020. Patterns of local, intercontinental and interseasonal variation of soil bacterial and eukaryotic microbial communities. FEMS Microbiol. Ecol. 96. https://doi.org/10.1093/femsec/fiaa018

de Hoyos-Martínez, P.L., Merle, J., Labidi, J., Charrier – El Bouhtoury, F., 2019. Tannins extraction: A key point for their valorization and cleaner production. J. Clean. Prod. 206, 1138–1155. https://doi.org/10.1016/j.jclepro.2018.09.243

de Vries, F.T., Manning, P., Tallowin, J.R.B., Mortimer, S.R., Pilgrim, E.S., Harrison, K.A., Hobbs, P.J., Quirk, H., Shipley, B., Cornelissen, J.H.C., Kattge, J., Bardgett, R.D., 2012. Abiotic drivers and plant traits explain landscape-scale patterns in soil microbial communities. Ecol. Lett. 15, 1230–1239. https://doi.org/10.1111/j.1461-0248.2012.01844.x

Dedysh, S.N., Liesack, W., Khmelenina, V.N., Suzina, N.E., Trotsenko, Y.A., Semrau, J.D., Bares, A.M., Panikov, N.S., Tiedje, J.M., 2000. Methylocella palustris gen. nov., sp. nov., a new methane-oxidizing acidophilic bacterium from peat bogs, representing a novel subtype of serine- pathway methanotrophs. Int. J. Syst. Evol. Microbiol. 50, 955–969. https://doi.org/10.1099/00207713-50-3-955

Defossez, E., Pitteloud, C., Descombes, P., Glauser, G., Allard, P.-M., Walker, T.W.N., Fernandez-Conradi, P., Wolfender, J.-L., Pellissier, L., Rasmann, S., 2021. Spatial and evolutionary predictability of phytochemical diversity. Proc. Natl. Acad. Sci. 118, e2013344118. https://doi.org/10.1073/pnas.2013344118

Del Giudice, R., Lindo, Z., 2017. Short-term leaching dynamics of three peatland plant species reveals how shifts in plant communities may affect decomposition processes. Geoderma 285, 110–116. https://doi.org/10.1016/j.geoderma.2016.09.028

Delarue, F., Laggoun-Défarge, F., Buttler, A., Gogo, S., Jassey, V.E.J., Disnar, J.R., 2011. Effects of short-term ecosystem experimental warming on water-extractable organic matter in an ombrotrophic Sphagnum peatland (Le Forbonnet, France). Org. Geochem. 42, 1016–1024. https://doi.org/10.1016/j.orggeochem.2011.07.005

Delgado-Baquerizo, M., Eldridge, D.J., Hamonts, K., Reich, P.B., Singh, B.K., 2018. Experimentally testing the species-habitat size relationship on soil bacteria: A proof of concept. Soil Biol. Biochem. 123, 200–206. https://doi.org/10.1016/j.soilbio.2018.05.016

DeLucia, E.H., Turnbull, M.H., Walcroft, A.S., Griffin, K.L., Tissue, D.T., Glenny, D., McSeveny, T.M., Whitehead, D., 2003. The contribution of bryophytes to the carbon exchange for a

temperature rainforest. Glob. Chang. Biol. 9, 1158–1170. https://doi.org/10.1046/j.1365-2486.2003.00650.x

Dembitsky, V.M., 1993. Lipids of bryophytes. Prog. Lipid Res. 32, 281–356. https://doi.org/10.1016/0163-7827(93)90010-T

Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., De Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P., Zak, M.R., 2004. The plant traits that drive ecosystems: Evidence from three continents. J. Veg. Sci. 15, 295–304. https://doi.org/10.1111/j.1654-1103.2004.tb02266.x

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet Ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D., 2016. The global spectrum of plant form and function. Nature 529, 167–171. https://doi.org/10.1038/nature16489

Dieleman, C.M., Branfireun, B.A., McLaughlin, J.W., Lindo, Z., 2016a. Enhanced carbon release under future climate conditions in a peatland mesocosm experiment: the role of phenolic compounds. Plant Soil 400, 81–91. https://doi.org/10.1007/s11104-015-2713-0

Dieleman, C.M., Lindo, Z., McLaughlin, J.W., Craig, A.E., Branfireun, B.A., 2016b. Climate change effects on peatland decomposition and porewater dissolved organic carbon biogeochemistry. Biogeochemistry 128, 385–396. https://doi.org/10.1007/s10533-016-0214-8

Dixon, R.K., Turner, D.P., 1991. The global carbon cycle and climate change: Responses and feedbacks from below-ground systems. Environ. Pollut. 73, 245–262. https://doi.org/10.1016/0269-7491(91)90052-X

Dizdaroglu, M., 1994. Chemical determination of oxidative DNA damage by gas chromatography-mass spectrometry. Methods Enzymol. 234, 3–16. https://doi.org/10.1016/0076-6879(94)34072-2

Djurdjević, L., Dinić, A., Mitrović, M., Pavlović, P., Tešević, V., 2003. Phenolic acids distribution in a peat of the relict community with Serbian spruce in the Tara Mt. forest reserve (Serbia). Eur. J. Soil Biol. 39, 97–103. https://doi.org/10.1016/S1164-5563(03)00015-3

Do, T.H., Truong, H.B., Nguyen, H.C., 2020. Optimization of Extraction of Phenolic Compounds from Ocimum Basilicum Leaves and Evaluation of Their Antioxidant Activity. Pharm. Chem. J. 54, 162–169. https://doi.org/10.1007/s11094-020-02181-3

Dorrepaal, E., 2007. Are plant growth-form-based classifications useful in predicting northern ecosystem carbon cycling feedbacks to climate change? J. Ecol. 95, 1167–1180. https://doi.org/10.1111/j.1365-2745.2007.01294.x

Dorrepaal, E., Aerts, R., Cornelissen, J.H.C., Callaghan, T. V., Van Logtestijn, R.S.P., 2003. Summer warming and increased winter snow cover affect Sphagnum fuscum growth, structure and production in a sub-arctic bog. Glob. Chang. Biol. 10, 93–104. https://doi.org/10.1046/j.1529-8817.2003.00718.x

Dorrepaal, E., Cornelissen, J.H.C., Aerts, R., Wallén, B., Van Logtestijn, R.S.P., 2005. Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? J. Ecol. 93, 817–828. https://doi.org/10.1111/j.1365-2745.2005.01024.x

Dorrepaal, E., Cornelissen, J.H.C., Logtestijn, R.S.P.V.A.N., 2006. Sphagnum modifies climate-change

impacts on subarctic 31–41. https://doi.org/10.1111/j.1365-2435.2006.01076.x

Dorrepaal, E., Toet, S., Logtestijn, R.S.P. Van, Swart, E., Weg, M.J. Van De, Callaghan, T. V, Aerts, R., 2009a. Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. Nature 460, 616–619. https://doi.org/10.1038/nature08216

Dorrepaal, E., Toet, S., Van Logtestijn, R.S.P., Swart, E., Van De Weg, M.J., Callaghan, T. V., Aerts, R., Logtestijn, R.S.P. Van, Swart, E., Weg, M.J. Van De, Callaghan, T. V., Aerts, R., 2009b. Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. Nature 460, 616–619. https://doi.org/10.1038/nature08216

Dunfield, P., knowles, R., Dumont, R., Moore, T.R., 1993. Methane production and consumption in temperate and subarctic peat soils: Response to temperature and pH. Soil Biol. Biochem. 25, 321–326. https://doi.org/10.1016/0038-0717(93)90130-4

During, H.J., van Tooren, B., 1990. Bryophyte interactions with other plants. Bot. J. Linn. Soc. 104, 79–98. https://doi.org/10.1111/j.1095-8339.1990.tb02212.x

Eigemann, F., Vogts, A., Voss, M., Zoccarato, L., Schulz-Vogt, H., 2019. Distinctive tasks of different cyanobacteria and associated bacteria in carbon as well as nitrogen fixation and cycling in a late stage Baltic Sea bloom. PLoS One 14, 1–20. https://doi.org/10.1371/journal.pone.0223294

El-Zayat, M.M., El-Amier, Y.A., El-Halawany, E.-S.F., Abo Aisha, I.A., 2020. Proximate Composition, Mineral Content and Secondary Metabolites of Three Medicinal Wild Fagonia Species. Food Biol. 9, 1–6. https://doi.org/10.25081/fb.0.v0.6290

Elliott, D.R., Caporn, S.J.M., Nwaishi, F., Nilsson, R.H., Sen, R., 2015. Bacterial and fungal communities in a degraded ombrotrophic peatland undergoing natural and managed re-vegetation. PLoS One 10, 1–20. https://doi.org/10.1371/journal.pone.0124726

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

Elstner, E.F., 1982. Oxygen Activation and Oxygen Toxicity. Annu. Rev. Plant Physiol. 33, 73–96. https://doi.org/10.1146/annurev.pp.33.060182.000445

Enkhtaivan, G., Maria John, K.M., Ayyanar, M., Sekar, T., Jin, K.J., Kim, D.H., 2015. Anti-influenza (H1N1) potential of leaf and stem bark extracts of selected medicinal plants of South India. Saudi J. Biol. Sci. 22, 532–538. https://doi.org/10.1016/j.sjbs.2015.01.011

Erb, M., Kliebenstein, D.J., 2020. Plant Secondary Metabolites as Defenses, Regulators, and Primary Metabolites: The Blurred Functional Trichotomy. Plant Physiol. 184, 39–52. https://doi.org/10.1104/PP.20.00433

Falkowski, P.G., Raven, J.A., 2007. Aquatic Photosynthesis, STU-Stud. ed. Princeton University Press. https://doi.org/10.2307/j.ctt4cgbxs

Falster, D.S., Brännström, Å., Dieckmann, U., Westoby, M., 2011. Influence of four major plant traits on average height, leaf-area cover, net primary productivity, and biomass density in single-species forests: A theoretical investigation. J. Ecol. 99, 148–164. https://doi.org/10.1111/j.1365-2745.2010.01735.x

Fan, Z.L., Li, L., Bai, X.L., Zhang, Hua, Liu, Q.R., Zhang, He, Fu, Y.J., Moyo, R., 2019. Extraction optimization, antioxidant activity, and tyrosinase inhibitory capacity of polyphenols from

Lonicera japonica. Food Sci. Nutr. 7, 1786–1794. https://doi.org/10.1002/fsn3.1021

Fatoyinbo, L., 2017. Ecology: Vast peatlands found in the Congo Basin. Nature 542, 38–39. https://doi.org/10.1038/542038b

Felsenstein, J., 1985. Phylogenies and the Comparative Method. Am. Nat. 125, 1–15. https://doi.org/10.1086/284325

Fenner, N., Freeman, C., 2011. Drought-induced carbon loss in peatlands. Nat. Geosci. 4, 895–900. https://doi.org/10.1038/ngeo1323

Fernandez-Conradi, P., Defossez, E., Delavallade, A., Descombes, P., Pitteloud, C., Glauser, G., Pellissier, L., Rasmann, S., 2021. The effect of community-wide phytochemical diversity on herbivory reverses from low to high elevation. J. Ecol. 1–11. https://doi.org/10.1111/1365-2745.13649

Fernandez, C., Monnier, Y., Santonja, M., Gallet, C., Weston, L.A., Prévosto, B., Saunier, A., Baldy, V., Bousquet-Mélou, A., 2016. The Impact of Competition and Allelopathy on the Trade-Off between Plant Defense and Growth in Two Contrasting Tree Species. Front. Plant Sci. 7, 1–14. https://doi.org/10.3389/fpls.2016.00594

Fernandez, C.W., Langley, J.A., Chapman, S., McCormack, M.L., Koide, R.T., 2016. The decomposition of ectomycorrhizal fungal necromass. Soil Biol. Biochem. 93, 38–49. https://doi.org/10.1016/j.soilbio.2015.10.017

Fernando, V., Ernesto, G., José, M.G., 2007. Ecological limits to plant phenotypic plasticity. New Phytol. 176, 749–763.

Fernie, A.R., Pichersky, E., 2015. Focus issue on metabolism: Metabolites, metabolites everywhere. Plant Physiol. 169, 1421–1423. https://doi.org/10.1104/pp.15.01499

Fernie, A.R., Trethewey, R.N., Krotzky, A.J., Willmitzer, L., 2004. Metabolite profiling: from diagnostics to systems biology. Nat. Rev. Mol. Cell Biol. 5, 763–769. https://doi.org/10.1038/nrm1451

Ferrer, J.L., Austin, M.B., Stewart, C., Noel, J.P., 2008. Structure and function of enzymes involved in the biosynthesis of phenylpropanoids. Plant Physiol. Biochem. 46, 356–370. https://doi.org/10.1016/j.plaphy.2007.12.009

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. https://doi.org/10.1002/joc.5086

Fiehn, O., 2002. Metabolomics - The link between genotypes and phenotypes. Plant Mol. Biol. 48, 155–171. https://doi.org/10.1023/A:1013713905833

Fiore-Donno, A.M., Richter-Heitmann, T., Degrune, F., Dumack, K., Regan, K.M., Marhan, S., Boeddinghaus, R.S., Rillig, M.C., Friedrich, M.W., Kandeler, E., Bonkowski, M., 2019. Functional traits and spatio-temporal structure of a major group of soil protists (rhizaria: Cercozoa) in a temperate grassland. Front. Microbiol. 10, 1–12. https://doi.org/10.3389/fmicb.2019.01332

Fischer, E.M., Knutti, R., 2016. Observed heavy precipitation increase confirms theory and early models. Nat. Clim. Chang. 6, 986–991. https://doi.org/10.1038/nclimate3110

Fisher, M.M., Graham, J.M., Graham, L.E., 1998. Bacterial abundance and activity across sites within two northern Wisconsin Sphagnum bogs. Microb. Ecol. 36, 259–269. https://doi.org/10.1007/s002489900113

Forlani, G., Funck, D., 2020. A Specific and Sensitive Enzymatic Assay for the Quantitation of L-Proline. Front. Plant Sci. 11, 1–12. https://doi.org/10.3389/fpls.2020.582026

Fort, M., 2015. Impact of climate change on mountain environment dynamics. Rev. géographie Alp.

0–7. https://doi.org/10.4000/rga.2877

Fraser, C.M., Chapple, C., 2011. The Phenylpropanoid Pathway in Arabidopsis. Arab. B. 9, e0152. https://doi.org/10.1199/tab.0152

Freeman, C., Evans, C.D., Monteith, D.T., Reynolds, B., Fenner, N., 2001a. Export of organic carbon from peat soils. Nature 412, 785–785. https://doi.org/10.1038/35090628

Freeman, C., Lock, M.A., Reynolds, B., 1992. Fluxes of CO2, CH4 and N2O from a Welsh peatland following simulation of water table draw-down: Potential feedback to climatic change. Biogeochemistry 19, 51–60. https://doi.org/10.1007/BF00000574

Freeman, C., Ostle, N., Kang, H., 2001b. An enzymic "latch" on a global carbon store: A shortage of oxygen locks up carbon in peatlands by restraining a single enzymes. Nature 409, 149. https://doi.org/10.1038/35051650

Frolking, S., Roulet, N., Lawrence, D., 2013. Issues Related to Incorporating Northern Peatlands into Global Climate Models. Carbon Cycl. North. Peatlands 19–35. https://doi.org/10.1029/2008GM000809

Frolking, S., Roulet, N.T., 2007. Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. Glob. Chang. Biol. 13, 1079–1088. https://doi.org/10.1111/j.1365-2486.2007.01339.x

Frolking, S., Talbot, J., Jones, M.C., Treat, C.C., Kauffman, J.B., Tuittila, E.S., Roulet, N., 2011. Peatlands in the Earth's 21st century climate system. Environ. Rev. 19, 371–396. https://doi.org/10.1139/a11-014

Fudyma, J.D., Lyon, J., AminiTabrizi, R., Gieschen, H., Chu, R.K., Hoyt, D.W., Kyle, J.E., Toyoda, J., Tolic, N., Hess, N.J., Heyman, H.M., Metz, T.O., Tfaily, M.M., Hess, N.J., Metz, T.O., Tfaily, M.M., 2019. Untargeted metabolomic profiling of Sphagnum fallax reveals novel antimicrobial metabolites. Plant Direct 3, 1–17. https://doi.org/10.1002/pld3.179

Fusco, G., Minelli, A., 2010. Phenotypic plasticity in development and evolution: Facts and concepts. Philos. Trans. R. Soc. B Biol. Sci. 365, 547–556. https://doi.org/10.1098/rstb.2009.0267

Fuss, R., Hueppi, R., Pedersen, Asger, R., 2020. Greenhouse gas flux calculation from chamber measurements 18.

Gaberščik, A., Martinčič, A., 1987. Seasonal dynamics of net photosynthesis and productivity of Sphagnum papillosum. Oikos 13, 105–110.

Gajewski, K., 2015. Impact of Holocene climate variability on Arctic vegetation. Glob. Planet. Change 133, 272–287. https://doi.org/10.1016/j.gloplacha.2015.09.006

Gallego-Sala, A. V., Charman, D.J., Brewer, S., Page, S.E., Prentice, I.C., Friedlingstein, P., Moreton, S., Amesbury, M.J., Beilman, D.W., Björck, S., Blyakharchuk, T., Bochicchio, C., Booth, R.K., Bunbury, J., Camill, P., Carless, D., Chimner, R.A., Clifford, M., Cressey, E., Courtney-Mustaphi, C., De Vleeschouwer, F., de Jong, R., Fialkiewicz-Koziel, B., Finkelstein, S.A., Garneau, M., Githumbi, E., Hribjlan, J., Holmquist, J., Hughes, P.D.M., Jones, C., Jones, M.C., Karofeld, E., Klein, E.S., Kokfelt, U., Korhola, A., Lacourse, T., Le Roux, G., Lamentowicz, M., Large, D., Lavoie, M., Loisel, J., Mackay, H., MacDonald, G.M., Makila, M., Magnan, G., Marchant, R., Marcisz, K., Martínez Cortizas, A., Massa, C., Mathijssen, P., Mauquoy, D., Mighall, T., Mitchell, F.J.G., Moss, P., Nichols, J., Oksanen, P.O., Orme, L., Packalen, M.S., Robinson, S., Roland, T.P., Sanderson, N.K., Sannel, A.B.K., Silva-Sánchez, N., Steinberg, N., Swindles, G.T., Turner, T.E., Uglow, J., Väliranta, M., van Bellen, S., van der Linden, M., van Geel, B., Wang, G., Yu, Z., Zaragoza-Castells, J., Zhao, Y., 2018. Latitudinal limits to the predicted increase of the peatland carbon sink with warming. Nat. Clim. Chang. 8, 907–913. https://doi.org/10.1038/s41558-018-0271-1

Gargallo-Garriga, A., Sardans, J., Granda, V., Llusià, J., Peguero, G., Asensio, D., Ogaya, R., Urbina,

I., Van Langenhove, L., Verryckt, L.T., Chave, J., Courtois, E.A., Stahl, C., Grau, O., Klem, K., Urban, O., Janssens, I.A., Peñuelas, J., 2020. Different "metabolomic niches" of the highly diverse tree species of the French Guiana rainforests. Sci. Rep. 10, 1–10. https://doi.org/10.1038/s41598-020-63891-y

Garnier, E., Navas, M.L., 2012a. A trait-based approach to comparative functional plant ecology: Concepts, methods and applications for agroecology. A review, Agronomy for Sustainable Development. https://doi.org/10.1007/s13593-011-0036-y

Garnier, E., Navas, M.L., 2012b. A trait-based approach to comparative functional plant ecology: Concepts, methods and applications for agroecology. A review. Agron. Sustain. Dev. https://doi.org/10.1007/s13593-011-0036-y

Gavazov, K., Albrecht, R., Buttler, A., Dorrepaal, E., Garnett, M.H., Gogo, S., Hagedorn, F., Mills, R.T.E., Robroek, B.J.M., Bragazza, L., 2018. Vascular plant-mediated controls on atmospheric carbon assimilation and peat carbon decomposition under climate change. Glob. Chang. Biol. 24, 3911–3921. https://doi.org/10.1111/gcb.14140

Geisen, S., 2020. Protists as catalyzers of microbial litter breakdown and carbon cycling at different temperature regimes. ISME J. 10–13. https://doi.org/10.1038/s41396-020-00792-y

Geisen, S., Tveit, A.T., Clark, I.M., Richter, A., Svenning, M.M., Bonkowski, M., Urich, T., 2015. Metatranscriptomic census of active protists in soils. ISME J. 9, 2178–2190. https://doi.org/10.1038/ismej.2015.30

Gerdol, R., 1996. The seasonal growth of Sphagnum magellanicum Brid. in different microhabitats on a mire in the southern Alps. Oecologia Mont. 5, 13–20.

Gerdol, R., Bonora, A., Poli, F., 1994. The Vertical Pattern of Pigment Concentrations in Chloroplasts of Sphagnum capillifolium. Bryologist 97, 158–161.

Gessner, M.O., 1997. Fungal biomass, production and sporulation associated with particulate organic matter in streams. Limnetica 13, 33–44.

Gessner, M.O., Bauchrowitz, M.A., Escautier, M., 1991. Extraction and quantification of ergosterol as a measure of fungal biomass in leaf litter. Microb. Ecol. 22, 285–291. https://doi.org/10.1007/BF02540230

Ghalambor, C.K., McKay, J.K., Carroll, S.P., Reznick, D.N., 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Funct. Ecol. 21, 394–407. https://doi.org/10.1111/j.1365-2435.2007.01283.x

Gilbert, D., Amblard, C., Bourdier, G., Francez, A.J., 1998. The microbial loop at the surface of a peatland: Structure, function, and impact of nutrient input. Microb. Ecol. 35, 83–93. https://doi.org/10.1007/s002489900062

Gilbert, D., Mitchell, E.A.D., 2006. Microbial diversity in Sphagnum peatlands. Biotechnol. Apl. 23, 202–210.

Gilbert, D., Mitchell, E.A.D., Amblard, C., Bourdier, G., Francez, A.J., 2003. Population dynamics and food preferences of the testate amoeba Nebela tincta major-bohemica-collaris complex (Protozoa) in a Sphagnum peatland. Acta Protozool. 42, 99–104.

Glime, J.M., 2006. Bryophytes and Herbivory. Cryptogamie 27, 191–203.

Goffinet, B., Shaw, A.J., 2008. Bryophyte biology. Cambridge University press.

Gong, J., Roulet, N., Frolking, S., Peltola, H., Laine, A.M., Kokkonen, N., Tuittila, E.-S., 2020a. Modelling the habitat preference of two key Sphagnum species in a poor fen as controlled by capitulum water retention. Biogeosciences 17, 5693–5719. https://doi.org/10.5194/bg-17-5693-2020

Gong, J., Roulet, N., Frolking, S., Peltola, H., Laine, A.M., Kokkonen, N., Tuittila, E.-S., 2020b. Modelling the habitat preference of two key Sphagnum species in a poor fen as controlled by capitulum water content. Biogeosciences 17, 5693–5719. https://doi.org/10.5194/bg-17-5693-2020

Gorham, E., 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol. Appl. 1, 182–195. https://doi.org/10.2307/1941811

Gornall, J.L., Jónsdóttir, I.S., Woodin, S.J., Van Der Wal, R., 2007. Arctic mosses govern below-ground environment and ecosystem processes. Oecologia 153, 931–941. https://doi.org/10.1007/s00442-007-0785-0

Gotelli, N.J., Ulrich, W., 2012. Statistical challenges in null model analysis. Oikos 121, 171–180. https://doi.org/10.1111/j.1600-0706.2011.20301.x

Goud, E.M., Watt, C., Moore, T.R., 2018. Plant community composition along a peatland margin follows alternate successional pathways after hydrologic disturbance. Acta Oecologica 91, 65–72. https://doi.org/10.1016/j.actao.2018.06.006

Grabowski, M., Porto, A., 2017. How many more? Sample size determination in studies of morphological integration and evolvability. Methods Ecol. Evol. 8, 592–603. https://doi.org/10.1111/2041-210X.12674

Grace, J.B., Adler, P.B., Stanley Harpole, W., Borer, E.T., Seabloom, E.W., 2014. Causal networks clarify productivity-richness interrelations, bivariate plots do not. Funct. Ecol. 28, 787–798. https://doi.org/10.1111/1365-2435.12269

Grace, J.B., Anderson, T.M., Olff, H., Scheiner, S.M., 2010. On the specification of structural equation models for ecological systems. Ecol. Monogr. 80, 67–87. https://doi.org/10.1890/09-0464.1

Graglia, E., Julkunen-Tiitto, R., Shaver, G.R., Schmidt, I.K., Jonasson, S., Michelsen, A., 2001. Environmental control and intersite variations of phenolics in Betula nana in tundra ecosystems. New Phytol. 151, 227–236. https://doi.org/10.1046/j.1469-8137.2001.00149.x

Graham, L.E., Kim, E., Arancibia-Avila, P., Graham, J.M., Wilcox, L.W., 2010. Evolutionary and ecophysiological significance of sugar utilization by the peat moss Sphagnum compactum (Sphagnaceae) and the common charophycean associates cylindrocystis brebissonii and Mougeotia sp. (zygnemataceae). Am. J. Bot. 97, 1485–1491. https://doi.org/10.3732/ajb.0900341

Gralka, M., Szabo, R., Stocker, R., Cordero, O.X., 2020. Trophic Interactions and the Drivers of Microbial Community Assembly. Curr. Biol. 30, R1176–R1188. https://doi.org/10.1016/j.cub.2020.08.007

Granath, G., Strengbom, J., Breeuwer, A., Heijmans, M.M.P.D., Berendse, F., Rydin, H., 2009. Photosynthetic performance in Sphagnum transplanted along a latitudinal nitrogen deposition gradient. Oecologia 159, 705–715. https://doi.org/10.1007/s00442-008-1261-1

Griffiths, M.J., Harrison, S.T.L., 2009. Lipid productivity as a key characteristic for choosing algal species for biodiesel production. J. Appl. Phycol. 21, 493–507. https://doi.org/10.1007/s10811-008-9392-7

Grime, J.P., 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. Am. Nat. 111, 1169–1194. https://doi.org/10.1086/283244

Grime, P.J., 2006. Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences, Journal of Vegetation Science.

Gui, H., Hyde, K., Xu, J., Mortimer, P., 2017. Arbuscular mycorrhiza enhance the rate of litter decomposition while inhibiting soil microbial community development. Sci. Rep. 7, 1–10. https://doi.org/10.1038/srep42184

Gunnarsson, U., 2005. Global patterns of Sphagnum productivity. J. Bryol. 27, 269–279. https://doi.org/10.1179/174328205X70029

Gunnarsson, U., Granberg, G., Nilsson, M., 2004. Growth , production and interspecific competition in Sphagnum : effects of temperature , nitrogen and sulphur treatments on a boreal mire. New Phytol. 1, 349–359. https://doi.org/10.1111/j.1469-8137.2004.01108.x

Guo, C., Ma, L., Yuan, S., Wang, R., 2017. Morphological, physiological and anatomical traits of plant functional types in temperate grasslands along a large-scale aridity gradient in northeastern China. Sci. Rep. 7, 1–10. https://doi.org/10.1038/srep40900

Hadacek, F., Bachmann, G., 2015. Low-molecular-weight metabolite systems chemistry. Front. Environ. Sci. 3, 1–21. https://doi.org/10.3389/fenvs.2015.00012

Hájek, T., 2020. Interlinking moss functional traits. A commentary on: 'Water economy responses to water level drawdown in peat mosses.' Ann. Bot. 126, iv–v. https://doi.org/10.1093/aob/mcaa108

Hájek, T., 2014. Photosynthesis in Bryophytes and Early Land Plants, in: Hanson, D.T., Rice, S.K. (Eds.), Photosynthesis in Bryophytes and Early Land Plants. Springer, pp. 233–252. https://doi.org/10.1007/978-94-007-6988-5

Hájek, T., Ballance, S., Limpens, J., Zijlstra, M., Verhoeven, J.T.A., 2011. Cell-wall polysaccharides play an important role in decay resistance of Sphagnum and actively depressed decomposition in vitro. Biogeochemistry 103, 45–57. https://doi.org/10.1007/s10533-010-9444-3

Hájek, T., Vicherová, E., 2014. Desiccation tolerance of Sphagnum revisited: A puzzle resolved. Plant Biol. 16, 765–773. https://doi.org/10.1111/plb.12126

Hallingbäck, T., Hodgetts, N., 2000. Mosses, Liverworts, and Hornworts. Status Survey and Conservation Action Plan for Bryophytes.

Hamard, S., Robroek, B.J.M., Allard, P.-M., Signarbieux, C., Zhou, S., Saesong, T., de Baaker, F., Buttler, A., Chiapusio, G., Wolfender, J.-L., Bragazza, L., Jassey, V.E.J., 2019. Effects of Sphagnum Leachate on Competitive Sphagnum Microbiome Depend on Species and Time. Front. Microbiol. 10, 1–17. https://doi.org/10.3389/fmicb.2019.02042

Handakumbura, P.P., Stanfill, B., Rivas-Ubach, A., Fortin, D., Vogel, J.P., Jansson, C., 2019. Metabotyping as a Stopover in Genome-to-Phenome Mapping. Sci. Rep. 9, 1–12. https://doi.org/10.1038/s41598-019-38483-0

Hansen, A.H., Jonasson, S., Michelsen, A., Julkunen-Tiitto, R., 2006. Long-term experimental warming, shading and nutrient addition affect the concentration of phenolic compounds in arctic-alpine deciduous and evergreen dwarf shrubs. Oecologia 147, 1–11. https://doi.org/10.1007/s00442-005-0233-y

Hansen, A.M., Kraus, T.E.C., Pellerin, B.A., Fleck, J.A., Downing, B.D., Bergamaschi, B.A., 2016. Optical properties of dissolved organic matter (DOM): Effects of biological and photolytic degradation. Limnol. Oceanogr. 61, 1015–1032. https://doi.org/10.1002/lno.10270

Hanson, D.T., Swanson, S., Graham, L.E., Sharkey, T.D., 1999. Evolutionary significance of isoprene emission from mosses. Am. J. Bot. 86, 634–639. https://doi.org/10.2307/2656571

Harris, A., Bryant, R.G., Baird, A.J., 2005. Detecting near-surface moisture stress in Sphagnum spp. Remote Sens. Environ. 97, 371–381. https://doi.org/10.1016/j.rse.2005.05.001

Harrison, S., 2020. Plant community diversity will decline more than increase under climatic warming. Philos. Trans. R. Soc. B Biol. Sci. 375. https://doi.org/10.1098/rstb.2019.0106

Hartmann, T., 2007. From waste products to ecochemicals: Fifty years research of plant secondary metabolism. Phytochemistry 68, 2831–2846. https://doi.org/10.1016/j.phytochem.2007.09.017

Hättenschwiler, S., Vitousek, P.M., 2000. The role of polyphenols in terrestrial ecosystem nutrient cycling. Trends Ecol. Evol. https://doi.org/10.1016/S0169-5347(00)01861-9

Hayat, S., Hayat, Q., Alyemeni, M.N., Wani, A.S., Pichtel, J., Ahmad, A., 2012. Role of proline under changing environments: A review. Plant Signal. Behav. 7, 1456–1466. https://doi.org/10.4161/psb.21949

Hayward, P.M., Clymo, R.S., 1983. The Growth of Sphagnum: Experiments on, and Simulation of, Some Effects of Light Flux and Water-Table Depth. J. Ecol. 71, 845. https://doi.org/10.2307/2259597

Hayward, P.M., Clymo, R.S., 1982. Profiles of water content and pore size in Sphagnum and peat, and their relation to peat bog ecology. Proc. R. Soc. London - Biol. Sci. 215, 299–325. https://doi.org/10.1098/rspb.1982.0044

He, X., He, K.S., Hyvönen, J., 2016. Will bryophytes survive in a warming world? Perspect. Plant Ecol. Evol. Syst. 19, 49–60. https://doi.org/10.1016/j.ppees.2016.02.005

Heijmans, M.M.P.D., Klees, H., Berendse, F., 2002. Competition between Sphagnum magellanicum and Eriophorum angustifolium as affected by raised CO2 and increased N deposition. Oikos 97, 415–425. https://doi.org/10.1034/j.1600-0706.2002.970311.x

Heinselman, M.L., 1970. Landscape Evolution, Peatland Types, and the Environment in the Lake Agassiz Peatlands Natural Area, Minnesota. Ecol. Monogr. 40, 235–261. https://doi.org/10.2307/1942297

Hengl, T., De Jesus, J.M., MacMillan, R.A., Batjes, N.H., Heuvelink, G.B.M., Ribeiro, E., Samuel-Rosa, A., Kempen, B., Leenaars, J.G.B., Walsh, M.G., Gonzalez, M.R., 2014. SoilGrids1km - Global soil information based on automated mapping. PLoS One 9. https://doi.org/10.1371/journal.pone.0105992

Henn, J.J., Buzzard, V., Enquist, B.J., Halbritter, A.H., Klanderud, K., Maitner, B.S., Michaletz, S.T., Pötsch, C., Seltzer, L., Telford, R.J., Yang, Y., Zhang, L., Vandvik, V., 2018. Intraspecific trait variation and phenotypic plasticity mediate alpine plant species response to climate change. Front. Plant Sci. 871, 1–11. https://doi.org/10.3389/fpls.2018.01548

Herms, D.A., Mattson, W.J., 1992. The Dilemma of Plants : To Grow or Defend. Q. Rev. Biol. 67, 283–335.

Herrera, M.C., Luque De Castro, M.D., 2005. Ultrasound-assisted extraction of phenolic compounds from strawberries prior to liquid chromatographic separation and photodiode array ultraviolet detection. J. Chromatogr. A 1100, 1–7. https://doi.org/10.1016/j.chroma.2005.09.021

Hiruma, K., 2019. Roles of Plant-Derived Secondary Metabolites during Interactions with Pathogenic and Beneficial Microbes under Conditions of Environmental Stress. Microorganisms 7, 362. https://doi.org/10.3390/microorganisms7090362

Hodgkins, S.B., Tfaily, M.M., McCalley, C.K., Logan, T.A., Crill, P.M., Saleska, S.R., Rich, V.I., Chanton, J.P., 2014. Changes in peat chemistry associated with permafrost thaw increase greenhouse gas production. Proc. Natl. Acad. Sci. 111, 5819–5824. https://doi.org/10.1073/pnas.1314641111

Hoffmann, A.A., Parsons, P.A., 1991. Evolutionary genetics and environmental stress. Oxford University Press, New York.

Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L., Connor, M.I., 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486, 105–108. https://doi.org/10.1038/nature11118

Hosseini, H., Bolourian, S., Yaghoubi Hamgini, E., Ghanuni Mahababadi, E., 2018. Optimization of heat- and ultrasound-assisted extraction of polyphenols from dried rosemary leaves using response surface methodology. J. Food Process. Preserv. 42, 1–15.

https://doi.org/10.1111/jfpp.13778

Hu, L., Robert, C.A.M., Cadot, S., Zhang, X., Ye, M., Li, B., Manzo, D., Chervet, N., Steinger, T., Van Der Heijden, M.G.A., Schlaeppi, K., Erb, M., 2018. Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. Nat. Commun. 9, 1–13. https://doi.org/10.1038/s41467-018-05122-7

Huang, X., Xue, J., Zhang, J., Qin, Y., Meyers, P.A., Wang, H., 2012. Effect of different wetness conditions on Sphagnum lipid composition in the Erxianyan peatland, central China. Org. Geochem. 44, 1–7. https://doi.org/10.1016/j.orggeochem.2011.12.005

Hugelius, G., Loisel, J., Chadburn, S., Jackson, R.B., Jones, M., MacDonald, G., Marushchak, M., Olefeldt, D., Packalen, M., Siewert, M.B., Treat, C., Turetsky, M., Voigt, C., Yu, Z., 2020. Large stocks of peatland carbon and nitrogen are vulnerable to permafrost thaw. Proc. Natl. Acad. Sci. U. S. A. 117, 20438–20446. https://doi.org/10.1073/pnas.1916387117

Iason, G.R., Dicke, M., Hartley, S.E., 2012a. The integrative roles of plant secondary metabolites in natural systems. Ecol. Plant Second. Metab. 1–9. https://doi.org/10.1017/cbo9780511675751.002

Iason, G.R., Dicke, M., Hartley, S.E., 2012b. The Ecology of Plant Secondary Metabolites, The Ecology of Plant Secondary Metabolites. https://doi.org/10.1017/cbo9780511675751

Iglesias-Carres, L., Mas-Capdevila, A., Bravo, F.I., Aragonès, G., Muguerza, B., Arola-Arnal, A., 2019. Optimization of a polyphenol extraction method for sweet orange pulp (Citrus sinensis L.) to identify phenolic compounds consumed from sweet oranges. PLoS One 14, 1–17. https://doi.org/10.1371/journal.pone.0211267

Ingram, H.A.P., 1978. Soil layers in mires: function and terminology. J. Soil Sci. 29, 224–227. https://doi.org/10.1111/j.1365-2389.1978.tb02053.x

Isah, T., 2019. Stress and defense responses in plant secondary metabolites production. Biol. Res. 52, 39. https://doi.org/10.1186/s40659-019-0246-3

Isoviita, P., 1966. Studies on Sphagnum L . I . Nomenclatural revision of the European taxa. Ann. Bot. Fenn. 3, 199–264.

Issa, A.A., Abd-Alla, M.H., Ohyam, T., 2014. Nitrogen Fixing Cyanobacteria: Future Prospect, in: Advances in Biology and Ecology of Nitrogen Fixation. InTech, p. 13. https://doi.org/https://doi.org/10.5772/56995

Jaffrain, J., Gérard, F., Meyer, M., Ranger, J., 2007. Assessing the Quality of Dissolved Organic Matter in Forest Soils Using Ultraviolet Absorption Spectrophotometry. Soil Sci. Soc. Am. J. 71, 1851–1858. https://doi.org/10.2136/sssaj2006.0202

James, A.S.R., Yavitt, J.B., Zinder, S.H., Richardson, R.E., 2021. Linking microbial Sphagnum degradation and acetate mineralization in acidic peat bogs: from global insights to a genome-centric case study. ISME J. 15, 293–303. https://doi.org/10.1038/s41396-020-00782-0

Jassey, V., Meyer, C., Dupuy, C., Bernard, N., Toussaint, M., Metian, M., Chatelain, A., Jassey, V., Meyer, C., Dupuy, C., Bernard, N., Mitchell, E., 2016. To What Extent Do Food Preferences Explain the Trophic Position of Heterotrophic and Mixotrophic Microbial Consumers in a Sphagnum Peatland ?

Jassey, V.E.J., Chiapusio, G., Binet, P., Buttler, A., Laggoun-Défarge, F., Delarue, F., Bernard, N., Mitchell, E.A., Toussaint, M.-L., Francez, A.-J., Gilbert, D., 2013. Above- and belowground linkages in Sphagnum peatland: climate warming affects plant-microbial interactions. Glob. Chang. Biol. 19, 811–823. https://doi.org/10.1111/gcb.12075

Jassey, V.E.J., Chiapusio, G., Gilbert, D., Buttler, A., Toussaint, M.-L., Binet, P., 2011a. Experimental climate effect on seasonal variability of polyphenol/phenoloxidase interplay along a narrow fen-bog ecological gradient in Sphagnum fallax. Glob. Chang. Biol. 17, 2945–2957.

https://doi.org/10.1111/j.1365-2486.2011.02437.x

Jassey, V.E.J., Chiapusio, G., Gilbert, D., Toussaint, M.L., Binet, P., 2012. Phenoloxidase and peroxidase activities in Sphagnum-dominated peatland in a warming climate. Soil Biol. Biochem. 46, 49–52. https://doi.org/10.1016/j.soilbio.2011.11.011

Jassey, V.E.J., Chiapusio, G., Mitchell, E.A.D., Binet, P., Toussaint, M.L., Gilbert, D., 2011b. Fine-Scale Horizontal and Vertical Micro-distribution Patterns of Testate Amoebae Along a Narrow Fen/Bog Gradieant. Microb. Ecol. 61, 374–385. https://doi.org/10.1007/s00248-010-9756-9

Jassey, V.E.J., Gilbert, D., Binet, P., Toussaint, M.-L., Chiapusio, G., 2011c. Effect of a temperature gradient on Sphagnum fallax and its associated living microbial communities: a study under controlled conditions. Can. J. Microbiol. 57, 226–235. https://doi.org/10.1139/w10-116

Jassey, V.E.J., Lamentowicz, L., Robroek, B.J.M., Gabka, M., Rusińska, A., Lamentowicz, M., 2014. Plant functional diversity drives niche-size-structure of dominant microbial consumers along a poor to extremely rich fen gradient. J. Ecol. 102, 1150–1162. https://doi.org/10.1111/1365-2745.12288

Jassey, V.E.J., Lamentowicz, M., Bragazza, L., Hofsommer, M.L., Mills, R.T.E., Buttler, A., Signarbieux, C., Robroek, B.J.M., 2016. Loss of testate amoeba functional diversity with increasing frost intensity across a continental gradient reduces microbial activity in peatlands. Eur. J. Protistol. 55, 190–202. https://doi.org/10.1016/j.ejop.2016.04.007

Jassey, V.E.J., Reczuga, M.K., Zielińska, M., Słowińska, S., Robroek, B.J.M., Mariotte, P., Seppey, C.V.W., Lara, E., Barabach, J., Słowiński, M., Bragazza, L., Chojnicki, B.H., Lamentowicz, M., Mitchell, E.A.D., Buttler, A., 2018. Tipping point in plant–fungal interactions under severe drought causes abrupt rise in peatland ecosystem respiration. Glob. Chang. Biol. 24, 972–986. https://doi.org/10.1111/gcb.13928

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

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

Jassey, V.E.J.J., Signarbieux, C., 2019. Effects of climate warming on Sphagnum photosynthesis in peatlands depend on peat moisture and species-specific anatomical traitsa. Glob. Chang. Biol. 25, 1–12. https://doi.org/10.1111/gcb.14788

Joabsson, A., Christensen, T.R., Wallén, B., 1999. Vascular plant controls on methane emissions from northern peatforming wetlands. Trends Ecol. Evol. 14, 385–388. https://doi.org/10.1016/S0169-5347(99)01649-3

Johnson, L.C., Damman, A.W.H., 1991. Species-Controlled Sphagnum Decay on a South Swedish Raised Bog Published by : Wiley on behalf of Nordic Society Oikos Stable URL : http://www.jstor.org/stable/3545341 REFERENCES Linked references are available on JSTOR for this artic. Oikos 61, 234–242.

Johnson, M.G., Granath, G., Tahvanainen, T., Pouliot, R., Stenøien, H.K., Rochefort, L., Rydin, H., Shaw, A.J., 2015. Evolution of niche preference in Sphagnum peat mosses. Evolution (N. Y). 69, 90–103. https://doi.org/10.1111/evo.12547

Johnston, A.S.A., Sibly, R.M., 2018. The influence of soil communities on the temperature sensitivity of soil respiration. Nat. Ecol. Evol. 2, 1597–1602. https://doi.org/10.1038/s41559-018-0648-6

Jones, C.G., Hartley, S.E., 1999. A Protein Competition Model of Phenolic Allocation. Oikos 86, 27–

44. https://doi.org/https://doi.org/3546567

Jones, C.G., Lawton, J.H., Shachak, M., Organisms, M., 1994. Organisms as Ecosystem Engineers Author. Oikos 69, 373–386.

Joosten, H., Clarke, D., 2002. Wise use of mires and peatlands -Background and principles including a framework for decision-making, International Mire Conservation Group and International Peat Society.

Kallam, K., Cai, Y.M., Bickerton, P., 2019. Using synthetic biology to unleash the potential of plants. Biochem. (Lond). 41, 20–23. https://doi.org/10.1042/bio04103020

Kapoor, D., Bhardwaj, S., Landi, M., Sharma, Arti, Ramakrishnan, M., Sharma, Anket, 2020. The impact of drought in plant metabolism: How to exploit tolerance mechanisms to increase crop production. Appl. Sci. 10. https://doi.org/10.3390/app10165692

Karunen, P., Salin, M., Lindbergia, S., 1982. Seasonal Changes in Lipids of Photosynthetically Active and Senescent Parts of Sphagnum fuscum. Lindbergia 8, 35–44.

Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., Van Bodegom, P.M., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., Ackerly, D.D., Anand, M., Atkin, O., Bahn, M., Baker, T.R., Baldocchi, D., Bekker, R., Blanco, C.C., Blonder, B., Bond, W.J., Bradstock, R., Bunker, D.E., Casanoves, F., Cavender-Bares, J., Chambers, J.Q., Chapin, F.S., Chave, J., Coomes, D., Cornwell, W.K., Craine, J.M., Dobrin, B.H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W.F., Fang, J., Fernández-Méndez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.T., Fyllas, N.M., Gallagher, R. V., Green, W.A., Gutierrez, A.G., Hickler, T., Higgins, S.I., Hodgson, J.G., Jalili, A., Jansen, S., Joly, C.A., Kerkhoff, A.J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J.M.H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D., Lee, T.D., Leishman, M., Lens, F., Lenz, T., Lewis, S.L., Lloyd, J., Llusià, J., Louault, F., Ma, S., Mahecha, M.D., Manning, P., Massad, T., Medlyn, B.E., Messier, J., Moles, A.T., Müller, S.C., Nadrowski, K., Naeem, S., Niinemets, Ü., Nöllert, S., Nüske, A., Ogaya, R., Oleksyn, J., Onipchenko, V.G., Onoda, Y., Ordoñez, J., Overbeck, G., Ozinga, W.A., Patiño, S., Paula, S., Pausas, J.G., Peñuelas, J., Phillips, O.L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J.F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S.J., Yguel, B., Zaehle, S., Zanne, A.E., Wirth, C., 2011. TRY - a global database of plant traits. Glob. Chang. Biol. 17, 2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x

Keddy, P.A., 2010. Wetland ecology:Principles and conservation, Wetland Ecology: Principles and Conservation. https://doi.org/10.1017/CBO9780511778179

Keddy, P.A., 1992. Assembly and response rules: two goals for predictive community ecology. J. Veg. Sci. 3, 157–164. https://doi.org/10.2307/3235676

Kelly, R., Healy, K., Anand, M., Baudraz, M.E.A., Bahn, M., Cerabolini, B.E.L., Cornelissen, J.H.C., Dwyer, J.M., Jackson, A.L., Kattge, J., Niinemets, Ü., Penuelas, J., Pierce, S., Salguero-Gómez, R., Buckley, Y.M., 2021. Climatic and evolutionary contexts are required to infer plant life history strategies from functional traits at a global scale. Ecol. Lett. 24, 970–983. https://doi.org/10.1111/ele.13704

Kéry, M., Matthies, D., Spillmann, H.H., 2000. Reduced fecundity and offspring performance in small populations of the declining grassland plants Primula veris and Gentiana lutea. J. Ecol. 88, 17–30. https://doi.org/10.1046/j.1365-2745.2000.00422.x

Khare, S., Singh, N.B., Singh, A., Hussain, I., Niharika, K., Yadav, V., Bano, C., Yadav, R.K., Amist, N., 2020. Plant secondary metabolites synthesis and their regulations under biotic and abiotic constraints. J. Plant Biol. 63, 203–216. https://doi.org/10.1007/s12374-020-09245-7

Kishor, P.B.K., Sreenivasulu, N., 2014. Is proline accumulation per se correlated with stress tolerance

or is proline homeostasis a more critical issue? Plant, Cell Environ. 37, 300–311. https://doi.org/10.1111/pce.12157

Klavina, L., 2018. Composition of mosses , their metabolites and environmental stress impacts. University of Latvia, Riga.

Klavina, L., Springe, G., Nikolajeva, V., Martsinkevich, I., Nakurte, I., Dzabijeva, D., Steinberga, I., 2015. Chemical composition analysis, antimicrobial activity and cytotoxicity screening of moss extracts (Moss Phytochemistry). Molecules 20, 17221–17243. https://doi.org/10.3390/molecules200917221

Klavina, L., Springe, G., Steinberga, I., Mezaka, A., Ievinsh, G., 2018. Seasonal changes of chemical composition in boreonemoral moss species. Environ. Exp. Biol. 16, 9–19. https://doi.org/10.22364/eeb.16.02

Kleessen, S., Laitinen, R., Fusari, C.M., Antonio, C., Sulpice, R., Fernie, A.R., Stitt, M., Nikoloski, Z., 2014. Metabolic efficiency underpins performance trade-offs in growth of Arabidopsis thaliana. Nat. Commun. 5. https://doi.org/10.1038/ncomms4537

Kliebenstein, D.J., Osbourn, A., 2012. Making new molecules - evolution of pathways for novel metabolites in plants. Curr. Opin. Plant Biol. 15, 415–423. https://doi.org/10.1016/j.pbi.2012.05.005

Korrensalo, A., 2017. Behind the stability of boreal bog carbon sink : Compositional and functional variation of vegetation across temporal and spatial scales.

Korrensalo, A., Alekseychik, P., Hï¿½jek, T., Rinne, J., Vesala, T., Mehtï¿½talo, L., Mammarella, I., Tuittila, E.S., 2017. Species-specific temporal variation in photosynthesis as a moderator of peatland carbon sequestration. Biogeosciences 14, 257–269. https://doi.org/10.5194/bg-14-257-2017

Kostka, J.E., Weston, D.J., Glass, J.B., Lilleskov, E.A., Shaw, A.J., Turetsky, M.R., 2016. The Sphagnum microbiome: New insights from an ancient plant lineage. New Phytol. 211, 57–64. https://doi.org/10.1111/nph.13993

Kruk, M., Podbielska, K., 2018. Potential changes of elemental stoichiometry and vegetation production in an ombrotrophic peatland in the condition of moderate nitrogen deposition. Aquat. Bot. 147, 24–33. https://doi.org/10.1016/j.aquabot.2018.03.004

Kuzuyama, T., 2002. Mevalonate and nonmevalonate pathways for the biosynthesis of isoprene units. Biosci. Biotechnol. Biochem. 66, 1619–1627. https://doi.org/10.1271/bbb.66.1619

Laborde, J.L., Bouyer, C., Caltagirone, J.P., Gérard, A., 1998. Acoustic bubble cavitation at low frequencies. Ultrasonics 36, 589–594. https://doi.org/10.1016/S0041-624X(97)00105-4

Lafleur, P.M., Roulet, N.T., Admiral, S.W., 2001. Annual cycle of CO2 exchange at a bog peatland. J. Geophys. Res. Atmos. 106, 3071–3081. https://doi.org/10.1029/2000JD900588

Laine, A.M., Lindholm, T., Nilsson, M., Kutznetsov, O., Jassey, V.E.J., Tuittila, E., 2021. Functional diversity and trait composition of vascular plant and Sphagnum moss communities during peatland succession across land uplift regions . J. Ecol. https://doi.org/10.1111/1365-2745.13601

Laine, A.M., Mäkiranta, P., Laiho, R., Mehtätalo, L., Penttilä, T., Korrensalo, A., Minkkinen, K., Fritze, H., Tuittila, E.-S., 2019. Warming impacts on boreal fen CO 2 exchange under wet and dry conditions . Glob. Chang. Biol. 1–14. https://doi.org/10.1111/gcb.14617

Laing, C.G., Granath, G., Belyea, L.R., Allton, K.E., Rydin, H., 2014. Tradeoffs and scaling of functional traits in Sphagnum as drivers of carbon cycling in peatlands. Oikos 123, 817–828. https://doi.org/10.1111/oik.01061

Laliberté, E., Legendre, P., Shipley, B., 2015. FD: measuring functional diversity from multiple traits,

and other tools for functional ecology. R Packag. Version 1.0-12.

Lambers, H., Chapin, F.S., Pons, T.L., 2008. Plant physiological ecology: Second edition, Plant Physiological Ecology: Second Edition. https://doi.org/10.1007/978-0-387-78341-3

Lamentowicz, M., Gałka, M., Lamentowicz, T., Obremska, M., Kühl, N., Lücke, A., Jassey, V.E.J., 2015. Reconstructing climate change and ombrotrophic bog development during the last 4000years in northern Poland using biotic proxies, stable isotopes and trait-based approach. Palaeogeogr. Palaeoclimatol. Palaeoecol. 418, 261–277. https://doi.org/10.1016/j.palaeo.2014.11.015

Lamentowicz, M., Gałka, M., Marcisz, K., Kajukało-drygalska, K., Dayras, M.D., Jassey, V.E.J., 2019. Unveiling tipping points in long-term ecological records from Sphagnum- dominated peatlands. Biol. Lett. 15. https://doi.org/https://dx.doi.org/10.6084/m9

Lang, S.I., Cornelissen, J.H.C., Klahn, T., Van Logtestijn, R.S.P., Broekman, R., Schweikert, W., Aerts, R., 2009. An experimental comparison of chemical traits and litter decomposition rates in a diverse range of subarctic bryophyte, lichen and vascular plant species. J. Ecol. 97, 886–900. https://doi.org/10.1111/j.1365-2745.2009.01538.x

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. Funct. Ecol. 16, 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Lee, M.R., Kim, C.S., Park, T., Choi, Y.S., Lee, K.H., 2018. Optimization of the ninhydrin reaction and development of a multiwell plate-based high-throughput proline detection assay. Anal. Biochem. 556, 57–62. https://doi.org/10.1016/j.ab.2018.06.022

Lefcheck, J.S., 2016. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods Ecol. Evol. 7, 573–579. https://doi.org/10.1111/2041-210X.12512

Leff, J.W., Bardgett, R.D., Wilkinson, A., Jackson, B.G., Pritchard, W.J., De Long, J.R., Oakley, S., Mason, K.E., Ostle, N.J., Johnson, D., Baggs, E.M., Fierer, N., 2018. Predicting the structure of soil communities from plant community taxonomy, phylogeny, and traits. ISME J. 12, 1794–1805. https://doi.org/10.1038/s41396-018-0089-x

Leflaive, J., Ten-Hage, L., 2007. Algal and cyanobacterial secondary metabolites in freshwaters: A comparison of allelopathic compounds and toxins. Freshw. Biol. 52, 199–214. https://doi.org/10.1111/j.1365-2427.2006.01689.x

Legendre, P., Legendre, L., 2012. Numerical Ecology. Elsevier Science.

Lehtonen, K., Ketola, M., 1993. Solvent-extractable lipids of Sphagnum, Carex, Bryales and Carex-Bryales peats: content and compositional features vs peat humification. Org. Geochem. 20, 363–380. https://doi.org/10.1016/0146-6380(93)90126-V

Leprince, O., Harren, F.J.M., Buitink, J., Alberda, M., Hoekstra, F.A., 2000. Metabolic dysfunction and unabated respiration precede the loss of membrane integrity during dehydration of germinating radicles. Plant Physiol. 122, 597–608. https://doi.org/10.1104/pp.122.2.597

Liang, C., Amelung, W., Lehmann, J., Kästner, M., 2019. Quantitative assessment of microbial necromass contribution to soil organic matter. Glob. Chang. Biol. 25, 3578–3590. https://doi.org/10.1111/gcb.14781

Liang, C., Schimel, J.P., Jastrow, J.D., 2017. The importance of anabolism in microbial control over soil carbon storage. Nat. Microbiol. 2, 1–6. https://doi.org/10.1038/nmicrobiol.2017.105

Limpens, J., Berendse, F., Blodau, C., Canadell, J.G., Freeman, C., Holden, J., Roulet, N., Rydin, H., Schaepman-Strub, G., 2008. Peatlands and the carbon cycle: From local processes to global implications - A synthesis. Biogeosciences 5, 1475–1491. https://doi.org/10.5194/bg-5-1475-2008

Limpens, J., Bohlin, E., Nilsson, M.B., 2017. Phylogenetic or environmental control on the elemental and organo-chemical composition of Sphagnum mosses? Plant Soil 417, 69–85. https://doi.org/10.1007/s11104-017-3239-4

Lindo, Z., Gonzalez, A., 2010. The bryosphere: An integral and influential component of the Earth's biosphere. Ecosystems 13, 612–627. https://doi.org/10.1007/s10021-010-9336-3

Liu, B., Lei, C., Jin, J., Guan, Y., Li, S., Zhang, Y., Liu, W., 2016. Physiological responses of two moss species to the combined stress of water deficit and elevated N deposition (II): Carbon and nitrogen metabolism. Ecol. Evol. 6, 7596–7609. https://doi.org/10.1002/ece3.2521

Liu, C., Bu, Z., Mallik, A., 2019. Resource competition and allelopathy in two peat mosses : implication for niche differentiation. Plant Soil Soil 446, 229–242.

Liu, C., Bu, Z.J., Mallik, A., Chen, Y. Da, Hu, X.F., Lu, F., 2020. Inhibition or facilitation? Contrasted inter-specific interactions in sphagnum under laboratory and field conditions. Plants 9, 1–13. https://doi.org/10.3390/plants9111554

Ljungqvist, F.C., Krusic, P.J., Sundqvist, H.S., Zorita, E., Brattström, G., Frank, D., 2016. Northern Hemisphere hydroclimate variability over the past twelve centuries. Nature 532, 94–98. https://doi.org/10.1038/nature17418

Loisel, J., Gallego-Sala, A. V., Yu, Z., 2012. Global-scale pattern of peatland Sphagnum growth driven by photosynthetically active radiation and growing season length. Biogeosciences 9, 2737–2746. https://doi.org/10.5194/bg-9-2737-2012

Loka, J., Philipose, K.K., Sonali, S.M., 2016. Effect of microalgal diets on filtration and ingestion rates of the rotifer Brachionus plicatilis. Indian J. Fish. 63, 76–80. https://doi.org/10.21077/ijf.2016.63.3.58554-10

Ludwiczuk, A., Odrzykoski, I.J., Asakawa, Y., 2013. Identification of cryptic species within liverwort Conocephalum conicum based on the volatile components. Phytochemistry 95, 234–241. https://doi.org/10.1016/j.phytochem.2013.06.011

Lyakh A.M., 2012. 3D-Microalgae software used for the estimation of microalgae biovolumes and surface area. Mod. Phytomorphology 1, 89–91. https://doi.org/10.5281/zenodo.162745

Maass, W.S.G., Craigie, J.S., 1964. Examination of Some Soluble Constituents of Sphagnum Gametophytes. Can. J. Bot. 42, 805–813. https://doi.org/10.1139/b64-072

Maehly, A.C., Chance, B., 1954. The Assay of Catalse and Peroxidases. Methods Biochem. Anal. 1, 358–423.

Malik, A.A., Martiny, J.B.H., Brodie, E.L., Martiny, A.C., Treseder, K.K., Allison, S.D., 2020. Defining trait-based microbial strategies with consequences for soil carbon cycling under climate change. ISME J. 14, 1–9. https://doi.org/10.1038/s41396-019-0510-0

Malmer, N., Albinsson, C., Svensson, B.M., Wallén, B., 2003. Interferences between Sphagnum and vascular plants: Effects on plant community structure and peat formation. Oikos 100, 469–482. https://doi.org/10.1034/j.1600-0706.2003.12170.x

Malmer, N., Svensson, B.M., Wallén, B., 1994. Interactions between Sphagnum mosses and field layer vascular plants in the development of peat-forming systems. Folia Geobot. Phytotaxon. 29, 483–496. https://doi.org/10.1007/BF02883146

Mandi, M.R., De, M.M.O., Sabovljevi, A.D., 2022. The Influence of Seasonality on Secondary Metabolite Profiles and Neuroprotective Activities of Moss Hypnum cupressiforme.

Mariotte, P., Robroek, B.J.M., Jassey, V.E.J., Buttler, A., 2015. Subordinate plants mitigate drought effects on soil ecosystem processes by stimulating fungi. Funct. Ecol. 29, 1578–1586. https://doi.org/10.1111/1365-2435.12467

Maseyk, K.S., Green, T.G.A., Klinac, D., 1999. Photosynthetic responses of New Zealand Sphagnum species. New Zeal. J. Bot. 37, 155–165. https://doi.org/10.1080/0028825X.1999.9512621

Massalha, H., Korenblum, E., Tholl, D., Aharoni, A., 2017. Small molecules below-ground : the role of specialized metabolites in the rhizosphere 788–807. https://doi.org/10.1111/tpj.13543

Matić, P., Sabljić, M., Jakobek, L., 2017. Validation of Spectrophotometric Methods for the Determination of Total Polyphenol and Total Flavonoid Content. J. AOAC Int. 100, 1795–1803. https://doi.org/10.5740/jaoacint.17-0066

Mattson, W.J., Julkunen-Tiitto, R., Herms, D.A., 2005. CO2 enrichment and carbon partitioning to phenolics: Do plant responses accord better with the protein competition or the growth-differentiation balance models? Oikos 111, 337–347. https://doi.org/10.1111/j.0030-1299.2005.13634.x

Matzek, V., Vitousek, P., 2003. Nitrogen fixation in bryophytes, lichens, and decaying wood along a soil-age gradient in Hawaiian montane rain forest. Biotropica 35, 12–19. https://doi.org/10.1111/j.1744-7429.2003.tb00257.x

Mazziotta, A., Granath, G., Rydin, H., Bengtsson, F., Norberg, J., 2019. Scaling functional traits to ecosystem processes: Towards a mechanistic understanding in peat mosses. J. Ecol. 107, 843–859. https://doi.org/10.1111/1365-2745.13110

Mazziotta, A., Granath, G., Rydin, H., Bengtsson, F., Norberg, J., 2018. Scaling functional traits to ecosystem processes: towards a mechanistic understanding in peat mosses. J. Ecol. 107, 1365-2745.13110. https://doi.org/10.1111/1365-2745.13110

Mccarter, C.P.R., Price, J.S., 2014. Ecohydrology of Sphagnum moss hummocks: Mechanisms of capitula water supply and simulated effects of evaporation. Ecohydrology 7, 33–44. https://doi.org/10.1002/eco.1313

McCue, K.F., Hanson, A.D., 1990. Drought and salt tolerance: towards understanding and application. Trends Biotechnol. 8, 358–362. https://doi.org/10.1016/0167-7799(90)90225-M

Mcguire, A.D., Anderson, L.G., Christensen, T.R., Scott, D., Laodong, G., Hayes, D.J., Martin, H., Lorenson, T.D., Macdonald, R.W., Nigel, R., 2009. Sensitivity of the carbon cycle in the Arctic to climate change. Ecol. Monogr. 79, 523–555. https://doi.org/10.1890/08-2025.1

McLaughlin, J., Webster, K., North, F., 2013. Effects of a Changing Climate on Peatlands in Permafrost Zones : A Literature Review and Application to Ontario ' s. https://doi.org/10.13140/RG.2.2.14743.98721

Medvigy, D., Beaulieu, C., 2012. Trends in daily solar radiation and precipitation coefficients of variation since 1984. J. Clim. 25, 1330–1339. https://doi.org/10.1175/2011JCLI4115.1

Mekinić, I.G., Skroza, D., Ljubenkov, I., Katalinić, V., Šimat, V., 2019. Antioxidant and antimicrobial potential of phenolic metabolites from traditionally used Mediterranean herbs and spices. Foods 8. https://doi.org/10.3390/foods8110579

Mellegård, H., Stalheim, T., Hormazabal, V., Granum, P.E., Hardy, S.P., 2009. Antibacterial activity of sphagnum acid and other phenolic compounds found in Sphagnum papillosum against food-borne bacteria. Lett. Appl. Microbiol. 49, 85–90. https://doi.org/10.1111/j.1472-765X.2009.02622.x

Meng, M., Ni, J., Zong, M., 2011. Impacts of changes in climate variability on regional vegetation in China: NDVI-based analysis from 1982 to 2000. Ecol. Res. 26, 421–428. https://doi.org/10.1007/s11284-011-0801-z

Merilä, J., Hendry, A.P., 2014. Climate change, adaptation, and phenotypic plasticity: The problem and the evidence. Evol. Appl. 7, 1–14. https://doi.org/10.1111/eva.12137

Metlen, K.L., Aschehoug, E.T., Callaway, R.M., 2009. Plant behavioural ecology : dynamic plasticity

in secondary metabolites 641–653. https://doi.org/10.1111/j.1365-3040.2008.01910.x

Michel, P., Lee, W.G., During, H.J., Cornelissen, J.H.C., 2012. Species traits and their non-additive interactions control the water economy of bryophyte cushions. J. Ecol. 100, 222–231. https://doi.org/10.1111/j.1365-2745.2011.01898.x

Mierziak, J., Kostyn, K., Kulma, A., 2014. Flavonoids as important molecules of plant interactions with the environment. Molecules 19, 16240–16265. https://doi.org/10.3390/molecules191016240

Mikami, K., Hartmann, E., 2004. Lipid Metabolism in Mosses, in: New Frontiers in Bryology. Springer Netherlands, Dordrecht, pp. 133–155. https://doi.org/10.1007/978-0-306-48568-8_8

Minasny, B., Berglund, Ö., Connolly, J., Hedley, C., de Vries, F., Gimona, A., Kempen, B., Kidd, D., Lilja, H., Malone, B., McBratney, A., Roudier, P., O'Rourke, S., Rudiyanto, Padarian, J., Poggio, L., ten Caten, A., Thompson, D., Tuve, C., Widyatmanti, W., 2019. Digital mapping of peatlands – A critical review. Earth-Science Rev. 196, 102870. https://doi.org/10.1016/j.earscirev.2019.05.014

Minayeva, T.Y., Sirin, A.A., 2012. Peatland biodiversity and climate change. Biol. Bull. Rev. 2, 164–175. https://doi.org/10.1134/s207908641202003x

Minibayeva, F., Beckett, R.P., 2001. High rates of extracellular superoxide production in bryophytes and lichens, and an oxidative burst in response to rehydration following desiccation. New Phytol. 152, 333–341. https://doi.org/10.1046/j.0028-646X.2001.00256.x

Mitchell, E.A.D., Gilbert, D., Buttler, A., Amblard, C., Grosvernier, P., Gobat, J.-M., 2003. Structure of microbial communities in Sphagnum peatlands and effect of atmospheric carbon dioxide enrichment. Microb. Ecol. 46, 187–199. https://doi.org/10.1007/BF03036882

Mithöfer, A., Boland, W., 2012. Plant defense against herbivores: Chemical aspects. Annu. Rev. Plant Biol. 63, 431–450. https://doi.org/10.1146/annurev-arplant-042110-103854

Mommer, L., Cotton, T.E.A., Raaijmakers, J.M., Termorshuizen, A.J., van Ruijven, J., Hendriks, M., van Rijssel, S.Q., van de Mortel, J.E., van der Paauw, J.W., Schijlen, E.G.W.M., Smit-Tiekstra, A.E., Berendse, F., de Kroon, H., Dumbrell, A.J., 2018. Lost in diversity: the interactions between soil-borne fungi, biodiversity and plant productivity. New Phytol. 218, 542–553. https://doi.org/10.1111/nph.15036

Moor, H., Hylander, K., Norberg, J., 2015. Predicting climate change effects on wetland ecosystem services using species distribution modeling and plant functional traits. Ambio 44, 113–126. https://doi.org/10.1007/s13280-014-0593-9

Moore, P.D., 1991. Ups and downs in peatland. Nature 353, 299–300. https://doi.org/10.1038/353299a0

Moore, T.R., Bubier, J.L., Frolking, S.E., Lafleur, P.M., Roulet, N.T., 2002. Plant biomass and production and CO2 exchange in an ombrotrophic bog. J. Ecol. 90, 25–36. https://doi.org/10.1046/j.0022-0477.2001.00633.x

Munir, T.M., Perkins, M., Kaing, E., Strack, M., 2015. Carbon dioxide flux and net primary production of a boreal treed bog: Responses to warming and water-table-lowering simulations of climate change. Biogeosciences 12, 1091–1111. https://doi.org/10.5194/bg-12-1091-2015

Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., Thuiller, W., 2012. How to measure and test phylogenetic signal. Methods Ecol. Evol. 3, 743–756. https://doi.org/10.1111/j.2041-210X.2012.00196.x

Murren, C.J., Maclean, H.J., Diamond, S.E., Steiner, U.K., Heskel, M.A., Handelsman, C.A., Ghalambor, C.K., Auld, J.R., Callahan, H.S., Pfennig, D.W., Relyea, R.A., Schlichting, C.D., Kingsolver, J., 2014. Evolutionary change in continuous reaction norms. Am. Nat. 183, 453–467. https://doi.org/10.1086/675302

Muscarella, R., Uriarte, M., 2016. Do community-weighted mean functional traits reflect optimal strategies? Proc. R. Soc. B Biol. Sci. 283. https://doi.org/10.1098/rspb.2015.2434

Naeem, S., Ali, M., Mahmood, A., 2012. Optimization of extraction conditions for the extraction of phenolic compounds from Moringa oleifera leaves. Pak. J. Pharm. Sci. 25, 535–541.

Nakabayashi, R., Yonekura-Sakakibara, K., Urano, K., Suzuki, M., Yamada, Y., Nishizawa, T., Matsuda, F., Kojima, M., Sakakibara, H., Shinozaki, K., Michael, A.J., Tohge, T., Yamazaki, M., Saito, K., 2014. Enhancement of oxidative and drought tolerance in Arabidopsis by overaccumulation of antioxidant flavonoids. Plant J. 77, 367–379. https://doi.org/10.1111/tpj.12388

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Nakano, Y., Asada, K., 1981. Hydrogen Peroxide is Scavenged by Ascorbate-specific Peroxidase in Spinach Chloroplasts. Plant Cell Physiol. 22, 867–880. https://doi.org/10.1093/oxfordjournals.pcp.a076232

National Wetlands Working Group, 1997. The canadian wetland classification system, 2nd ed, National Wetlands Working Group. University of Waterloo, Waterloo, Ontario.

Nichols, J.E., Peteet, D.M., 2019. Rapid expansion of northern peatlands and doubled estimate of carbon storage. Nat. Geosci. 12, 917–921. https://doi.org/10.1038/s41561-019-0454-z

Nijp, J.J., Limpens, J., Metselaar, K., van der Zee, S.E.A.T.M., Berendse, F., Robroek, B.J.M., 2014. Can frequent precipitation moderate the impact of drought on peatmoss carbon uptake in northern peatlands? New Phytol. 203, 70–80. https://doi.org/10.1111/nph.12792

Noctor, G., Reichheld, J.P., Foyer, C.H., 2018. ROS-related redox regulation and signaling in plants. Semin. Cell Dev. Biol. 80, 3–12. https://doi.org/10.1016/j.semcdb.2017.07.013

Norby, R.J., Childs, J., Hanson, P.J., Warren, J.M., 2019. Rapid loss of an ecosystem engineer: Sphagnum decline in an experimentally warmed bog. Ecol. Evol. 1–15. https://doi.org/10.1002/ece3.5722

Nungesser, M.K., 2003. Modelling microtopography in boreal peatlands: Hummocks and hollows. Ecol. Modell. 165, 175–207. https://doi.org/10.1016/S0304-3800(03)00067-X

O'Donnell, M.S., Ignizio, D.A., 2012. Bioclimatic Predictors for Supporting Ecological Applications in the Conterminous United States. U.S Geol. Surv. Data Ser. 691 10.

Obata, T., Fernie, A.R., 2012. The use of metabolomics to dissect plant responses to abiotic stresses. Cell. Mol. Life Sci. 69, 3225–3243. https://doi.org/10.1007/s00018-012-1091-5

Oke, T.A., Turetsky, M.R., Weston, D.J., Shaw, J.A., 2020. Tradeoffs between phenotypic plasticity and local adaptation influence the ecophysiology of the moss, Sphagnum magellanicum. Oecologia 193, 867–877. https://doi.org/10.1007/s00442-020-04735-4

Oksanen, A.J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P.R., Hara, R.B.O., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., 2019. Vegan. Encycl. Food Agric. Ethics 2395–2396. https://doi.org/10.1007/978-94-024-1179-9_301576

Okumoto, S., Anjum, N.A., Signorelli, S., Kishor, P.B.K., Kavi Kishor, P.B., Kumari, P.H., Sunita, L., Sreenivasulu, N., 2015. Role of proline in cell wall synthesis and plant development and its implications in plant ontogeny. https://doi.org/10.3389/fpls.2015.00544

Opelt, K., Berg, C., Schönmann, S., Eberl, L., Berg, G., 2007a. High specificity but contrasting biodiversity of Sphagnum-associated bacterial and plant communities in bog ecosystems independent of the geographical region. ISME J. 1, 502–516. https://doi.org/10.1038/ismej.2007.58

Opelt, K., Chobot, V., Hadacek, F., Schönmann, S., Eberl, L., Berg, G., 2007b. Investigations of the structure and function of bacterial communities associated with Sphagnum mosses. Environ. Microbiol. 9, 2795–2809. https://doi.org/10.1111/j.1462-2920.2007.01391.x

Opelt, K., Chobot, V., Hadacek, F., Schönmann, S., Eberl, L., Berg, G., 2007c. Investigations of the structure and function of bacterial communities associated with Sphagnum mosses. Environ. Microbiol. 9, 2795–2809. https://doi.org/10.1111/j.1462-2920.2007.01391.x

Opelt, K., Chobot, V., Hadacek, F., Schönmann, S., Eberl, L., Berg, G., 2007d. Investigations of the astructure and function of bacterial communities associated with Sphagnum mosses. Environ. Microbiol. 9, 2795–2809. https://doi.org/10.1111/j.1462-2920.2007.01391.x

Ordoñez, J.C., Van Bodegom, P.M., Witte, J.P.M., Wright, I.J., Reich, P.B., Aerts, R., 2009. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. Glob. Ecol. Biogeogr. 18, 137–149. https://doi.org/10.1111/j.1466-8238.2008.00441.x

Page, S.E., Baird, A.J., 2016. Peatlands and Global Change: Response and Resilience. Annu. Rev. Environ. Resour. 41, 35–57. https://doi.org/10.1146/annurev-environ-110615-085520

Painter, T.J., 1991. Lindow man, tollund man and other peat-bog bodies: The preservative and antimicrobial action of Sphagnan, a reactive glycuronoglycan with tanning and sequestering properties. Carbohydr. Polym. 15, 123–142. https://doi.org/10.1016/0144-8617(91)90028-B

Painter, T.J., 1983. Carbohydrate origin of aquatic humus from peat. Carbohydr. Res. 124, 22–26. https://doi.org/10.1016/0008-6215(83)88374-8

Painter, T.J., Shrensen, N.A., 1978. The cationexchanger of Sphagnum mosses: an unusual form of holocellulose. Carbohydr. Res. 66, 20–22.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change. Nature 421, 37–42.

Peñuelas, J., Sardans, J., 2009. Ecological metabolomics. Josep Peñuelas & Jordi Sardans 25, 305–309. https://doi.org/10.1080/02757540903062517

Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variation partitioning of species data matrices: Estimation and comparison of fractions. Ecology 87, 2614–2625. https://doi.org/10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2

Peters, K., Gorzolka, K., Bruelheide, H., Neumann, S., 2018. Seasonal variation of secondary metabolites in nine different bryophytes. Ecol. Evol. 8, 9105–9117. https://doi.org/10.1002/ece3.4361

Peters, K., Treutler, H., Döll, S., Kindt, A.S.D., Hankemeier, T., Neumann, S., 2019. Chemical diversity and classification of secondary metabolites in nine bryophyte species. Metabolites 9. https://doi.org/10.3390/metabo9100222

Pew, J.C., 1948. Structural Aspects of the Color Reaction of Lignin with Phenols. J. Am. Chem. Soc. 73, 1678–1685.

Piatkowski, B.T., Shaw, A.J., 2019. Functional trait evolution in Sphagnum peat mosses and its relationship to niche construction. New Phytol. 223, 939–949. https://doi.org/10.1111/nph.15825

Pichersky, E., Lewinsohn, E., 2011. Convergent evolution in plant specialized metabolism. Annu. Rev. Plant Biol. 62, 549–566. https://doi.org/10.1146/annurev-arplant-042110-103814

Pigliucci, M., 2001. Phenotypic Plasticity: Beyond Nature and Nurture. The Johns Hopkins University Press, Baltimore, Maryland.

Pinheiro, J.C., Bates, D.M., 2000. Mixed-Effects Models in S and S-PLUS. Springer.

Pinton, R., Varanini, Z., Paolo, N., 2001. The rhizosphere: biochemistry and organic substances at the soil–plant interface. Marcel Dekker, Inc., New York.

Plas, F. Van Der, Schröder-georgi, T., Weigelt, A., Barry, K., Meyer, S., Alzate, A., Barnard, R.L., Buchmann, N., Kroon, H. De, Ebeling, A., Eisenhauer, N., Engels, C., Fischer, M., Gleixner, G., 2020. Properties and Long-Term Ecosystem Functioning. Nat. Ecol. Evol. https://doi.org/10.1038/s41559-020-01316-9

Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O, R.B., Parris, K.M., Vesk, P.A., McCarthy, M.A., 2014. Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). https://doi.org/10.1111/2041-210X.12180

Porra, R.J., Thompson, W.., Kriedemann, P.E., 1989. Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophylls a and b extracted with four different solvents: verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. Biochim. Biophys. Acta - Bioenerg. 975, 384–394. https://doi.org/10.1016/S0005-2728(89)80347-0

Pourrut, B., 2008. Implication du stress oxydatif dans la toxicité du plomb sur une plante modèle, Vicia faba 284.

Prasad, K.N., Hassan, F.A., Yang, B., Kong, K.W., Ramanan, R.N., Azlan, A., Ismail, A., 2011. Response surface optimisation for the extraction of phenolic compounds and antioxidant capacities of underutilised Mangifera pajang Kosterm. peels. Food Chem. 128, 1121–1127. https://doi.org/10.1016/j.foodchem.2011.03.105

Price, M.L., Scoyoc, S. Van, Butler, L.G., 1978. A Critical Evaluation of the Vanillin Reaction as an Assay for Tannin in Sorghum Grain. J. Agric. Food Chem. 26, 1214–1218. https://doi.org/10.1021/jf60219a031

Proctor, M.C.F., 1990. The physiological basis of bryophyte production. Bot. J. Linn. Soc. 104, 61–77. https://doi.org/10.1111/j.1095-8339.1990.tb02211.x

Putkinen, A., Larmola, T., Tuomivirta, T., Siljanen, H.M.P., Bodrossy, L., Tuittila, E.S., Fritze, H., 2012. Water dispersal of methanotrophic bacteria maintains functional methane oxidation in Sphagnum mosses. Front. Microbiol. 3, 1–10. https://doi.org/10.3389/fmicb.2012.00015

R Core Team, 2019. R: A language and environment for statistical computing.

Radu, D.D., Duval, T.P., 2018. Precipitation frequency alters peatland ecosystem structure and CO2 exchange: Contrasting effects on moss, sedge, and shrub communities. Glob. Chang. Biol. 24, 2051–2065. https://doi.org/10.1111/gcb.14057

Raghoebarsing, A.A., Smolders, A.J.P., Schmid, M.C., Rijpstra, W.I.C., Wolters-Arts, M., Derksen, J., Jetten, M.S.M., Schouten, S., Damsté, J.S.S., Lamers, L.P.M., Roelofs, J.G.M., Op Den Camp, H.J.M., Strous, M., 2005. Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. Nature 436, 1153–1156. https://doi.org/10.1038/nature03802

Ramawat, K.G., Dass, S., Mathur, M., 2009. The Chemical Diversity of Bioactive Molecules and Therapeutic Potential of Medicinal Plants, in: Herbal Drugs: Ethnomedicine to Modern Medicine. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 7–32. https://doi.org/10.1007/978-3-540-79116-4_2

Rasmussen, S., Peters, G., Rudolph, H., 1995a. Regulation of phenylpropanoid metabolism by exogenous precursors in axenic cultures of Sphagnum fallax. Physiol. Plant. 95, 83–90. https://doi.org/10.1111/j.1399-3054.1995.tb00812.x

Rasmussen, S., Wolff, C., Rudolph, H., 1995b. Compartmentalization of phenolic constituents in sphagnum. Phytochemistry 38, 35–39. https://doi.org/10.1016/0031-9422(94)00650-I

Rastogi, A., Antala, M., Gąbka, M., Rosadziński, S., Stróżecki, M., Brestic, M., Juszczak, R., 2020. Impact of warming and reduced precipitation on morphology and chlorophyll concentration in peat mosses (Sphagnum angustifolium and S . fallax). Sci. Rep. 1–9. https://doi.org/10.1038/s41598-020-65032-x

Ratcliffe, J.L., Peng, H., Nijp, J.J., Nilsson, M.B., 2021. Lateral expansion of northern peatlands calls into question a 1,055 GtC estimate of carbon storage. Nat. Geosci. 14, 468–469. https://doi.org/10.1038/s41561-021-00770-9

Reczuga, M.K., Lamentowicz, M., Mulot, M., Mitchell, E.A.D., Buttler, A., Chojnicki, B., Słowiński, M., Binet, P., Chiapusio, G., Gilbert, D., Słowińska, S., Jassey, V.E.J., 2018a. Predator–prey mass ratio drives microbial activity under dry conditions in Sphagnum peatlands. Ecol. Evol. 8, 5752–5764. https://doi.org/10.1002/ece3.4114

Reczuga, M.K., Lamentowicz, M., Mulot, M., Mitchell, E.A.D., Buttler, A., Chojnicki, B., Słowiński, M., Binet, P., Chiapusio, G., Gilbert, D., Słowińska, S., Jassey, V.E.J., 2018b. Predator–prey mass ratio drives microbial activity under dry conditions in Sphagnum peatlands. Ecol. Evol. 8, 5752–5764. https://doi.org/10.1002/ece3.4114

Reich, P.B., Wright, I.J., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M., Walters, M.B., 2003. The Evolution of Plant Functional Variation: Traits, Spectra, and Strategies. Int. J. Plant Sci. 164, S143–S164. https://doi.org/10.1086/374368

Renato, G., 1995. Community and species-performance patterns along an alpine poor-rich mire gradient 175–182.

Rice, S.K., 2009. Mosses (Bryophytes), in: Encyclopedia of Inland Waters. Elsevier, pp. 88–96. https://doi.org/10.1016/B978-012370626-3.00219-2

Rice, S.K., Aclander, L., Hanson, D.T., 2008. Do bryophyte shoot systems function like vascular plant leaves or canopies? Functional trait relationships in Sphagnum mosses (Sphagnaceae). Am. J. Bot. 95, 1366–1374. https://doi.org/10.3732/ajb.0800019

Rice, S.K., Giles, L., 1996. The influence of water content and leaf anatomy on carbon isotope discrimination and photosynthesis in Sphagnum. Plant, Cell Environ. 19, 118–124. https://doi.org/10.1111/j.1365-3040.1996.tb00233.x

Rice, S.K., Schneider, N., 2004. Cushion Size , Surface Roughness , and the Control of Water Balance and Carbon Flux in the Cushion Moss Leucobryum glaucum (Leucobryaceae). Am. J. Bot. 91, 1164–1172.

Rishmawi, K., Prince, S.D., Xue, Y., 2016. Vegetation responses to climate variability in the northern arid to sub-humid zones of sub-Saharan Africa. Remote Sens. 8. https://doi.org/10.3390/rs8110910

Ritchie, R.J., 2006. Consistent sets of spectrophotometric chlorophyll equations for acetone, methanol and ethanol solvents. Photosynth. Res. 89, 27–41. https://doi.org/10.1007/s11120-006-9065-9

Roberts, A.W., Roberts, E.M., Haigler, C.H., 2012. Moss cell walls: structure and biosynthesis. Front. Plant Sci. 3, 1–7. https://doi.org/10.3389/fpls.2012.00166

Robroek, Bjorn J M, Jassey, V.E.J., Hefting, M.M., 2017. Diverse fen plant communities enhance multifunctionality , but do not mitigate negative effects of drought. R. Soc. open Sci. 4, 1–11. https://doi.org/http://dx.doi.org/10.1098/rsos.170449

Robroek, B.J.M., Jassey, V.E.J., Kox, M.A.R., Berendsen, R.L., Mills, R.T.E., Cécillon, L., Puissant, J., Meima-Franke, M., Bakker, P.A.H.M., Bodelier, P.L.E., 2015. Peatland vascular plant functional types affect methane dynamics by altering microbial community structure. J. Ecol. 103, 925–934. https://doi.org/10.1111/1365-2745.12413

Robroek, Bjorn J.M., Jassey, V.E.J., Payne, R.J., Martí, M., Bragazza, L., Bleeker, A., Buttler, A., Caporn, S.J.M., Dise, N.B., Kattge, J., Zajac, K., Svensson, B.H., Van Ruijven, J., Verhoeven, J.T.A., 2017. Taxonomic and functional turnover are decoupled in European peat bogs. Nat. Commun. 8. https://doi.org/10.1038/s41467-017-01350-5

Robroek, B.J.M., Limpens, J., Breeuwer, A., Schouten, M.G.C., 2007. Effects of water level and

temperature on performance of four Sphagnum mosses. Plant Ecol. 190, 97–107. https://doi.org/10.1007/s11258-006-9193-5

Robroek, B.J.M., Martí, M., Svensson, B.H., Dumont, M.G., Veraart, A.J., Jassey, V.E.J., 2021. Rewiring of peatland plant–microbe networks outpaces species turnover. Oikos 130, 339–353. https://doi.org/10.1111/oik.07635

Robroek, B.J.M., Schouten, M.G.C., Limpens, J., Berendse, F., Poorter, H., 2009. Interactive effects of water table and precipitation on net CO2 assimilation of three co-occurring Sphagnum mosses differing in distribution above the water table. Glob. Chang. Biol. 15, 680–691. https://doi.org/10.1111/j.1365-2486.2008.01724.x

Rohmer, M., 1999. The discovery of a mevalonate-independent pathway for isoprenoid biosynthesis in bacteria, algae and higher plants. Nat. Prod. Rep. 16, 565–574. https://doi.org/10.1039/a709175c

Rosseel, Y., 2012. lavaan : An R Package for Structural Equation Modeling. J. Stat. Softw. 48. https://doi.org/10.18637/jss.v048.i02

Roulet, N., Moore, T., Bubier, J., Lafleur, P., 1992. Northern fens: methane flux and climatic change. Tellus B 44, 100–105. https://doi.org/10.1034/j.1600-0889.1992.t01-1-00002.x

Rousk, J., Bååth, E., 2011. Growth of saprotrophic fungi and bacteria in soil. FEMS Microbiol. Ecol. 78, 17–30. https://doi.org/10.1111/j.1574-6941.2011.01106.x

Rousk, K., Pedersen, P.A., Dyrnum, K., Michelsen, A., 2017. The interactive effects of temperature and moisture on nitrogen fixation in two temperate-arctic mosses. Theor. Exp. Plant Physiol. 29, 25–36. https://doi.org/10.1007/s40626-016-0079-1

Rudolph, H., Engmann, B., 1967. Neue Ergebnisse zur Konstitution des Sphagnols. Ber. Dtsch. Bot. Ges. 80, 114.

Rudolph, H., Samland, J., 1985. Occurrence and metabolism of sphagnum acid in the cell walls of bryophytes. Phytochemistry 24, 745–749. https://doi.org/10.1016/S0031-9422(00)84888-8

Ruppel, M., Väliranta, M., Virtanen, T., Korhola, A., 2013. Postglacial spatiotemporal peatland initiation and lateral expansion dynamics in North America and northern Europe. Holocene 23, 1596–1606. https://doi.org/10.1177/0959683613499053

Rydin, H., Jeglum, J.K., 2013. The Biology of Peatlands. Oxford University Press, United Kingdom Oxford.

Rydin, H., Jeglum, J.K., 2006. The biology of peatlands. Oxford University Press, United Kingdom Oxford.

Samanta, A., Das, G., Das, S., 2011. Roles of flavonoids in plants. Carbon N. Y. 100, 6.

Sanchez, D.H., Redestig, H., Krämer, U., Udvardi, M.K., Kopka, J., 2008. Metabolome-ionome-biomass interactions: What can we learn about salt stress by multiparallel phenotyping? Plant Signal. Behav. 3, 598–600. https://doi.org/10.4161/psb.3.8.6347

Sardans, J., Gargallo-Garriga, A., Urban, O., Klem, K., Walker, T.W.N., Holub, P., Janssens, I.A., Peñuelas, J., 2020. Ecometabolomics for a better understanding of plant responses and acclimation to abiotic factors linked to global change. Metabolites 10, 1–20. https://doi.org/10.3390/metabo10060239

Sarkar, S.K., Howarth, R.E., 1976. Specificity of the Vanillin Test for Flavanols. J. Agric. Food Chem. 24, 317–320. https://doi.org/10.1021/jf60204a041

Såstad, S.M., Flatberg, K.I., 1993. Leaf morphology of Sphagnum strictum in Norway, related to habitat characteristics. Lindbergia 18, 71–77. https://doi.org/10.2307/20149834

Såstad, S.M., Pedersen, B., Digre, K., 1999. Habitat-specific genetic effects on growth rate and

morphology across pH and water-level gradients within a population of the moss Sphagnum angustifolium (Sphagnaceae). Am. J. Bot. 86, 1687–1698. https://doi.org/10.2307/2656667

Scheffer, R.A., Van Logtestijn, R.S.P., Verhoeven, J.T.A., 2001. Decomposition of Carex and Sphagnum litter in two mesotrophic fens differing in dominant plant species. Oikos 92, 44–54. https://doi.org/10.1034/j.1600-0706.2001.920106.x

Schellekens, J., Bindler, R., Martínez-Cortizas, A., McClymont, E.L., Abbott, G.D., Biester, H., Pontevedra-Pombal, X., Buurman, P., 2015. Preferential degradation of polyphenols from Sphagnum – 4-Isopropenylphenol as a proxy for past hydrological conditions in Sphagnum-dominated peat. Geochim. Cosmochim. Acta 150, 74–89. https://doi.org/https://doi.org/10.1016/j.gca.2014.12.003

Schimel, J.P., Cates, R.G., Ruess, R., 1998. The Role of Balsam Poplar Secondary Chemicals in Controlling Soil Nutrient Dynamics through Succession in the Alaskan Taiga. Biogeochemistry 42, 221–234.

Schlesinger, W.H., Andrews, J.A., 2000. Soil respiration and the global carbon cycle. Biogeochemistry 48, 7–20. https://doi.org/10.1023/A:1006247623877

Schmidt-Stohn, G., 1977. Änderungen der plastidenpigmente bei Sphagnum magellanicumBrid. in abhängigkeit von standort, verfärbungsgrad und alter. Zeitschrift für Pflanzenphysiologie 81, 289–303. https://doi.org/10.1016/s0044-328x(77)80095-0

Schuman, M.C., Van Dam, N.M., Beran, F., Harpole, W.S., 2016. How does plant chemical diversity contribute to biodiversity at higher trophic levels? Curr. Opin. Insect Sci. 14, 46–55. https://doi.org/10.1016/j.cois.2016.01.003

Sedio, B.E., 2017. Recent breakthroughs in metabolomics promise to reveal the cryptic chemical traits that mediate plant community composition, character evolution and lineage diversification. New Phytol. 214, 952–958. https://doi.org/10.1111/nph.14438

Sedio, B.E., Echeverri, J.C.R., Boya, C.A., Wright, S.J., 2017. Sources of variation in foliar secondary chemistry in a tropical forest tree community. Ecology 98, 616–623. https://doi.org/10.1002/ecy.1689

Settharaksa, S., Madaka, F., Sueree, L., Kittiwisut, S., Sakunpak, A., Moton, C., Charoenchai, L., 2014. Effect of solvent types on phenolic, flavonoid contents and antioxidant activities of Syzygium gratum (wight) S.N. Int. J. Pharm. Pharm. Sci. 6, 114–116. https://doi.org/http://dx.doi.org/10.4314/njbas.v24i2.16

Sharma, V., Gupta, P., Priscilla, K., Sharankumar, Hangargi, B., Veershetty, A., Ramrao, D.P., Suresh, S., Narasanna, R., Naik, G.R., Kumar, A., Guo, B., Zhuang, W., Varshney, R.K., Pandey, M.K., Kumar, R., 2021. Metabolomics intervention towards better understanding of plant traits. Cells 10, 1–32. https://doi.org/10.3390/cells10020346

Shetler, G., Turetsky, M.R., Kane, E., Kasischke, E., 2008. Sphagnum mosses limit total carbon consumption during fire in Alaskan black spruce forests. Can. J. For. Res. 38, 2328–2336. https://doi.org/10.1139/X08-057

Silvola, J., Aaltomen, H., 1984. Water content and photosynthesis in the peat mosses Sphagnum fuscum and S . angustifolium. Ann. Bot. Fenn. 21, 1–6.

Simola, L.K., 1975. The Effect of Several Protein Amino Acids and Some Inorganic Nitrogen Sources on the Growth of Sphagnum nemoreum. Physiol. Plant. 35, 194–199. https://doi.org/10.1111/j.1399-3054.1975.tb03892.x

Singh, B.K., Bardgett, R.D., Smith, P., Reay, D.S., 2010. Microorganisms and climate change: Terrestrial feedbacks and mitigation options. Nat. Rev. Microbiol. 8, 779–790. https://doi.org/10.1038/nrmicro2439

Singh, B.K., Dawson, L.A., Macdonald, C.A., Buckland, S.M., 2009. Impact of biotic and abiotic

interaction on soil microbial communities and functions: A field study. Appl. Soil Ecol. 41, 239–248. https://doi.org/10.1016/j.apsoil.2008.10.003

Singleton, V.L., Orthofer, R., Lamuela-Raventós, R.M., 1999. [14] Analysis of total phenols and other oxidation substrates and antioxidants by means of folin-ciocalteu reagent, in: Scientia Horticulturae. pp. 152–178. https://doi.org/10.1016/S0076-6879(99)99017-1

Singleton, V.L., Rossi, J.A., 1965. Colorimetry of Total Phenolics with Phosphomolybdic-Phosphotungstic Acid Reagents. Am. J. Enol. Vitic. 16, 144 LP – 158.

Skoneczny, D., Weston, P.A., Weston, L.A., 2018. Metabolomics and Metabolic Profiling: Investigation of Dynamic Plant-Environment Interactions at the Functional Level, in: Sánchez-Moreiras, A.M., Reigosa, M.J. (Eds.), Advances in Plant Ecophysiology Techniques. Springer International Publishing, Cham, pp. 323–345. https://doi.org/10.1007/978-3-319-93233-0_20

Skre, O., Oechel, W.C., Miller, P.M., 1983. Patterns of translocation of carbon in four common moss species in a black spruce (Picea mariana) dominated forest in interior Alaska. Can. J. For. Res. 13, 869–878. https://doi.org/10.1139/x83-117

Sonesson, M., Carlsson, B.Å., Callaghan, T. V., Halling, S., Björn, L.O., Bertgren, M., Johanson, U., 2002. Growth of two peat-forming mosses in subarctic mires: Species interactions and effects of simulated climate change. Oikos 99, 151–160. https://doi.org/10.1034/j.1600-0706.2002.990115.x

Song, L., Gilbert, D., Wu, D., 2016. Vertical micro-distribution of microbial communities living in Sphagnum fallax. Aquat. Microb. Ecol. 77, 1–10. https://doi.org/10.3354/ame01783

Soudzilovskaia, N.A., Cornelissen, J.H.C., During, H.J., Van Logtestun, R.S.P., Lang, S.I., Aerts, R., 2010. Similar cation exchange capacities among bryophyte species refute a presumed mechanism of peatland acidification. Ecology 91, 2716–2726. https://doi.org/10.1890/09-2095.1

Spatt, P.D., Miller, M.C., 1981. Growth Conditions and Vitality of *Sphagnum* in a Tundra Community Along the Alaska Pipeline Haul Road. Arctic 34, 48–54. https://doi.org/10.14430/arctic2503

Spigno, G., Tramelli, L., De Faveri, D.M., 2007. Effects of extraction time, temperature and solvent on concentration and antioxidant activity of grape marc phenolics. J. Food Eng. 81, 200–208. https://doi.org/10.1016/j.jfoodeng.2006.10.021

St. Martin, P., Mallik, A.U., 2017. The status of non-vascular plants in trait-based ecosystem function studies. Perspect. Plant Ecol. Evol. Syst. 27, 1–8. https://doi.org/10.1016/j.ppees.2017.04.002

Stalheim, T., Ballance, S., Christensen, B.E., Granum, P.E., 2009. Sphagnan - A pectin-like polymer isolated from Sphagnum moss can inhibit the growth of some typical food spoilage and food poisoning bacteria by lowering the pH. J. Appl. Microbiol. 106, 967–976. https://doi.org/10.1111/j.1365-2672.2008.04057.x

Stephanopoulos, G.N., Aristidou, A.A., Nielsen, J., 1998. Review of Cellular Metabolism. Metab. Eng. 21–79. https://doi.org/10.1016/b978-012666260-3/50003-0

Stępniewska, Z., Goraj, W., Kuźniar, A., Szafranek-Nakonieczna, A., Banach, A., Górski, A., Pytlak, A., Urban, D., 2018. Methane Oxidation by Endophytic Bacteria Inhabiting Sphagnum sp. and Some Vascular Plants. Wetlands 38, 411–422. https://doi.org/10.1007/s13157-017-0984-3

Stevenson, T.J., Visser, M.E., Arnold, W., Barrett, P., Biello, S., Dawson, A., Denlinger, D.L., Dominoni, D., Ebling, F.J., Elton, S., Evans, N., Ferguson, H.M., Foster, R.G., Hau, M., Haydon, D.T., Hazlerigg, D.G., Heideman, P., Hopcraft, J.G.C., Jonsson, N.N., Kronfeld-Schor, N., Kumar, V., Lincoln, G.A., Macleod, R., Martin, S.A.M., Martinez-Bakker, M., Nelson, R.J., Reed, T., Robinson, J.E., Rock, D., Schwartz, W.J., Steffan-Dewenter, I., Tauber, E., Thackeray, S.J., Umstatter, C., Yoshimura, T., Helm, B., 2015. Disrupted seasonal biology impacts health, food security and ecosystems. Proc. R. Soc. B Biol. Sci. 282. https://doi.org/10.1098/rspb.2015.1453

Stitt, M., Lunn, J., Usadel, B., 2010. Arabidopsis and primary photosynthetic metabolism - More than

the icing on the cake. Plant J. 61, 1067–1091. https://doi.org/10.1111/j.1365-313X.2010.04142.x

Stolter, C., Niemela, P., Ball, J.P., Julkunen-tiitto, R., Ganzhorn, U., 2009. Comparison of plant secondary metabolites and digestibility of three different boreal coniferous trees 10, 19–26. https://doi.org/10.1016/j.baae.2007.12.001

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Díaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T., Navas, M.L., 2008. Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. Glob. Chang. Biol. 14, 1125–1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x

Sulpice, R., McKeown, P.C., 2015. Moving toward a comprehensive map of central plant metabolism. Annu. Rev. Plant Biol. 66, 187–210. https://doi.org/10.1146/annurev-arplant-043014-114720

Sultan, S., 2001. Phenotypic plasticity for fitness components in Polygonum species of contrasting ecological breadth. Ecology 82, 328.

Sultan, S.E., 2000. Phenotypic plasticity for plant development, function and life history. Trends Plant Sci. 5, 537–542. https://doi.org/10.1016/S1360-1385(00)01797-0

Sultan, S.E., 1987. Evolutionary Implications of Phenotypic Plasticity in Plants, in: Hecht, M.K., Wallace, B., Prance, G.T. (Eds.), Evolutionary Biology: Volume 21. Springer US, Boston, MA, pp. 127–178. https://doi.org/10.1007/978-1-4615-6986-2_7

Sunil, B., Talla, S.K., Aswani, V., Raghavendra, A.S., 2013. Optimization of photosynthesis by multiple metabolic pathways involving interorganelle interactions: Resource sharing and ROS maintenance as the bases. Photosynth. Res. 117, 61–71. https://doi.org/10.1007/s11120-013-9889-z

Sweeney, C.J., de Vries, F.T., van Dongen, B.E., Bardgett, R.D., 2020. Root traits explain rhizosphere fungal community composition among temperate grassland plant species. New Phytol. 53, nph.16976. https://doi.org/10.1111/nph.16976

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

Sytiuk, A., Céréghino, R., Hamard, S., Delarue, F., Dorrepaal, E., Küttim, M., Lamentowicz, M., Pourrut, B., Robroek, B.J.M., Tuittila, E.-S., Jassey, V.E.J., 2022. Biochemical traits enhance the trait concept in Sphagnum ecology. Oikos e09119, 1–15. https://doi.org/10.1111/oik.09119

Sytiuk, A., Céréghino, R., Hamard, S., Delarue, F., Guittet, A., Barel, J.M., Dorrepaal, E., Küttim, M., Lamentowicz, M., Pourrut, B., Robroek, B.J.M., Tuittila, E., Jassey, V.E.J., 2021. Predicting the structure and functions of peatland microbial communities from Sphagnum phylogeny, anatomical and morphological traits and metabolites. J. Ecol. 1365-2745.13728. https://doi.org/10.1111/1365-2745.13728

Sytiuk, A., Cereghino, R., Hamard, S., Delarue, F.F., Dorrepaal, E., Kuttim, M., Lamentowicz, M., Pourrut, B., Robroek, B.J.M., Tuittila, E.-S., Jassey, V.E.J., Céréghino, R., Hamard, S., Delarue, F.F., Dorrepaal, E., Lamentowicz, M., Pourrut, B., Robroek, B.J.M., Tuittila, E.-S., Jassey, V.E.J., 2020. Morphological and biochemical responses of Sphagnum mosses to environmental changes. bioRxiv 2020.10.29.360388. https://doi.org/10.1101/2020.10.29.360388

Tan, B.C., Pócs, T., 2000. Bryogeography and conservation of bryophytes, in: Shaw, J.A., Goffinet, B. (Eds.), Bryophyte Biology. Cambridge University Press, pp. 403–448.

https://doi.org/10.1017/CBO9781139171304.014

Tetemadze, N., Bakuridze, A., Jokhadze, M., Machutadze, I., 2018. Peculiarities of the composition of acids in Sphagnum species of the percolation bog of the Kolkheti lowland. Ann. Agrar. Sci. 16, 222–225. https://doi.org/10.1016/j.aasci.2018.04.012

Thakur, S., Kapila, S., 2017. Seasonal changes in antioxidant enzymes, polyphenol oxidase enzyme, flavonoids and phenolic content in three leafy liverworts. Lindbergia 40, 39–44. https://doi.org/10.25227/linbg.01076

Tian, J., Branfireun, B.A., Lindo, Z., 2020. Global change alters peatland carbon cycling through plant biomass allocation. Plant Soil 455, 53–64. https://doi.org/10.1007/s11104-020-04664-4

Tissier, A., Ziegler, J., Vogt, T., 2014. Specialized Plant Metabolites: Diversity and Biosynthesis, in: Krauss, G.-J., Nies, D.H. (Eds.), Ecological Biochemistry. Wiley-VCH Verlag GmbH & Co. KGaA, Weinheim, Germany, pp. 14–37. https://doi.org/10.1002/9783527686063.ch2

Titus, J.E., Wagner, D.J., 1984. Carbon Balance for Two Sphagnum Mosses: Water Balance Resolves a Physiological Paradox. Ecology 65, 1765–1774. https://doi.org/10.2307/1937772

Toftegaard, T., Posledovich, D., Navarro-Cano, J.A., Wiklund, C., Gotthard, K., Ehrlén, J., 2016. Variation in plant thermal reaction norms along a latitudinal gradient - more than adaptation to season length. Oikos 125, 622–628. https://doi.org/10.1111/oik.02323

Trease, G.E., Evans, W.C., 2009. Trease and Evans' Pharmacognosy : 16th Edition.

Tsuneda, A., Thormann, M.N., Currah, R.S., 2001. Modes of cell-wall degradation of Sphagnum fuscum by Acremonium cf. curvulum and Oidiodendron maius. Can. J. Bot. 79, 93–100. https://doi.org/10.1139/cjb-79-1-93

Turetsky, M.R., 2003. New Frontiers in Bryology and Lichenology The Role of Bryophytes in Carbon and Nitrogen Cycling. Bryologist 106, 395–409. https://doi.org/10.1016/S1364-8152(03)00155-5

Turetsky, M.R., Crow, S.E., Evans, R.J., Vitt, D.H., Wieder, R.K., 2008. Trade-offs in resource allocation among moss species control decomposition in boreal peatlands. J. Ecol. 96, 1297–1305. https://doi.org/10.1111/j.1365-2745.2008.01438.x

Turner, M.F., Heuberger, A.L., Kirkwood, J.S., Collins, C.C., Wolfrum, E.J., Broeckling, C.D., Prenni, J.E., Jahn, C.E., 2016. Non-targeted metabolomics in diverse sorghum breeding lines indicates primary and secondary metabolite profiles are associated with plant biomass accumulation and photosynthesis. Front. Plant Sci. 7. https://doi.org/10.3389/fpls.2016.00953

Tutschek, R., 1982. An evaluation of phenylpropanoid metabolism during cold-induced sphagnorubin synthesis in Sphagnum magellanicum BRID. Planta 155, 301–306.

Tveit, A.T., Kiss, A., Winkel, M., Horn, F., Hájek, T., Svenning, M.M., Wagner, D., Liebner, S., 2020. Environmental patterns of brown moss- and Sphagnum-associated microbial communities. Sci. Rep. 10, 1–17. https://doi.org/10.1038/s41598-020-79773-2

Urbanová, Z., Bárta, J., 2016. Effects of long-term drainage on microbial community composition vary between peatland types. Soil Biol. Biochem. 92, 16–26. https://doi.org/10.1016/j.soilbio.2015.09.017

Valladares, F., Sanchez-Gomez, D., Zavala, M.A., 2006. Quantitative estimation of phenotypic plasticity: Bridging the gap between the evolutionary concept and its ecological applications. J. Ecol. 94, 1103–1116. https://doi.org/10.1111/j.1365-2745.2006.01176.x

Valladares, F., Wright, S.J., Lasso, E., Kitajima, K., Pearcy, R.W., 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. Ecology 81, 1925–1936. https://doi.org/https://doi.org/10.1890/0012-9658(2000)081[1925:PPRTLO]2.0.CO;2

van Breemen, N., 1995. How Sphagnum bogs down other plants. Trends Ecol. Evol. 10, 270–275. https://doi.org/10.1016/0169-5347(95)90007-1

van Dam, N.M., Bouwmeester, H.J., 2016. Metabolomics in the Rhizosphere: Tapping into Belowground Chemical Communication. Trends Plant Sci. 21, 256–265. https://doi.org/10.1016/j.tplants.2016.01.008

Van Den Elzen, E., Bengtsson, F., Fritz, C., Rydin, H., Lamers, L.P.M., 2020. Variation in symbiotic N2 fixation rates among Sphagnum mosses. PLoS One 15, 1–14. https://doi.org/10.1371/journal.pone.0228383

Van der Heijden, E., 1994. A combined anatomical and pyrolysis mass spectrometric study of peatified plant tissues. University of Amsterdam.

Van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T., Kardol, P., Klironomos, J.N., Kulmatiski, A., Schweitzer, J.A., Suding, K.N., Van de Voorde, T.F.J., Wardle, D.A., 2013. Plant-soil feedbacks: The past, the present and future challenges. J. Ecol. 101, 265–276. https://doi.org/10.1111/1365-2745.12054

Veen, G.F. (Ciska), ten Hooven, F.C., Weser, C., Hannula, S.E., 2021. Steering the soil microbiome by repeated litter addition. J. Ecol. 9, 1365-2745.13662. https://doi.org/10.1111/1365-2745.13662

Verbruggen, N., Hermans, C., 2008. Proline accumulation in plants: A review. Amino Acids 35, 753–759. https://doi.org/10.1007/s00726-008-0061-6

Verhoeven, J.T.A., Liefveld, W.M., 1997. The ecological significance of organochemical compounds in Sphagnum. Acta Bot. Neerl. 46, 117–130. https://doi.org/10.1111/plb.1997.46.2.117

Verhoeven, J.T.A., Toth, E., 1995. Decomposition of Carex and Sphagnum litter in fens: Effect of litter quality and inhibition by living tissue homogenates. Soil Biol. Biochem. 27, 271–275. https://doi.org/10.1016/0038-0717(94)00183-2

Veteli, T.O., Mattson, W.J., Niemelä, P., Julkunen-Tiitto, R., Kellomäki, S., Kuokkanen, K., Lavola, A., 2007. Do elevated temperature and CO2 generally have counteracting effects on phenolic phytochemistry of boreal trees? J. Chem. Ecol. 33, 287–296. https://doi.org/10.1007/s10886-006-9235-4

Via, S., 1994. The Evolution of Phenotypic Plasticity: What Do We Really Know?, in: Real, L. (Ed.), Ecological Genetics. Princeton University Press, pp. 35–57. https://doi.org/10.1515/9781400887262-005

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaced framework in functional ecology. Ecology 89, 2290–2301. https://doi.org/10.1890/07-1206.1

Vinatoru, M., 2001. An overview of the ultrasonically assisted extraction of bioactive principles from herbs. Ultrason. Sonochem. 8, 303–313. https://doi.org/10.1016/S1350-4177(01)00071-2

Vinatoru, M., Toma, M., Radu, O., Filip, P.I., Lazurca, D., Mason, T.J., 1997. The use of ultrasound for the extraction of bioactive principles from plant materials. Ultrason. Sonochem. 4, 135–139. https://doi.org/10.1016/S1350-4177(97)83207-5

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V., Messier, J., 2012. The return of the variance: Intraspecific variability in community ecology. Trends Ecol. Evol. 27, 244–252. https://doi.org/10.1016/j.tree.2011.11.014

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116, 882–892. https://doi.org/10.1111/j.2007.0030-1299.15559.x

Visser, M.E., 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. Proc. R. Soc. B Biol. Sci. 275, 649–659. https://doi.org/10.1098/rspb.2007.0997

Visser, M.E., Both, C., 2005. Shifts in phenology due to global climate change: The need for a yardstick. Proc. R. Soc. B Biol. Sci. 272, 2561–2569. https://doi.org/10.1098/rspb.2005.3356

Vitt, D.H., 2008. Peatlands. Encycl. Ecol. Five-Volume Set 2656–2664. https://doi.org/10.1016/B978-008045405-4.00318-9

Vitt, D.H., 2000. Peatlands : ecosystems dominated by bryophytes.

von Rudolph, H., 1972. Identifikation der Czapek schen Sphagnolkristalle. Biochem. und Physiol. der Pflanz. 163, 110–112. https://doi.org/10.1016/s0015-3796(17)31207-6

Waddington, J.M., Warner, K.D., Kennedy, G.W., 2002. Cutover peatlands: A persistent source of atmospheric CO2. Global Biogeochem. Cycles 16, 1–7. https://doi.org/10.1029/2001gb001398

Walker, A.P., Carter, K.R., Gu, L., Hanson, P.J., Malhotra, A., Norby, R.J., Sebestyen, S.D., Wullschleger, S.D., Weston, D.J., 2017. Biophysical drivers of seasonal variability in Sphagnum gross primary production in a northern temperate bog. J. Geophys. Res. Biogeosciences 122, 1078–1097. https://doi.org/10.1002/2016JG003711

Walker, T.N., Garnett, M.H., Ward, S.E., Oakley, S., Bardgett, R.D., Ostle, N.J., 2016. Vascular plants promote ancient peatland carbon loss with climate warming. Glob. Chang. Biol. 22, 1880–1889. https://doi.org/10.1111/gcb.13213

Walker, T.W.N., Alexander, J.M., Allard, P., Baines, O., Baldy, V., Bardgett, R.D., Capdevila, P., Coley, P.D., David, B., Defossez, E., Endara, M., Ernst, M., Fernandez, C., Forrister, D., Gargallo-Garriga, A., Jassey, V.E.J., Marr, S., Neumann, S., Pellissier, L., Peñuelas, J., Peters, K., Rasmann, S., Roessner, U., Sardans, J., Schrodt, F., Schuman, M.C., Soule, A., Uthe, H., Weckwerth, W., Wolfender, J., Dam, N.M., Salguero-Gómez, R., 2022. Functional Traits 2.0: The power of the metabolome for ecology. J. Ecol. 110, 4–20. https://doi.org/10.1111/1365-2745.13826

Walker, T.W.N., Weckwerth, W., Bragazza, L., Fragner, L., Forde, B.G., Ostle, N.J., Signarbieux, C., Sun, X., Ward, S.E., Bardgett, R.D., 2019. Plastic and genetic responses of a common sedge to warming have contrasting effects on carbon cycle processes. Ecol. Lett. 22, 159–169. https://doi.org/10.1111/ele.13178

Wang, C., Michalet, R., Liu, Z., Jiang, X., Wang, X., Zhang, G., An, L., Chen, S., Xiao, S., 2020. Disentangling Large- and Small-Scale Abiotic and Biotic Factors Shaping Soil Microbial Communities in an Alpine Cushion Plant System. Front. Microbiol. 11, 1–17. https://doi.org/10.3389/fmicb.2020.00925

Wang, H., Richardson, C.J., Ho, M., 2015. Dual controls on carbon loss during drought in peatlands. Nat. Clim. Chang. 5, 584–587. https://doi.org/10.1038/nclimate2643

Wang, S., Alseekh, S., Fernie, A.R., Luo, J., 2019. The Structure and Function of Major Plant Metabolite Modifications. Mol. Plant 12, 899–919. https://doi.org/10.1016/j.molp.2019.06.001

Ward, S.E., Ostle, N.J., Oakley, S., Quirk, H., Henrys, P.A., Bardgett, R.D., 2013. Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation composition. Ecol. Lett. 16, 1285–1293. https://doi.org/10.1111/ele.12167

Wardle, D.A., Bardgett, R.D.R.D., Klironomos, J.N., Setala, H., van der Putten, W.H., Wall, D.H., Setälä, H., van der Putten, W.H., Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. Science (80-.). 304, 1629–1633. https://doi.org/10.1126/science.1094875

Weckwerth, W., 2011. Green systems biology - From single genomes, proteomes and metabolomes to ecosystems research and biotechnology. J. Proteomics 75, 284–305. https://doi.org/10.1016/j.jprot.2011.07.010

Weckwerth, W., Kahl, G., 2013. The Handbook of Plant Metabolomics. Handb. Plant Metabolomics. https://doi.org/10.1002/9783527669882

Weltzin, J.F., Bridgham, S.D., Pastor, J., Chen, J., Harth, C., 2003. Potential effects of warming and drying on peatland plant community composition. Glob. Chang. Biol. 9, 141–151. https://doi.org/10.1046/j.1365-2486.2003.00571.x

Weltzin, J.F., Harth, C., Bridgham, S.D., Pastor, J., Vonderharr, M., 2001. Production and microtopography of bog bryophytes: Response to warming and water-table manipulations. Oecologia 128, 557–565. https://doi.org/10.1007/s004420100691

Weltzin, J.F., Pastor, J., Harth, C., Bridgham, S.D., Updegraff, K., Chapin, C.T., 2000. Response of bog and fen plant communities to warming and water-table manipulations. Ecology 81, 3464–3478. https://doi.org/https://doi.org/10.1890/0012-9658(2000)081[3464:ROBAFP]2.0.CO;2

Weng, J.K., 2014. The evolutionary paths towards complexity: A metabolic perspective. New Phytol. 201, 1141–1149. https://doi.org/10.1111/nph.12416

Weng, J.K., Chapple, C., 2010. The origin and evolution of lignin biosynthesis. New Phytol. 187, 273–285. https://doi.org/10.1111/j.1469-8137.2010.03327.x

Weng, J.K., Lynch, J.H., Matos, J.O., Dudareva, N., 2021. Adaptive mechanisms of plant specialized metabolism connecting chemistry to function. Nat. Chem. Biol. 17, 1037–1045. https://doi.org/10.1038/s41589-021-00822-6

West-Eberhard, M.J., 2008. Phenotypic Plasticity. Encycl. Ecol. Five-Volume Set 2701–2707. https://doi.org/10.1016/B978-008045405-4.00837-5

Weston, D.J., Timm, C.M., Walker, A.P., Gu, L., Muchero, W., Schmutz, J., Shaw, A.J., Tuskan, G.A., Warren, J.M., Wullschleger, S.D., 2015. Sphagnum physiology in the context of changing climate: Emergent influences of genomics, modelling and host-microbiome interactions on understanding ecosystem function. Plant, Cell Environ. 38, 1737–1751. https://doi.org/10.1111/pce.12458

Weston, L.A., Skoneczny, D., Weston, P. a., Weidenhamer, J.D., 2015. Metabolic profiling: an overview - new approaches for the detection and functional analysis of biologically active secondary plant products. J. Allelochem. Interact. 1, 15–27.

Wheeler, B.D., Proctor, M.C.F., 2000. Ecological gradients, subdivisions and terminology of north-west European mires. J. Ecol. 88, 187–203. https://doi.org/10.1046/j.1365-2745.2000.00455.x

Whitehead, J., Wittemann, M., Cronberg, N., 2018. Allelopathy in bryophytes - A review. Lindbergia 41. https://doi.org/10.25227/linbg.01097

Whitham, T.G., Bailey, J.K., Schweitzer, J.A., Shuster, S.M., Bangert, R.K., Leroy, C.J., Lonsdorf, E. V., Allan, G.J., DiFazio, S.P., Potts, B.M., Fischer, D.G., Gehring, C.A., Lindroth, R.L., Marks, J.C., Hart, S.C., Wimp, G.M., Wooley, S.C., 2006. A framework for community and ecosystem genetics: From genes to ecosystems. Nat. Rev. Genet. 7, 510–523. https://doi.org/10.1038/nrg1877

Wilken, S., Huisman, J., Naus-Wiezer, S., Van Donk, E., 2013. Mixotrophic organisms become more heterotrophic with rising temperature. Ecol. Lett. 16, 225–233. https://doi.org/10.1111/ele.12033

Williams, T.G., Flanagan, L.B., 1998. Measuring and modelling environmental influences on photosynthetic gas exchange in Sphagnum and Pleurozium. Plant, Cell Environ. 21, 555–564. https://doi.org/10.1046/j.1365-3040.1998.00292.x

Wink, M., 2010. Introduction: Biochemistry, Physiology and Ecological Functions of Secondary Metabolites, in: M. Wink (Ed.), Biochemistry of Plant Secondary Metabolism. Wiley-Blackwell, Oxford, UK, pp. 1–19. https://doi.org/10.1002/9781444320503.ch1

Wink, M., 2003. Evolution of secondary metabolites from an ecological and molecular phylogenetic perspective. Phytochemistry 64, 3–19. https://doi.org/10.1016/S0031-9422(03)00300-5

Xie, C.F., Lou, H.X., 2009. Secondary metabolites in bryophytes: An ecological aspect. Chem. Biodivers. 6, 303–312. https://doi.org/10.1002/cbdv.200700450

Xu, J., Morris, P.J., Liu, J., Holden, J., 2018. Catena PEATMAP : Re fi ning estimates of global peatland distribution based on a 160, 134–140. https://doi.org/10.1016/j.catena.2017.09.010

Yan, Y., Yang, X., Tang, Z., 2013. Patterns of species diversity and phylogenetic structure of vascular plants on the Qinghai-Tibetan Plateau. Ecol. Evol. 3, 4584–4595. https://doi.org/10.1002/ece3.847

Yan, Z., Guo, Z., Serbin, S.P., Song, G., Zhao, Y., Chen, Y., Wu, S., Wang, J., Wang, X., Li, J., Wang, B., Wu, Y., Su, Y., Wang, H., Rogers, A., Liu, L., Wu, J., 2021. Spectroscopy outperforms leaf trait relationships for predicting photosynthetic capacity across different forest types. New Phytol. 232, 134–147. https://doi.org/10.1111/nph.17579

Yang, L., Wen, K.S., Ruan, X., Zhao, Y.X., Wei, F., Wang, Q., 2018. Response of plant secondary metabolites to environmental factors. Molecules 23, 1–26. https://doi.org/10.3390/molecules23040762

Yu, Z., Joos, F., Bauska, T.K., Stocker, B.D., Fischer, H., Loisel, J., Brovkin, V., Hugelius, G., Nehrbass-Ahles, C., Kleinen, T., Schmitt, J., 2021. No support for carbon storage of >1,000 GtC in northern peatlands. Nat. Geosci. 14, 465–467. https://doi.org/10.1038/s41561-021-00769-2

Yu, Z., Loisel, J., Brosseau, D.P., Beilman, D.W., Hunt, S.J., 2010. Global peatland dynamics since the Last Glacial Maximum. Geophys. Res. Lett. 37, 1–5. https://doi.org/10.1029/2010GL043584

Zak, D., Roth, C., Unger, V., Goldhammer, T., Fenner, N., Freeman, C., Jurasinski, G., 2019. Unraveling the Importance of Polyphenols for Microbial Carbon Mineralization in Rewetted Riparian Peatlands. Front. Environ. Sci. 7, 1–14. https://doi.org/10.3389/fenvs.2019.00147

Zhao, Y., Liu, C., Wang, S., Wang, Y., Liu, X., Luo, W., Feng, X., 2021. "Triple locks" on soil organic carbon exerted by sphagnum acid in wetlands. Geochim. Cosmochim. Acta 315, 24–37. https://doi.org/10.1016/j.gca.2021.09.028

Zhu, X., Nimmo, V., Wu, J., Thomas, R., 2019. Sphagnum outcompetes feathermosses in their photosynthetic adaptation to postharvest black spruce forests. Botany 97, 585–597. https://doi.org/10.1139/cjb-2019-0076

Ziegler, J., Facchini, P.J., 2008. Alkaloid biosynthesis: Metabolism and trafficking. Annu. Rev. Plant Biol. 59, 735–769. https://doi.org/10.1146/annurev.arplant.59.032607.092730

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R, Journal of Statistical Software, Statistics for Biology and Health. Springer New York, New York, NY. https://doi.org/10.1007/978-0-387-87458-6

Résumé de vulgarisation

Les changements climatiques affectent gravement le fonctionnement des écosystèmes, notamment les tourbières qui jouent un rôle clé dans la dynamique du carbone mondiale en tant que puits de carbone. Les sphaignes jouent un rôle clé dans le fonctionnement des tourbières. Grâce à leurs caractéristiques morphologiques et biochimiques, elles jouent un rôle important dans la dynamique du carbone des tourbières et contribuent à l'accumulation de C à long terme. Certains composés chimiques produits par les sphaignes se sont révélés importants dans la capacité des tourbières à stocker du carbone. Cependant, l'effet du changement climatique sur ces composés reste largement inconnu. Ce travail de doctorat avait pour but d'étudier la réponse des composés chimiques produits par les sphaignes aux changements climatiques et de déterminer les conséquences de ces changements pour le cycle du carbone à travers les effets sur les microorganismes du sol et l'assimilation de carbone du système. Mes résultats améliorent notre capacité à prédire le devenir des communautés microbiennes du sol dans un contexte d'environnement changeant grâce à l'inclusion des composés chimiques dans les modèles prédictifs. De plus, mes résultats montrent que la réponse des composés chimiques de la sphaigne aux changements climatiques influence directement l'assimilation de carbone des tourbières, notamment au printemps et en automne. Cela suggère que les composés chimiques des sphaignes pourraient être utilisés comme des signaux indicateurs des changements climatiques à l'avenir.

Abstract for general auditory

Climate change is severely affecting the functioning of ecosystems, including peatlands that play a key role in global carbon dynamics as carbon sinks, where one third of soil organic carbon is locked belowground. *Sphagnum* mosses are ecosystem engineers that create and maintain boreal peatlands and contribute to long-term C accumulation. Certain metabolites produced by *Sphagnum* have been pointed out to be important in deterring decomposers or providing structural resistance to decay. The effect of climate change on *Sphagnum* metabolites *per se* remains largely unknown, as most of studies are concentrated on the effect of the climate change on vegetation communities and ecosystem functions. We used a reciprocal transplantation along a latitudinal gradient spanning five countries thus emulating shifts in climate conditions. Our results bring information about the *Sphagnum* trait functional space, relationships with microbes and dynamics of *Sphagnum* metabolites. Our results have important implications for understanding the plasticity of *Sphagnum* metabolites and how it will feedback to C assimilation in peatlands under climate warming.