Helmholtz-Zentrum Potsdam Deutsches GeoForschungsZentrum (GFZ)

Geomikrobiologie

Moss-associated bacterial and archaeal communities of northern peatlands: key taxa, environmental drivers and potential functions

Andrea Kiss

Dissertation zur Erlangung des akademischen Grades „doctor rerum naturalium"
(Dr. rer. nat.) in der Wissenschaftsdisziplin „Mikrobiologie"

Vorgelegt an der
Mathematisch-Naturwissenschaftlichen Fakultät der Universität Potsdam

Eingereicht: 29.06.2023
Datum der Disputation: 18.03.2024

Erstbetreuerin: Prof. Dr. Susanne Liebner

Zweitbetreuer: Prof. Dr. Dirk Wagner

Gutachter:innen: Prof. Dr. Susanne Liebner, Prof. Dr. Ulrike Herzschuh, Prof. Dr. Steffen Kolb

The picture on the front cover was taken during the field campaign on Svalbard 2014, showing the pond Gluudneset with dense carpets of thriving brown mosses.

Published online on the
Publication Server of the University of Potsdam:
https://doi.org/10.25932/publishup-63064
https://nbn-resolving.org/urn:nbn:de:kobv:517-opus4-630641

Selbstständigkeitserklärung

Hiermit erkläre ich, Andrea Kiss, dass ich diese Arbeit bisher nicht an der Mathematisch-Naturwissenschaftlichen Fakultät der Universität Potsdam oder an einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion eingereicht habe. Ich erkläre weiterhin, dass ich diese Arbeit selbstständig verfasst und nur die in dieser Arbeit angegebenen Quellen und Hilfsmittel verwendet habe.

Statement of authorship

I, Andrea Kiss, hereby declare that I did not previously submit this thesis to the Faculty of Mathematics and Natural Science at the University of Potsdam or to any other scientific institution. I further state that I wrote this thesis on my own by using only the sources and aids named in this work.

Rathenow, June 2023

Preface

The following study focuses on key prokaryotic taxa that are associated with peatland bryophytes, their environmental drivers and their possible ecological functions.

This thesis was embedded into the *ArcBiont* project and conducted within the frame of the Helmholtz International Research Group (HIRG 0007). The thesis was further supported by the Helmholtz Association of German Research Centres within the frame of a Helmholtz Young Investigators Group to Susanne Liebner (grant VH-NG-919). The field work carried out in Svalbard was supported by the Arctic Field Grant (RiS-ID: 6547) with support of the Svalbard Science Forum (SSF). The infrastructure was further funded by the Terrestrial Environmental Observatories Network (TERENO), specifically the North-Eastern German Lowland Observatory (TERENO-NE).

Field sampling campaigns were conducted in Svalbard, Samoylov, Neiden and in the Mueritz National Park from 2014 to 2015. The expeditions were organised by the Helmholtz Centre Potsdam, German Research Centre of Geosciences (GFZ) in collaboration with the Arctic University of Norway (UiT) and the Alfred-Wegener-Institute in Potsdam (AWI). The laboratory work here described was mainly performed at GFZ Potsdam in the section Geomicrobiology, and furthermore at the department of Arctic and Marine Biology, headed at the Arctic University of Norway, as well as at the department of Experimental Plant Biology, headed at the University of South Bohemia (USB) in České Budějovice.

This thesis is written in British English and organised as a monograph to the Faculty of Mathematics and Natural Science at the University of Potsdam (UP). It contains an introduction to the scientific background and the particular research field, the description of materials and methods including the study sites and the objectives of the study, followed by a discussion of the results. The main outcomes are highlighted in a final conclusion and future prospects are mentioned in a general outlook. A large part of the achieved results was already published in a shared first-authorship manuscript as well as within the following conference contributions:

Tveit, A.T., Kiss, A., Winkel, M. *et al.* Environmental patterns of brown moss- and *Sphagnum*-associated microbial communities. *Sci Rep* 10, 22412 (2020). https://doi.org/10.1038/s41598-020-79773-2

A. Kiss, M. Winkel, A.T. Tveit, M. M. Svenning, D. Wagner, T. Hájek, S. Liebner, 2015, Epi- and endophytic microbial communities of arctic and subarctic peatland mosses. Conference on Polar and Alpine Microbiology (PAM), September 6-10. 2015, České Budějovice, Czech Republic (Abstract, Poster)

A. Kiss, A.T. Tveit, M. Winkel, F. Horn, T. Hájek; M. M. Svenning, D. Wagner, S. Liebner, 2016, Global and local patterns of bacterial communities associated with peatland bryophytes. Annual Conference of the Association for General and Applied Microbiology (VAAM), March 13-16. 2016, Jena, Germany (Abstract, Oral Presentation)

A. Kiss, A.T. Tveit, M. Winkel, F. Horn, T. Hájek; M. M. Svenning, D. Wagner, S. Liebner, 2016, Global and local patterns of bacterial communities associated with peatland bryophytes. Annual PhD Day at GFZ German Research Centre for Geosciences, Section 3.7 Geomicrobiology, April 07. 2016, Potsdam, Germany (Abstract, Oral Presentation)

Acknowledgements

I gratefully acknowledge my PhD supervisor Prof. Dr. Susanne Liebner who consistently supported me in realising my ideas and in accomplishing my work in every possible way. I sincerely thank you for always being a straightforward and patient supervisor who guided me through my PhD with an exemplary attitude.

Further, I would like to thank Prof. Dr. Dirk Wagner for his support and encouragement during my time as a PhD student. I want to thank also all former and current ‘Geomics’ members who contributed to a joyful time at the GFZ, namely Lars Ganzert, Julia Mitzscherling, Janine Heise, Fabian Horn, Sizhong Yang, Paloma Serrano, Mashal Alawi, Jens Kallmeyer, Matthias Winkel, Patryk Krauze and André Friese. I am especially grateful to my dear colleagues and friends Nadine Manke, Steffi Genderjahn and Roman Osudar.

I am very grateful to Prof. Dr. Mette Marianne Svenning for giving me the unique opportunity to travel to Svalbard and do field work within such an impressive landscape. Further, I want to acknowledge Dr. Tomáš Hájek who kindly invited me to the University of Southern Bohemia and helped me together with Eliška Vicherová to carry out the laboratory work. At both journeys, I felt very comfortable and in good company.

I want to express my sincere thanks to Alexander Tøsdal Tveit for the constructive cooperation and his valuable, ambitious work on the bioinformatical analysis.

Sincere thanks are given to Anke Saborowski and Oliver Burckhardt for their essential technical support in the laboratory and the organisation of a smooth lab workflow. I especially acknowledge Axel Kitte and Alena Didriksen for their irreplaceable practical assistance and mental support during the field campaigns in the Lena Delta, respectively in Neiden. In particular, I want to thank Sybille Hahmann for her engagement and essential work which substantially facilitates the whole staff´s lives.

Furthermore, I want to thank Dyke Scheidemann and Antje Eulenburg for laboratory support as well as Christian Knoblauch, Tiemo Timmermann and Knut Kaiser for field work. All Tiksi Hydrobase staff members, in particular Dmitry Melnichenko and Waldemar Schneider from the Alfred Wegener Institute, are acknowledged for organisation and logistics in Siberia.

Sincere thanks are given to Michael Zauft (Stiftung Naturschutzfonds Brandenburg) for sharing his expertise on brown moss ecology.

Not least, I want to express my gratitude to my whole family for their support and understanding, and especially to my 'co-pilote' Ulf for his continuous encouragement in daily life, as well as to our beloved children Valeska and Géza for their light-hearted tempers.

Further, I greatly thank Zsuzsanna Kiss and Oliver Rapphahn for proofreading.

Finally, I want to acknowledge Alexandra Elbakyan and all activists who help "to remove all barriers in the way of science".

This thesis is dedicated to my father András Imre Kiss who inspired me to become a biologist.

In making theories, always keep a window open

so that you can throw one out if necessary.

Béla Lugosi

Summary

Moss-microbe associations are often characterised by syntrophic interactions between the microorganisms and their hosts, but the structure of the microbial consortia and their role in peatland development remain unknown.

In order to study microbial communities of dominant peatland mosses, *Sphagnum* and brown mosses, and the respective environmental drivers, four study sites representing different successional stages of natural northern peatlands were chosen on a large geographical scale: two brown moss-dominated, circumneutral peatlands from the Arctic and two *Sphagnum*-dominated, acidic peat bogs from subarctic and temperate zones.

The family Acetobacteraceae represented the dominant bacterial taxon of *Sphagnum* mosses from various geographical origins and displayed an integral part of the moss core community. This core community was shared among all investigated bryophytes and consisted of few but highly abundant prokaryotes, of which many appear as endophytes of *Sphagnum* mosses. Moreover, brown mosses and *Sphagnum* mosses represent habitats for archaea which were not studied in association with peatland mosses so far. Euryarchaeota that are capable of methane production (methanogens) displayed the majority of the moss-associated archaeal communities. Moss-associated methanogenesis was detected for the first time, but it was mostly negligible under laboratory conditions. Contrarily, substantial moss-associated methane oxidation was measured on both, brown mosses and *Sphagnum* mosses, supporting that methanotrophic bacteria as part of the moss microbiome may contribute to the reduction of methane emissions from pristine and rewetted peatlands of the northern hemisphere.

Among the investigated abiotic and biotic environmental parameters, the peatland type and the host moss taxon were identified to have a major impact on the structure of moss-associated bacterial communities, contrarily to archaeal communities whose structures were similar among the investigated bryophytes. For the first time it was shown that different bog development stages harbour distinct bacterial communities, while at the same time a small core community is shared among all investigated bryophytes independent of geography and peatland type.

The present thesis displays the first large-scale, systematic assessment of bacterial and archaeal communities associated both with brown mosses and *Sphagnum* mosses. It suggests that some host-specific moss taxa have the potential to play a key role in host moss establishment and peatland development.

Zusammenfassung

Während die Beziehungen zwischen Moosen und den mit ihnen assoziierten Mikroorganismen oft durch syntrophische Wechselwirkungen charakterisiert sind, ist die Struktur der Moos-assoziierten mikrobiellen Gemeinschaften sowie deren Rolle bei der Entstehung von Mooren weitgehend unbekannt.

Die vorliegende Arbeit befasst sich mit mikrobiellen Gemeinschaften, die mit Moosen nördlicher, naturnaher Moore assoziiert sind, sowie mit den Umweltfaktoren, die sie beeinflussen. Entlang eines groß angelegten geographischen Gradienten, der von der Hocharktis bis zur gemäßigten Klimazone reicht, wurden vier naturbelassene Moore als Probenstandorte ausgesucht, die stellvertretend für verschiedene Stadien der Moorentwicklung stehen: zwei Braunmoos-dominierte Niedermoore mit nahezu neutralem pH-Wert sowie zwei *Sphagnum*-dominierte Torfmoore mit saurem pH-Wert.

Die Ergebnisse der vorliegenden Arbeit machen deutlich, dass die zu den Bakterien zählenden Acetobacteraceae das vorherrschende mikrobielle Taxon der *Sphagnum*-Moose gleich welchen geographischen Ursprungs darstellen und insbesondere innerhalb des Wirtsmoosgewebes dominieren. Gleichzeitig gehörten die Acetobacteraceae zum wesentlichen Bestandteil der mikrobiellen Kerngemeinschaft aller untersuchten Moose, die sich aus einigen wenigen Arten, dafür zahlreich vorkommenden Prokaryoten zusammensetzt.

Die vorliegende Arbeit zeigt zudem erstmals, dass sowohl Braunmoose als auch Torfmoose ein Habitat für Archaeen darstellen. Die Mehrheit der Moos-assoziierten Archaeen gehörte dabei zu den methanbildenden Gruppen, wenngleich die metabolischen Aktivitätsraten unter Laborbedingungen meistens kaum messbar waren. Im Gegensatz hierzu konnte die Bakterien-vermittelte Methanoxidation sowohl an Braunmoosen als auch an *Sphagnum*-Moosen gemessen werden. Dies zeigt eindrucksvoll, dass Moos-assoziierte Bakterien potenziell zur Minderung von Methanemissionen aus nördlichen, aber auch wiedervernässten Mooren beitragen können.

Ein weiteres wichtiges Resultat der vorliegenden Arbeit ist die Bedeutung des Moortyps (Niedermoor oder Torfmoor), aber auch der Wirtsmoosart selbst für die Struktur der Moos-assoziierten Bakteriengemeinschaften, während die archaeellen Gemeinschaftsstrukturen weder vom Moortyp noch von der Wirtsmoosart beeinflusst wurden und sich insgesamt deutlich ähnlicher waren als die der Bakterien.

Darüber hinaus konnte erstmalig gezeigt werden, dass sich die bakteriellen Gemeinschaften innerhalb der unterschiedlichen Moorsukzessionsstadien zwar ganz erheblich voneinander unterscheiden, ein kleiner Teil der Bakterien dennoch Kerngemeinschaften bilden, die mit allen untersuchten Moosarten assoziiert waren.

Bei der hier präsentierten Arbeit handelt es sich um die erste systematische Studie, die sich auf einer großen geographischen Skala mit den bakteriellen und archaeellen Gemeinschaften von Braunmoosen und Torfmoosen aus naturbelassenen nördlichen

Mooren befasst. Die vorliegenden Ergebnisse machen deutlich, dass die untersuchten Moose ein ganz spezifisches mikrobielles Konsortium beherbergen, welches mutmaßlich eine Schlüsselrolle bei der Etablierung der Wirtspflanzen am Anfang der Moorentwicklung spielt und darüber hinaus das Potential hat, die charakteristischen Eigenschaften von Mooren sowie deren weitere Entwicklung zu prägen.

Abbreviations

°C .... *Degree Celsius*
µl .... *Microlitre*
µm........ *Micrometre*
µM .... *Micromole*
AAP .... *Aerobic Anoxygenic Phototrophs*
ACM .... *Amblystegiaceae Core Microbiome*
ASV .... *Amplicon Sequence Variants*
BChl*a*........ *Bacteriochlorophyll a*
BP........ *Before Past*
C .... *Carbon*
CA .... *Correspondence Analysis*
ca. .... *Circa*
CCA .... *Canonical Correspondence Analysis*
CDOM .... *Coloured Dissolved Organic Matter*
CEC .... *Cation Exchange Capacity*
CNS .... *Carbon Nitrogen Sulphur*
CTAB .... *Cetrimonium Bromide*
DEPC .... *Diethylpyrocarbonate*
dm .... *Dry Mass*
DNA .... *Deoxyribonucleic Acid*
DOC........ *Dissolved Organic Carbon*
dw .... *Dry Weight*
e.g. .... *Exempli Gratia*
g .... *Gramm*
GLU .... *Gluudneset*
h .... *Hours*
HC........ *Holocellulose*
HEI .... *Heidbergmoor*
IAA .... *Indole-3-Acetic Acid*

KIE .... *Kiebitzmoor*

KL .... *Klason-Lignin*

KLO .... *Klockenbruch*

KNU .... *Knudsenheia*

LLP .... *Lignin-like Polymers*

m .... *Metre*

min .... *Minute*

ml .... *Millilitre*

mm .... *Millimetre*

MO .... *Methane Oxidation*

MOB .... *Methane Oxidising Bacteria*

MUE .... *Mueritz National Park*

NEI .... *Neiden*

ng .... *Nanogramm*

nl .... *Nanolitre*

nmol .... *Nanomole*

OTU .... *Operational Taxonomic Unit*

PC .... *Polygonal Crack*

PCR .... *Polymerase Chain Reaction*

pH .... *Potentia Hydrogenii*

PP .... *Polygonal Pond*

rRNA .... *Ribosomal Ribonucleic Acid*

s .... *Second*

s.str. .... *Sensu Stricto ["in a narrower sense"]*

SA .... *Samoylov*

SCM .... *Sphagnum Core Microbiome*

SV .... *Svalbard*

TC .... *Total Carbon*

TCM .... *Total Core Microbiome*

TN .... *Total Nitrogen*

TW .... *Twin Water*

U .... *Units*

UV .... *Ultraviolet*

W .... *Watt*

VOC .... *Volatile Organic Compound*

List of figures and tables

Figure 1: Schematic peat bog succession.. 5

Figure 2: Characteristic peatlands of the northern hemisphere. 8

Figure 3: Submerged brown mosses form often thick mats under the water table. 15

Figure 4: Submerged and emerged *Sphagnum* species from a subarctic palsa mire. 17

Figure 5: Schematic illustration showing beneficial microorganisms inside the hyaline cells of *Sphagnum*.. 21

Figure 6: Sampling sites of Svalbard. 29

Figure 7: Sampling sites of Samoylov 31

Figure 8: Sampling sites of Neiden. 33

Figure 9: Sampling sites of Mueritz National Park. 35

Figure 10: Schematic overview of the investigated sites and the collected sample types. 37

Figure 11: Box plots showing the measurements of selected environmental variables. 52

Figure 12: Box plots illustrating bacterial alpha-diversities of all sample types. 55

Figure 13: Canonical correspondence analysis of moss-associated bacterial OTUs. 57

Figure 14: Dendrogram illustrating the clustering of bacterial communities in relation to abiotic and biotic characteristics of the sites. 60

Figure 15: Bubble plot displaying the relative abundances of bacterial families . 63

Figure 16: Bubble plot displaying the relative abundances of archaeal families. 64

Figure 17: Heatmap displaying the most abundant OTUs present at significantly higher abundance in putative endophytic than epiphytic libraries of the same sample. 67

Figure 18: Bar chart displaying the increase of the relative abundance of Acetobacteraceae within total moss bacteriomes of brown mosses towards *Sphagnum* mosses.. 69

Figure 19: Relative abundance of identified genera within the family Acetobacteraceae. 71

Figure 20: Venn diagrams showing the *Sphagnum* bacteriomes from all subsites within the Mueritz sampling site. 73

Figure 21: Moss-associated potential methane production and methane oxidation rates 75

Table 1: Cell wall and bulk moss litter analysis 53

Content

Preface IV

Acknowledgements VI

Summary IX

Zusammenfassung XI

Abbreviations XIV

1. Introduction 1

1.1. Peatlands 1

1.1.1. Peatland development and peat bog succession 2

1.1.2. Characteristic peatlands of the northern hemisphere 6

1.1.3. Anthropogenic threats of northern peatlands 9

1.1.4. Peat bog restoration 10

1.2. Peatland bryophytes 12

1.2.1. Brown mosses 13

1.2.2. *Sphagnum* mosses 15

1.3. Moss microbiota 18

1.3.1. Moss-associated bacteria 18

1.3.2. Moss-associated archaea 22

1.3.3. Endophytic prokaryotic communities 23

1.4. Biotic and abiotic influences on moss-associated microorganisms 25

1.5. Objectives 26

1.6. Study sites 28

1.6.1. High Arctic peatlands of Svalbard (SV) 28

1.6.2. Polygonal Tundra of Samoylov (SA) 30

1.6.3. Palsa Bogs of Neiden (NEI) 32

1.6.4. Kettle Bog Peatlands of Mueritz National Park (MUE) 34

2. Material and Methods 36

2.1. Sampling scheme overview 36

2.2. Sampling of pore water 38

2.3. Sampling of moss plantlets 38

2.4. Analysis of pore water chemistry 40

2.5. Cell wall analysis 41
2.5.1. Cation exchange capacity (CEC) 41
2.5.2. Holocellulose (HC) 42
2.5.3. Lignin and Lignin-like polymers (LLP) 42
2.5.4. Bulk moss litter analysis 43
2.6. Moss surface sterilisation and separation of putative epiphytic and endophytic microbial communities 43
2.7. DNA extraction and sequencing 44
2.8. Sequence analyses and bioinformatics 45
2.9. Statistical analyses 46
2.10. Potential methane production and oxidation assays 48
2.10.1. Surface sterilisation prior to activity tests 48
2.10.2. Methane production 49
2.10.3. Methane oxidation 49
3. Results 51
3.1. Peatland bulk and pore water characteristics 51
3.2. Diversity and structure of natural peatland microbial communities 54
3.3. Environmental drivers of moss-associated microbial communities 56
3.4. Microbial taxa associated with brown mosses and *Sphagnum* mosses 61
3.4.1. Moss-associated bacteria 61
3.4.2. Moss-associated archaea 63
3.4.3. Bacterial and archaeal core communities 65
3.4.4. Acetobacteraceae as dominant taxon of the bacterial core community 68
3.5. *Sphagnum* bacteriomes of disturbed, rewetted and pristine temperate kettle bog 71
3.6. Potential moss-associated methane production and methane oxidation rates 73
3.6.1. Moss-associated methane production 73
3.6.2. Moss-associated methane oxidation 74
4. Discussion 76
4.1. Environmental influences on moss-associated bacterial communities 76
4.2. Moss-associated archaeal communities and their environmental drivers 79
4.3. Distinct patterns of endophytic bacteria 82
4.4. The core microbiota and their possible role for peatland succession 84

4.5. The potential role of Acetobacteraceae for *Sphagnum* host mosses and bog ecosystems ... 85

4.6. Moss-associated microbial communities of the methane cycle and their potential metabolic activity ... 92

4.7. Diversity and structure of *Sphagnum* bacteriomes from pristine, disturbed and rewetted kettle bogs ... 96

5. Conclusion ... 103

6. Critical remarks and outlook ... 106

6.1. Critical remarks ... 106

6.2. Outlook ... 108

Bibliography ... 111

Supplementary ... i

1. Introduction

1.1. Peatlands

Neutral, mineral-rich fens and acidic, nutrient-poor bogs display unique environments that form peat, therefore called 'peatlands' (Zoltai and Vitt 1995, Rydin and Jeglum 2006). Together with non-peat forming habitats like marshes and swamps, peatlands are classified as wetlands which display water-saturated habitats with poorly drained soils, hydrophytic vegetation and biological activities that are adapted to these challenging conditions (Tarnocai et al. 1988).

Peatlands represent up to 70% of global wetlands and preserve a wealth of information and chronological records in remains of plants and animals (Chapman et al. 2003). 'Koelbjerg Man' and 'Tollund Man', two well-preserved bog bodies buried for thousands of years, belong to the best-known archaeological finds worldwide and illustrate the extraordinary preservative character of peat bogs (Painter 1991, Hansen et al. 2017, Chapman et al. 2020).

Peatlands are one of the most important ecosystems in the world (Holden 2005) and represent important habitats for highly adapted species. About 80% of all peatlands constitute natural and pristine environments (Joosten 2012). These vulnerable, long-existing ecosystems with widely constant conditions for over 1000 years appear mainly in remote and agricultural non-usable regions (Opelt, Chobot, et al. 2007). Due to extreme environmental conditions, such as low temperature, high water saturation, recalcitrant organic matter and low availability of plant nutrients, dead organic matter ('peat') accumulates (Freeman et al. 2001, Joosten and Clarke 2002, Holden 2005, MacDonald et al. 2006). Peatlands store approximately one third of the global soil carbon (C) and 10% of global freshwater resources (Holden 2005) and act as carbon sinks, therefore holding important ecosystem functions by regulating climate and water balance.

1.1.1. Peatland development and peat bog succession

Boreal and subarctic peatlands started to develop as a result of increasing insolation and temperatures during the Holocene Hypsithermal, when the Fennoscandian Ice Sheet covered most of the present boreal peatlands in Norway, Sweden, Finland and parts of western Russia (Kuhry and Turunen 2006). In the Northeast of Germany, complex paludification processes on larger scales took place during the late Holocene (9200-5700 BP), resulting from sea-level rise (Kaiser et al. 2012), while peat accumulation in polygonal peatlands of Western Siberia began about 9814 BP (Pastukhov et al. 2021). It is assumed that many of these newly developed peatlands were initially wet minerotrophic fens (MacDonald et al. 2006). Based on hydrology and vegetation, peatlands are roughly divided into fens and bogs (Rydin and Jeglum 2006, Soudzilovskaia et al. 2010, Tuittila et al. 2013). Fens are typically situated in landscape depressions and receive mineral-rich water from the belowground (minerotrophic), and the main vegetation comprises a taxonomically heterogenous group of aquatic bryophytes, so-called 'brown mosses'. Bogs are characterised by an elevated surface, which is solely fed by precipitation water (ombrotrophic); they are typically inhabited by aquatic and terrestrial peat mosses of the genus *Sphagnum* (Zoltai and Vitt 1995).

Fens and bogs represent peatland succession stages (Moore 1989, Kuhry et al. 1993, Fenton and Bergeron 2006, Soudzilovskaia et al. 2010), even though individual allogenic and autogenic factors characterise each mire succession (Klinger 1996, Hughes and Dumayne-Peaty 2002). Four processes can initiate peat bog development: primary peat formation, when peat develops directly on fresh, non-vegetated mineral soil; terrestrialisation, when shallow water bodies are infilled gradually by vegetation; paludification, when peat forms on drier, vegetated habitats over inorganic soil in the absence of water; and finally, peat formation of early Holocene lakes, which occurs mainly in glaciated areas (Wieder and Vitt 2006). In the boreal zone, terrestrialisation and subsequent paludification are the most common peat bog successional processes (Kuhry and Turunen 2006). The development starts with the establishment of sedges and brown mosses in shallow ponds, leading to a base-rich fen environment with circumneutral pH, which is strongly influenced by the chemistry of the surrounding mineral soil deposit. Over time, mesotrophic *Sphagnum* mosses invade and start to acidify the habitat, leading to the transition into a poor fen habitat with decreasing pH. Microbial degradation of organic material is additionally hindered by the decomposition-resistant litter of *Sphagnum* mosses and consecutively, peat accumulates. The subsequent raise of the surface leads to a loss of groundwater influence, resulting in the formation of an ombrotrophic (rain-fed), highly elevated bog with pH well below 4. Due to the oligotrophic and acidic conditions in the latter successional stages, *Sphagnum* mosses become ultimately dominant and outcompete brown mosses (Figure 1) (Gorham and Janssens 1992, Zoltai and Vitt 1995, Kuhry and Turunen 2006). While the upper bog layer, the acrotelm, consists of dense mats of living *Sphagnum* moss parts, the subjacent catotelm layer is characterised by already dead and compressed *Sphagnum* segments. Bulk density increases and dissolved oxygen (O_2) depletes towards the catotelm, and water velocity is so extremely low, that vertical transport of water and mineral nutrients into this layer is practically blocked (van Breemen 1995, Christen et al. 1995, Zaitseva 2009). The transition from a fen into a bog can take several thousands of years, and the bog development is accompanied by remarkable shifts in the moss vegetation and subsequent changes in pH, hydrology and nutrient regimes (Merilä et al. 2006, Oksanen 2006, Rozema et al. 2006, Tuittila et al. 2013, Gałka and Lamentowicz 2014, Putkinen et al. 2014). Furthermore, the bog development profoundly alters the ecosystem carbon budget, due to a doubling of net primary production and a fourfold decrease of the decomposition rate (Soudzilovskaia et al. 2010).

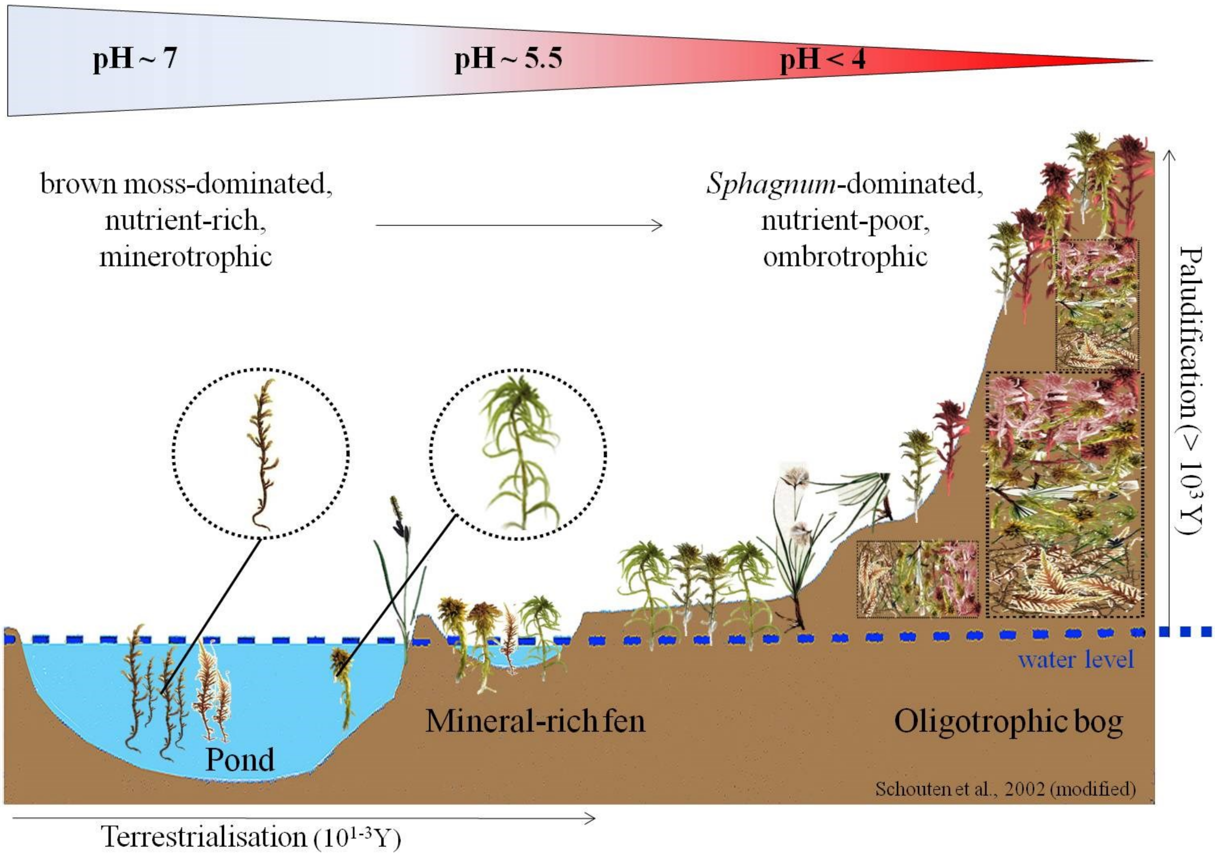


Figure 1: Schematic peat bog succession. The transition from brown moss-dominated, minerotrophic fens into *Sphagnum*-dominated, ombrotrophic bogs is accompanied by considerable shifts in vegetation and subsequent changes in pH, hydrology and nutrient levels. Mature bogs feature higher net primary production with simultaneously lower microbial decomposition rates compared to early successional stages. Taken from http://www.ipcc.ie/a-to-z-peatlands/raised-bogs (modified).

Peatlands exist globally where environmental conditions favour the accumulation of peat, especially in cold areas such as the boreal and subarctic regions, but also in wet regions, e.g. in oceanic areas and in the humid tropics (Gunnarsson 2005, Schumann and Joosten 2008). Although about 80% of the worldwide peatlands remained pristine, they are highly endangered in areas with high human population density and other anthropogenic impacts (Joosten 2012), which applies particularly for northern peatlands. In order to understand the complex mechanisms of peatland ecology and degradation processes, research on northern peatlands is therefore crucial.

1.1.2. Characteristic peatlands of the northern hemisphere

High Arctic ponds and bogs (Figure 2 a, b) are characterised by a low peat accumulation rate, since the short and cold arctic summer limits plant growth (Rozema et al. 2006). Swamps and wet tundra with moderately developed moss layers appear mainly in central fjord areas (Johansen et al. 2012). Typical bog formations in more dry areas of Svalbard are active layer mounds on moss-covered valley bottoms with ice-wedge polygon patterns, but also peat mounds similar to palsas (Åkerman and Boardman 1987). Fens and peat bogs on Svalbard display various microrelief structures and are typically inhabited by brown mosses and other members of the order Hypnales (leafy mosses) (Solheim et al. 1996, Tveit et al. 2015, Jaworski 2017); at the same time, the archipelago displays the northernmost dispersal border of *Sphagnum* species (Flatberg and Frisvoll 1984a, 1984b, Greilhuber et al. 2003).

Polygonal tundra (Figure 2 c, d) appears in the Arctic where seasonally rapidly decreasing temperatures lead to crack formations in the shrinking permafrost. Ice wedges form subsequently, when, after trickling into these open cracks, the water freezes again; the adjacent soil material heads up in a polygon pattern of low ridges and encloses wet depressions (MacKay 2000, Minke et al. 2007). The peat in these depressions is not frozen, but permafrost may occur at greater depths in the mineral soil (Zoltai and Tarnocai 1975). The prevailing moss vegetation of Siberian polygonal tundra environments comprises members of Hypnales, e.g. brown mosses (Sommerkorn et al. 1999, Kutzbach et al. 2004, Liebner et al. 2011, Zibulski et al. 2016).

Palsa peat bogs (Figure 2 e, f) are typical wetlands of the circumpolar zone, where permafrost is discontinuous or sporadic. Palsas are peat hummocks with a frozen core that rises above the mire surface, when frost penetrates the peat and frozen pore water expands. Palsa degradation occurs naturally when the frozen core reaches the till or silt layers of the mire, resulting in the collapse of the palsa and often a remaining open pond (Seppala 2006). In wet depressions and surrounding fen areas, various *Sphagnum* species are common (Oksanen 2005, Liebner and Svenning 2013, Kjellman et al. 2018, Hough et al. 2020), although brown moss-*Sphagnum*-communities appear at certain palsa development levels (Bhiry and Robert 2006, Oksanen 2006).

Kettle bogs (Figure 2 g, h) form in kettle hole-shaped basins that have developed by thawing of residual ice from retreating glaciers, or as a result of karst (Succow and Joosten 2012). Peat formation occurs either downwards from a floating mat under stable water level conditions or by peat forming upwards, as humus colloids seal off the basin, causing the water level to rise progressively ('kettle hole mire mechanism') (Gaudig et al. 2006). The stratigraphy of kettle bogs displays often basal brown moss peat layers, followed by layers of *Sphagnum* peat and mixed cyperaceous-*Sphagnum* peat (Vitt and Slack 1975, Andreas and Bryan 1990, Lamentowicz et al. 2008, Landgraf 2010).

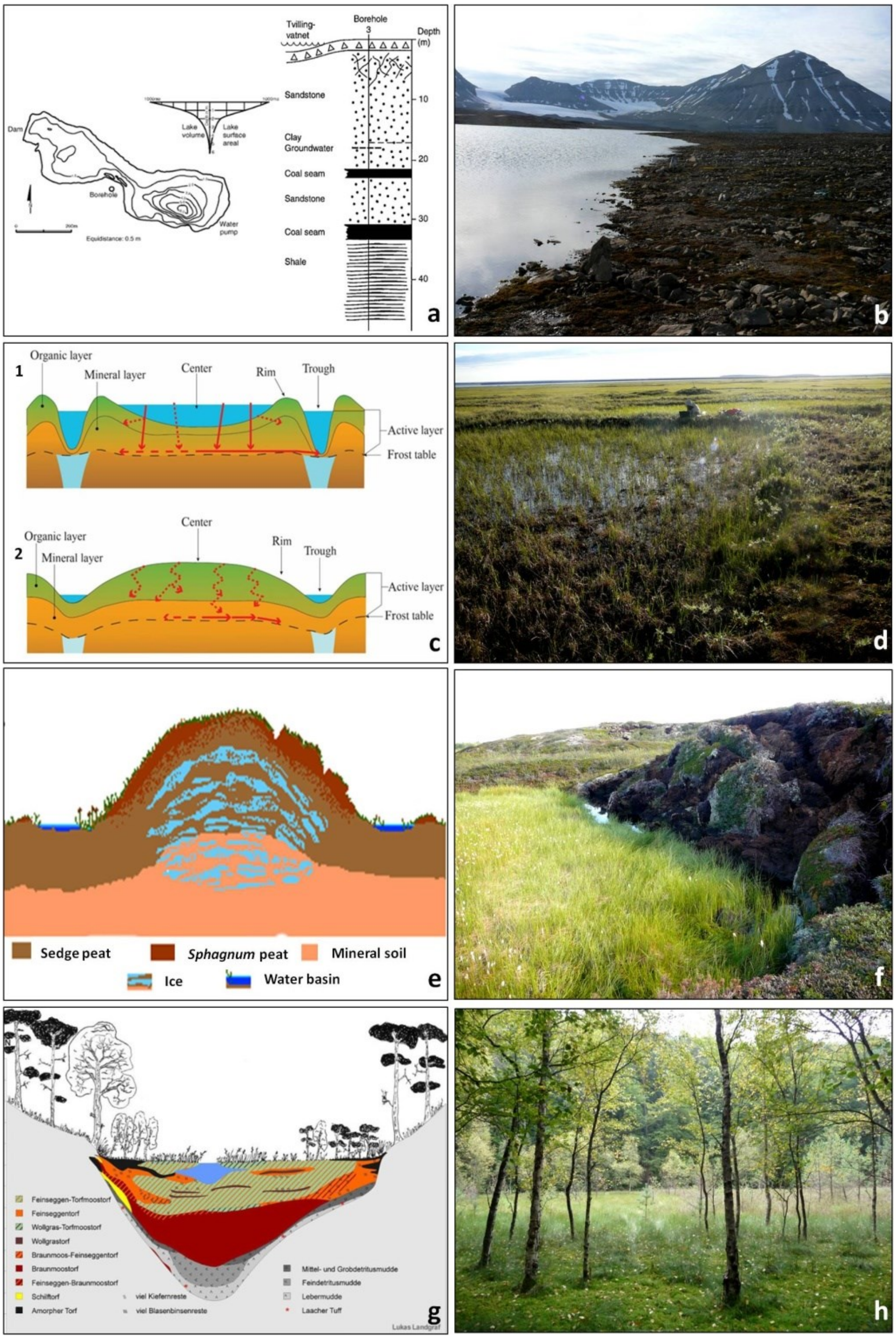


Figure 2: Characteristic peatlands of the northern hemisphere. a) Bathimetric map and geologic log of the High Arctic-pond Twin Water on Svalbard (b); c) schematic profiles of low-centred (1) and high-centred (2) polygons in the Arctic tundra; d) low-centred polygon on Samoylov Island, Siberia; e) schematic profile of a palsa frost mound; f) subarctic palsa peatland in Finnmark, Northern Norway; g) schematic profile of a kettle bog in the temperate zone; h) kettle bog in the Mueritz National Park, Northern Germany. Taken from a) Haldorsen, 2010 (modified), c) Wales, 2020, e) www.oulu.fi (modified); g) L. Landgraf. Photos by A. Kiss, except h): S. Liebner

1.1.3. Anthropogenic threats of northern peatlands

Northern peatlands are extremely sensitive to environmental changes induced by anthropogenic activities. Direct damage by humans is the most apparent threat to peatlands (Dise 2009). The exploitation of northern peatlands, like commercial extraction and drainage for agricultural demand, forestry or horticulture, destructed and shrank many of these habitats (Chapman et al. 2003). Peat fuel production and utilisation from pristine fens lead to similar magnitudes of greenhouse impact as from fossil coal (Kirkinen et al. 2007). The drainage of peatlands induces a loss of water, along with a loss of balance between accumulation, decomposition and therefore stability of the peat. Moreover, drained wetlands have negative influences on catchment hydrology. They increase flooding downstream and reduce water storage capacities, and the increased aeration enhances microbial induced peat decomposition (Holden et al. 2004).

Less obvious, but potentially as detrimental as direct human damage, and therefore of major concern, are long-term environmental disturbances, such as climate change (Dise 2009). Northern ecosystems currently experience a matchless era of altered temperature and precipitation patterns, influencing plant community structure and photosynthesis rates in northern ecosystems (Myers-Smith and Hik 2018, Jassey and Signarbieux 2019). Lately, a climate reconstruction study validated the unusual character of the warming in recent decades (Neukom et al. 2019). Temperatures rise rapidly in the Arctic (Overland et al. 2019) and turn the carbon sinks into sources, enhancing microbial driven emissions of powerful greenhouse gases like carbon dioxide (CO_2) and methane (CH_4) (Strack et al. 2008, Gorham 2014, Hopple et al. 2020). Further, peatlands are vulnerable, nutrient-limited environments where nitrogen (N) deposition can have severe impacts on local ecosystems. Reactive nitrogen acts as a potent fertilizer (Kühnel et al. 2013) and affects carbon balances by increasing microbial decomposition rates and subsequent rise of carbon emissions from ombrotrophic bogs (Aerts et al. 1992, Bragazza et al. 2006). High loads of atmospheric nitrogen can cause severe growth reduction and mortality of *Sphagnum* mosses (Woodin et al. 1985), resulting in the alteration of the typical peatland bryophyte vegetation towards vascular plant-dominated habitats, e.g. cyperaceous marshes and wooded fens (Bergamini and Pauli 2001, Turunen et al. 2004, Thormann and Landgraf 2010). Today, pristine peatlands can be found mainly in the northern latitudes, while many others are disturbed. For example, no further peat accumulation has been observed in more than a half of Europe´s peatlands, constituting them as degraded, while in Germany 99% of all peatlands are drained and therefore considered to be 'dead' (Joosten 2012). However, knowledge on the prerequisites of peatland recovery grows, since scientific research focussed lately also on the succession of peat-forming vegetation or the return of key microbial communities characteristic for peatlands (Emsens et al. 2020, Milner et al. 2020).

1.1.4. Peat bog restoration

Human impacts like airborne nutrient pollution, eutrophication and drainage are major threats to pristine peatlands (Tsujino et al. 2010). Nutrient loading may alter the bog vegetation and cause irreversible loss of highly adapted bog species plants such as

Sphagnum mosses (Bobbink et al. 1998, Gunnarsson et al. 2000, Tsujino et al. 2010), while improved pond water quality may effectively restore hummocks (Tsujino et al. 2010).

In the past, nearly 530.000 km^2 of natural peatlands had been drained, mostly in Europe (Kitson and Bell 2020). Main peatland restoration strategies include the reintroduction of peat-forming species, e.g., *Sphagnum*, and rewetting, while latter is a controversially debated issue.

The elevated CO_2 emissions from drained peatlands are caused by increased frequency of peat fires, enhanced microbial peat oxidation and the release and activation of extracellular hydrolase enzymes caused by phenol-oxidising organisms, a phenomenon known as *enzymatic latch theory* (Andersen et al. 2013, Kitson and Bell 2020). On the other hand, rewetted peatlands can enhance microbial driven methanogenesis, leading to elevated CH_4 emissions compared to pristine peatlands (Sachs et al. 2015, Günther et al. 2020). Consequently, peatland management has to decide on the emission of either CO_2 as a weak but persistent, or of CH_4 as a strong but short-living greenhouse gas, if considering radiative effects and atmospheric lifetimes of both gases (Günther et al. 2020). Peatland rewetting is cost-effective and simply feasible, but requires a strict water management to prevent permanently inundated areas and the subsequent formation of nutrient-rich, shallow lakes with unfavourable greenhouse gas balance (Sachs et al. 2015, Franz et al. 2016, Günther et al. 2020, Koebsch et al. 2020). Also, it has to be considered that bog vegetation and microbiota are already adapted to the dryer conditions and altered peat geochemistry after long-term drainages (Wen et al. 2018, Günther et al. 2020). Recently it was proposed that rewetted peatlands contribute to climate change mitigation, despite CH_4 emissions, and should be preferred over postponement of peatland rewetting (Günther et al. 2020).

However, it is not clear if rewetting alone is sufficient to fully restore drained peatlands. The restoration depends to a large extent on the return of the pristine microbial communities and the ecosystem functions they perform (Emsens et al. 2020). Therefore, the re-establishment of microorganisms may give a hint on the success of peatland restoration.

1.2. Peatland bryophytes

Bryophytes belong to the embryophyta and are the second largest group of green land plants. They comprise approximately about 15.000 species and are grouped into the three paraphyletic divisions Marchantiophyta (liverworts), Bryophyta (mosses) and Anthocerophyta (hornworts) (Frahm 2007, Von Konrat et al. 2014). These ancient organisms display the earliest diverging lineages of extant land plants and offer unique windows into early plant evolution (Shaw et al. 2011). Recent studies suggest that the embryophyta evolved from already terrestrial charophycean green algae ancestors (Harholt et al. 2016, Wang et al. 2020), and it is assumed that land plants appeared 700 million years ago (Heckman et al. 2001). Fundamental land plant characters such as water-conducting tissue, stomata and fungal symbiotic associations evolved primarily in the bryophyte grade (Ligrone et al. 2012).

Bryophytes are quiet inconspicuous, but surprisingly tough and literally spoken 'survivalists': they disperse over large distances - up to several hundreds of kilometres -

by anemochory of small spores or vegetative propagation organs (Frahm 2007). Due to their often narrow ecological niches, bryophytes occur in harsh habitats unfavourable for vascular plants, for example in cold biomes, where they contribute substantially to above-ground biomass, nitrogen input and soil chemistry control (Cornelissen et al. 2007). Mosses form 5500 years old banks of several metres depths on Antarctic maritime coasts (Bjorck 1991) and are able to regrow after 1400 years of glaciations (La Farge et al. 2013, Roads et al. 2014). They can further thrive in Antarctic lakes of well more than 80 metres depth (Wagner and Seppelt 2006) or grow unattached on bare ice or on ice pedestals as 'glacier mice' (Shacklette 1966, Heusser 1972, Belkina and Vilnet 2015). Thus, mosses are able to initiate plant succession even on Arctic glaciers (Dickson and Johnson 2014).

1.2.1. Brown mosses

In mire ecology, the term 'brown moss' includes calcium-tolerant, non-sphagnaceous mosses (Vicherová et al. 2017) which belong to the families Amblystegiaceae s.str. (including *Amblystegium*, *Campylium*, *Drepanocladus* and *Palustriella*) and Calliergonaceae (including *Calliergon*, *Scorpidium* and *Warnstorfia*) and comprise up to 170 species. Brown mosses were traditionally circumscribed by morphological features or habitat preferences (Hedenäs and Vanderpoorten 2007). Because of their ability to thrive under varying moisture conditions, brown mosses display a great phenotypic variability, and morphological characters are homoplastic (Vanderpoorten et al. 2002). Members of Amblystegiaceae and Calliergonaceae are probably the most important mosses in mineral-rich to calcareous wetlands within temperate to polar environments (Hedenäs and Vanderpoorten 2007, Kooijman 2012). Aquatic brown moss communities growing under the water table ('submerged') are often the exclusive macrophytic vegetation in Arctic lakes which are able to cope with low surface irradiance and long ice coverage (Welsh and Kalff 1974, Sand-Jensen et al. 1999). In low-centred, water-filled polygons of the Siberian tundra, brown mosses form thick swinging mats (Liebner et al. 2011, Zibulski et al. 2016). Remains of humified brown mosses in subarctic palsa peatlands and temperate bogs illustrate their wide distribution and importance at initial bog succession stages (Arlen-Pouliot and Bhiry 2005, Gaudig et al. 2006, Cai and Yu 2011, Kjellman et al. 2018). In Central Europe, brown moss-dominated rich fens were widely distributed during the Postglacial but declined rapidly due to anthropogenic caused acidification and eutrophication (Kooijman 1992, 2012, Landgraf 2010, Thormann and Landgraf 2010).

Figure 3: Submerged brown mosses form often thick mats under the water table. Brown moss communities in an Arctic pond on Svalbard; b) a mix of different brown moss species from the same habitat under the microscope; c) submerged *Scorpidium scorpioides* growing in water-filled polygonal ponds in the Siberian tundra, reaching lengths of approximately 20 cm (d) and well above. Photos: A. Kiss, except c): C. Knoblauch

1.2.2. *Sphagnum* mosses

The family Sphagnaceae comprises the only genus *Sphagnum*, which includes nearly 300 species (Daniels and Eddy 1990, Mcqueen and Andrus 2007, Zaitseva 2009). They are almost worldwide distributed and dominate moss community structures especially in the boreal zone. Certain *Sphagnum* species have broad ecological preferences according to water level, pH, conductivity and altitude, thriving therefore in dry hummocks as well as in wet hollows (Zaitseva 2009, Wojtuń et al. 2013).

Sphagnum mosses are ecosystem engineers that create and maintain boreal peatlands (Bengtsson et al. 2018). Owing to unique biochemistry, waterlogging and acidifying capacities, they reduce competition, impede decomposition and build up vast quantities of peat (Shaw et al. 2003, Bengtsson et al. 2018). *Sphagnum* species release a polysaccharide called ' Sphagnan', which displays in its acid form a powerful antimicrobial compound by lowering pH, inhibiting microbial mineralisation and decomposition more effectively than lignin-like polyphenols (Painter 1991, Stalheim et al. 2009, Hájek et al. 2011). Therefore, *Sphagnum* mosses were used for surgery and medical purposes as well as for transporting archaeological artifacts in the past (Zaitseva 2009, Drobnik and Stebel 2017).

Another unique feature of *Sphagnum* mosses is their ability to store enormous amounts of water, owing to dead and non-photosynthetic, hyaline cells ('hyalocytes'). The water-filled hyalocytes can retain multiple times their dry weight and are located in branch leaves or stems, accounting for up to 80% of the plant volume (van Breemen 1995, Rice 1995, Stalheim et al. 2009, Zaitseva 2009). In this way, hyalocytes can contribute to the acidification of the surrounding, as rainwater retention is linked with the separation of the bog surface from the groundwater, especially in combination with hardly decomposable *Sphagnum* litter (Vicherová et al. 2017).

Sphagnum mosses are known for their unusually high cation exchange capacity (CEC), which is accounted for the ability of peat mosses to acidify the surrounding environment by the exchange of tissue-bound protons for cations (Clymo 1963, Hájek and Adamec 2009, Raven and Edwards 2014). Yet, the role of the high CEC for *Sphagnum* and its biology is still under debate. Besides suppression of vascular plant competitors and microbial decomposition, high CEC may also enhance the intracellular uptake of cations and thus extends the availability of minerals in nutrient-limited habitats (Hájek and Adamec 2009). However, it has been shown that fen brown mosses possess substantial CEC similar to that of *Sphagnum* mosses (Soudzilovskaia et al. 2010).

Figure 4: Submerged and emerged *Sphagnum* species from a subarctic palsa mire. a) dense mats of *Sphagnum riparium* growing in a thermokarst pond besides a degrading palsa; b) divergent morphology of aquatic *S. riparium* plantlets; c, d) terrestrial *S. lindbergii* form large cushions in lawns and hollows. Photos by A. Kiss, except b): S. Liebner

1.3. Moss microbiota

Plants host diverse taxonomic microbial communities – the plant microbiota – which colonise accessible plant tissue. The plant microbiota comprises eukaryotic organisms, such as fungi, protists and nematodes, as well as prokaryotic bacteria and archaea, but also viruses (Stobbe and Roossinck 2014, Jung et al. 2020, Trivedi et al. 2020). Microbes can be pathogenic, commensal, symbiotic or transient (Alcaraz et al. 2018), and beneficial microbes confer fitness advantages like growth promotion, nutrient uptake and pathogen resistance to their host (Vandamme et al. 2007, Jung et al. 2020, Trivedi et al. 2020). The microbiota contains literally 'the plant´s second genome' and shapes the microbiome (entity of plant-associated microorganisms) by interacting with the host plant and the external environment (Berg et al. 2014, Alcaraz et al. 2018). Plant microbiomes represent highly specialised and co-evolved genetic pools and host a rich secondary metabolism (Müller et al. 2016).

1.3.1. Moss-associated bacteria

Knowledge on moss-associated bacteria, often referred to as 'moss bacteriome' (Marks et al. 2018, Bouchard et al. 2020, Renaudin et al. 2022), increased during the last decades and revealed fascinating insights into the interrelationship between hosts and their prokaryotic symbionts. Beneficial vitamin-producing, N_2 fixing (diazotrophic) and methane oxidising (methanotrophic) bacteria associated with streptophyte algae and bryophytes suggest that microbes fostered land colonisation by allowing early land plants to cope with nutrient poor soils (Knack et al. 2015). Phytohormone producing bacteria, which benefit from methanol emitted by bryophyte cells, stimulate in turn organ development in moss protonema, probably displaying a co-evolution of both symbiotic partners (Hornschuh et al. 2002, Kutschera 2007). Moss bacteriomes are important promoters of early succession in arid ecosystems and mediate stress resilience of pioneer moss vegetation exposed to high UV radiation (Graham et al. 2017, Cao et al. 2020). In polar regions, bacteria secrete ice-binding proteins on the surface of moss leaves (Raymond 2016) and contribute to the establishment and maintenance of important biochemical cycling in submerged 'moss pillars' from Antarctica (Nakai et al. 2012). Under nitrogen limitation, boreal feather mosses secrete chemo-attractants which guide cyanobacteria like *Nostoc* sp. towards them (Bay et al. 2013). It is further suggested that moss-associated diazotrophic bacteria display a major source of biologically fixed N_2 in nutrient-depleted boreal areas (Holland-Moritz et al. 2018). In Arctic ecosystems, brown mosses seem to be exceptionally well-adapted for harbouring epiphytic *Nostoc* communities (Solheim et al. 1996). A study on submerged *Scorpidium scorpioides* from Arctic polygonal tundra revealed even a mutualistic relationship between the moss host, which incorporates carbon deriving from microbial methane oxidation, and the associated methanotrophic bacteria which in turn benefit from the oxygen produced through photosynthesis. By this, methane emissions from these habitats may be reduced by at least 5% (Liebner et al. 2011). Brown moss-associated bacteria may contribute in different ways to habitat adaptation of their hosts (Wang et al. 2018), but studies on brown mosses and their associated microbiota remain sparse.

Sphagnum bacteriomes, on the contrary, attracted greater scientific interest. Although *Sphagnum* mosses create an inhospitable environment for most microbes, they simultaneously cultivate a diverse microbial community within their tissues, preferably in hyalocytes next to photosynthetic cells, where they provide expanded surface areas with regard to the inner cell walls and stable hydration to microorganisms (Granhall and Hofsten 1976, Raghoebarsing et al. 2005, Kostka et al. 2016). Bacterial community compositions vary vertically along the top, middle and bottom parts of *Sphagnum* mosses and underlying sediments, indicating diverse ecological functions of the microbiota (Xiang et al. 2013). However, the bacterial associates may contribute to the ecological dominance of *Sphagnum* and help the host to survive under changing environmental conditions (Kostka et al. 2016, Carrell et al. 2020). In *Sphagnum*-dominated bogs, where nitrogen is a growth-limiting factor, *Nostoc* spp. mediate N_2 fixation in and growths of *Sphagnum* mosses (Granhall and Hofsten 1976, Turetsky 2003, Berg et al. 2013). Diazotrophic microbial activity is highest in the green parts of mosses where photosynthesis takes place, indicating a light-dependency of bacterial mediated N_2 fixation (Basilier and Granhall 1978). Besides cyanobacteria, methanotrophic Alphaproteobacteria also possess *nifH* genes, but the extent of their contribution to N_2 input in nutrient depleted bogs remains controversial (Liebner and Svenning 2013, Larmola et al. 2014, Leppänen et al. 2014, Vile et al. 2014, Ho and Bodelier 2015). However, submerged *Sphagnum* mosses harbour symbiotic methanotrophic bacteria endophytically (living inside the cells), where they oxidise methane to carbon dioxide (Figure 5); in turn, the obtained carbon is subsequently fixed by the host (Basiliko et al.

2004, Raghoebarsing et al. 2005). Hence, they contribute significantly to the reduction of methane emissions from northern peatlands, especially in areas with high water levels (Kip et al. 2010, van Winden et al. 2010, Parmentier et al. 2011). Interestingly, methanotrophic bacteria can move through the water and initialise methanotrophic activity in former inactive *Sphagnum* plantlets from the same bog (Larmola et al. 2010, Putkinen et al. 2012).

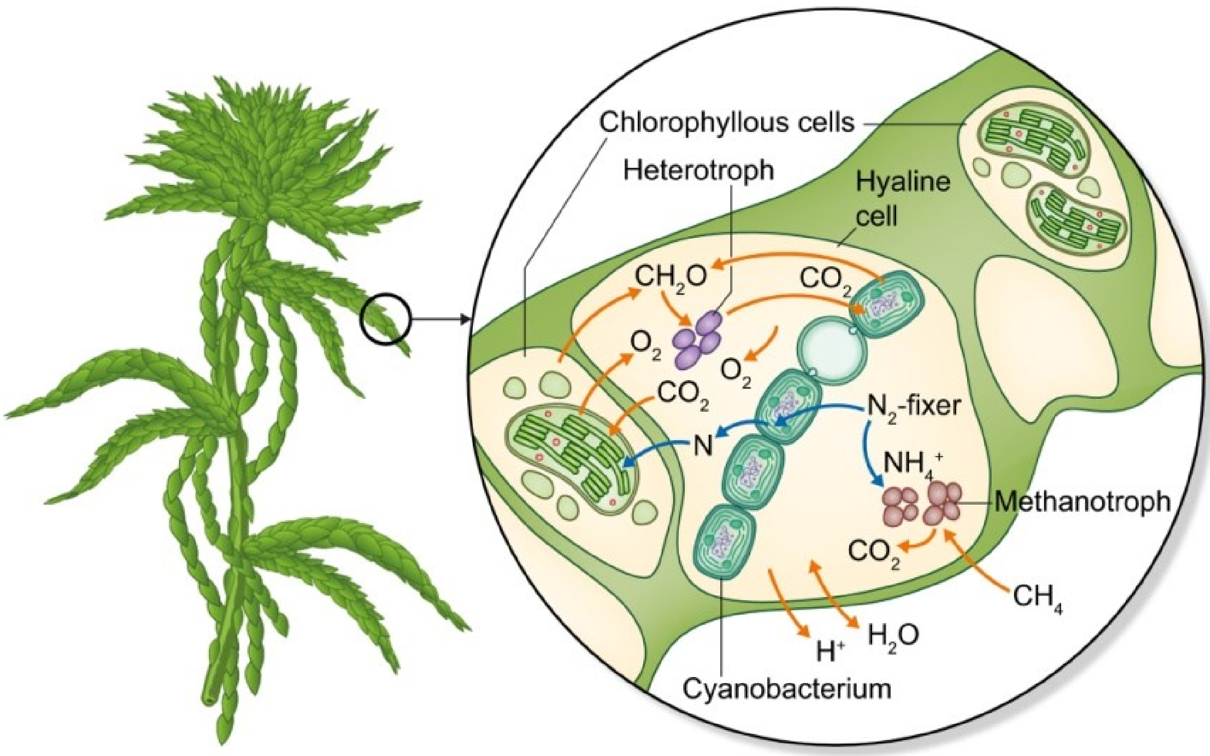


Figure 5: Schematic illustration showing beneficial microorganisms inside the hyaline cells of *Sphagnum*. Functional microbial guilds such as methanotrophic (methane oxidising) and diazotrophic (nitrogen fixing) bacteria may act as a source of carbon and nitrogen to the host. In turn, the microorganisms benefit from the photosynthetically produced oxygen, which diffuses through the hyaline cell walls. Taken from Kostka, 2016.

1.3.2. Moss-associated archaea

Analogous to bacteriomes, archaeomes are the entirety of archaeal cells, including their genetic material in a particular environment (Moissl-Eichinger et al. 2018); consequently, moss-associated archaea can be referred to as 'moss archaeome'. Archaea are often considered 'extremophiles' thriving in inhospitable environments such as deep sea vents, submarine permafrost sediments, salt pans, mine drainages and permafrost-affected soils (Ganzert et al. 2007, Morozova and Wagner 2007, Barbier et al. 2012, Cabrera and Blamey 2018, Genderjahn et al. 2018, Winkel et al. 2018). Owing to their often lithoautotrophic and anaerobic lifestyle and an extraordinary resistance against desiccation, UV radiation and sub-zero temperatures, methane producing (methanogenic) archaea have even been studied as model organisms for possible life on Mars (Wagner et al. 2002, Schirmack et al. 2015, Serrano et al. 2019, Maus et al. 2020).

However, there is a growing scientific interest in archaea inhabiting more moderate environments, for example as associates of eukaryotic hosts (Wrede et al. 2012, Borrel et al. 2020). Archaea appear in the phyllospheres (total above-ground plant surface) and rhizospheres (total root surface) of many plants (Buée et al. 2009, Timonen and Bomberg 2009). As part of prokaryotic communities living inside plant tissues, archaea promote plant growth and are involved in nutrient cyclings of plant ecosystems (Timonen and Bomberg 2009, Jung et al. 2020, Sellappan et al. 2020). It has been recently demonstrated that plant archaeomes are highly diverse and distinct for different plant parts and host plant-specific (Trivedi et al. 2020). Moreover, archaea are vertically transmitted in native alpine plants as part of seed microbiomes (Wassermann et al. 2019).

We face, however, a gap of knowledge regarding archaea and their probable role as moss symbionts, which is astonishing concerning the numerous studies on methanogenic archaea and their metabolic activity in northern bog habitats (Krumholz et al. 1995, Kotsyurbenko et al. 2004, Galand et al. 2005, Metje and Frenzel 2005, Merilä et al. 2006, Cadillo-Quiroz et al. 2008, Bridgham et al. 2013, Tveit et al. 2014, Liebner et al. 2015, Martí et al. 2015, Reumer et al. 2018, Putkinen et al. 2018, Vigneron et al. 2019). To date, only one study has investigated the archaeome of different moss and *Sphagnum* species as part of an alpine bog vegetation (Taffner et al. 2018). The authors have stated that functional groups of moss-associated archaea are related to osmotic stress, purine metabolism and auxin biosynthesis and are thus beneficial for the hosts. It has already been mentioned previously that archaea are part of the bog core microbiota and display potential microbial keystone species with importance for their hosts and the whole bog ecosystem (Bragina et al. 2015).

1.3.3. Endophytic prokaryotic communities

Endophytes are microorganisms residing within plant tissues – the endosphere - such as leaves, roots and stems (Trivedi et al. 2020). Noteworthy, each individual of the 300.000 plant species existing, is host to one or more endophytes (Strobel and Daisy 2003).

Diversity and network complexity of endophytic prokaryotes is low compared to epiphytic (living on the plant surface) or soil microbiomes (Tian et al. 2020). Bacteria inhabiting plant roots tend to be phylogenetically clustered, which points towards a greater influence of the host plant on endosphere microbiome assembly (Trivedi et al. 2020).

Endophytic prokaryotes can supply a range of substances that provide protection and survival value to the host (Strobel et al. 2004). Plant processes are directly influenced by both the bacteria and archaea, but there is not enough knowledge on the mechanism on how endophytic prokaryotes contribute to host performance (Trivedi et al. 2020).

Endophytic prokaryotes enter the moss host through the cell pores. The water-filled hyalocytes of *Sphagnum* provide favourable conditions in terms of nutrients and pH, where versatile bacterial microcolonies are attached to the cell wall or thrive inside the internal spaces of the hyalocytes (Figure 5) (Granhall and Hofsten 1976, Bragina et al. 2012a). Endophytic bacteria can grow actively as clusters in stem hyalocytes and inhabit both, the emerged (growing above the water table, terrestrial) and the submerged *Sphagnum* parts (Raghoebarsing et al. 2005). It has been observed that isolated endophytic bacteria from different *Sphagnum* species are able to suppress the growth of phytopathogenic and toxigenic fungi and are thus potentially antagonistic (Shcherbakov et al. 2013), while symbiotic functional groups, such as methanotrophs and diazotrophs, contribute to the carbon and nitrogen budget of their host (Basilier and Granhall 1978, Raghoebarsing et al. 2005, Kip et al. 2011, Stępniewska et al. 2018, Tian et al. 2020). Owing to individual habitat preferences and the production of bioactive secondary metabolites, *Sphagnum* species display distinct endo- and epiphytic bacterial communities (Opelt et al. 2007b).

1.4. Biotic and abiotic influences on moss-associated microorganisms

The prevailing water regime is a key environmental factor that shapes the microbiomes of terrestrial and aquatic mosses (Leppänen et al. 2014, Wang et al. 2018), influencing for example the metabolic activity of the moss bacteriome (Raghoebarsing et al. 2005, Kip et al. 2010, van Winden et al. 2010). Contrarily, the role of pH remains ambiguous due to the interactions with other abiotic factors (Bragina et al. 2012b, 2012a, Jean et al. 2020, Rousk and Rousk 2020). It has further been shown that the community structure of moss bacteriomes alters with changing bog succession stages (Putkinen et al. 2014), but also with changes in temperature (Markham 2009, van Winden et al. 2012). Interestingly, also light seems to have an influence on metabolic activity of both, diazotrophic an methanotrophic moss associates (Basilier and Granhall 1978, Liebner et al. 2011, Larmola et al. 2014, Kox et al. 2020a).

Besides abiotic environmental factors, the surrounding vegetation may also have an impact on microbial communities (Borga 1994, Opelt et al. 2007a). However, the impact of the moss host on its prokaryotic assemblages and their metabolic activities remains ambiguous (Basilier and Granhall 1978, Basilier 1979, Opelt et al. 2007b, 2007a, Gavazov et al. 2010, Bragina et al. 2012a, Kox et al. 2020b), while some studies point even towards a peat bog-specific ‘core microbiome’, meaning microbial taxa that are common across the same plant species or plant microhabitats and potentially fulfil important functions for both, the host plants and the ecosystem (Bragina et al. 2015).

1.5. Objectives

Despite several studies on *Sphagnum*-associated bacterial communities and their environmental drivers, we face a knowledge gap regarding bacterial and archaeal communities associated with both, *Sphagnum* and brown moss taxa from different peatland types with diverging environmental conditions across a large geographical scale. No studies exist on the core microbiome of natural northern peatlands spanning from the High Arctic to the temperate zone, and its presumed role in the transition from minerotrophic fens to ombrotrophic peat bogs. Moreover, our understanding on the community structure of moss-associated methanotrophic bacteria and especially of methanogenic archaea and their potential metabolic activity within their host mosses remain sparse. Finally, moss-associated prokaryotes from adjacent pristine, disturbed and rewetted bogs not investigated so far so the effect of peatland degradation and restoration on structure and metabolic activity of moss-associated bacteria and archaea remains to be studied.

Therefore, the aims of this thesis were to

I. Unravel the bacterial and archaeal communities (defined as 'microbiome') of both brown mosses and *Sphagnum* species from northern bogs with a focus on epiphytic and endophytic assemblages.

II. Investigate the environmental drivers on moss-associated microbial assemblages across different peatland types on a large geographical scale.

III. Examine the prokaryotic core community of brown mosses, *Sphagnum* mosses, adjacent higher peat bog plants and soil.

IV. Estimate potential methane oxidation and methane production rates of moss-associated bacteria and archaea.

V. Investigate the *Sphagnum*-associated microbial communities of adjacent intact, rewetted and degraded peat bogs on a local scale.

For this purpose, a comparative large-scale study was designed spanning four brown moss and *Sphagnum*-dominated peatlands in the Arctic, subarctic and temperate zones. Moss and reference samples were collected from altogether 26 sites and the associated microbial community structures were related to various local environmental parameters. Moreover, potential methane oxidation and methane production rates mediated by bacteria and archaea were determined for both, brown mosses and *Sphagnum* mosses. The following section gives an overview on the four peatlands and the corresponding sub-sites which were studied during the course of this thesis.

1.6. Study sites

1.6.1. High Arctic peatlands of Svalbard (SV)

Svalbard is an archipelago in the Arctic Ocean, and the research settlement Ny-Ålesund (78.9° N, 11.9° E) is located on the western coast of the main island Spitsbergen. The annual temperature of Ny-Ålesund was around - 4,5°C between 1993 – 2011 (Maturilli et al. 2013). Ny-Ålesund is located within an 'Arctic semi-desert' with an annual precipitation of up to 300 mm (Lakka 2013). The vegetation consists mainly of bryophytes (e.g. *Sanionia uncinata*, *Aulacomnium turgidum*) and vascular plants (e.g. *Saxifraga oppositifolia*, *Salix polaris*, *Dryas octopetala* and *Luzula confusa*) (Muraoka et al. 2002).

In the vicinity of Ny-Ålesund, three Arctic ponds were chosen as sub-sampling sites: Twin Water (Norwegian: Tvillingvatnet) (TW) has a surface of 3.50 ha and a maximum depth of 6.3 m. The pond is fed by inflowing ground water from the talus of the Zeppelinfjellet Mountain (Haldorsen et al. 2010). Gluudneset (GLU) is a sandy headland located about 150 m from the shore, on level ground about 3-4 m above sea level and influenced by Arctic tern (*Sterna paradisaea*) and Barnacle geese (*Branta leucopsis*) (Bengtson et al. 1974, Lakka 2013). Knudsenheia (KNU) is a small lake at a marine terrace, about 300 m from the shore (Bengtson et al. 2013), with surrounding dense waterlogged moss layer and influenced by grazing *Branta leucopsis* and Svalbard reindeers (*Rangifer tarandus plathyrynchus*) (Alves 2011).

Figure 6: Sampling sites of Svalbard. a) Twin Water with submerged brown moss communities on its shore (b); c) Gluudneset with moss carpets above and below the water table (d); e) Knudsenheia with thick moss mats on stony ground (f). Photos by A. Kiss

1.6.2. Polygonal Tundra of Samoylov (SA)

Samoylov Island (72.4° N, 126.5°) is located in the Arctic Siberian Lena Delta and has an area of 1200 ha. It is characterised by a mean annual temperature of -14.7°C and a mean annual precipitation of 190 mm. The landscape is covered by ice wedge polygons with typical tundra vegetation consisting of dwarf shrub *Dryas punctata*, various *Carex* species and mosses such as *Hylocomium splendens*, *Timmia austriaca*, *Limprichtia revolvens* and *Meesia longiseta*. (Hubberten et al. 2003), but also brown mosses like *Scorpidium scorpioides*, *Drepanocladus cossonii* and *Warnstorfia exannulata* (Liebner et al. 2011). Samples were taken from various sites represented by three different polygon types: low-centred polygonal ponds with an open pond surface and a deep waterbody, low-centred polygonal ponds with sedge coverage and a shallow water body, and high-centred, dry polygons.

Figure 7: Sampling sites of Samoylov. a) low-centred, deep polygonal pond with open water and submerged *Scorpidium scorpioides* growing completely under the water table (b); c) low-centred, shallow polygonal pond with *Carex aquatilis* and submerged *S. scorpioides* reaching the water table (d); e) dry low-centred polygon with various moss species and vascular plants (f). All depicted polygons are examples for sub-sampling sites. Photos by A. Kiss

1.6.3. Palsa Bogs of Neiden (NEI)

Neiden (69.7° N; 29.4° E) is located in the county of Troms of Finnmark, Northern Norway within the subarctic zone. The annual average temperature between 1965 and 2011 was -0.6°C and the annual mean precipitation was about 435 mm. (Liebner and Svenning 2013). The Bøttemyra mire is characterised by palsas which show a declining trend since the end of the 19th century, most likely due to global warming (Hofgaard 2003, Johnsen 2012). The vegetation consists of *Ledum palustre*, *Empetrum sp*., *Pleurozium sp*. and *Rubus chamaemorus* and various sedges such as *Eriophorum vaginatum* and *Carex* spp. Within the surrounding palsa peatland, three different successional palsa stages were selected as sub-sampling sites: currently degrading palsas with adjacent thermokarst ponds, inhabited by *Sphagnum riparium*, thermokarst ponds with *S. riparium* as remnants of collapsed palsas and hollows with *Sphagnum lindbergii*, representing old successional stages of previously collapsed palsas.

Figure 8: Sampling sites of Neiden. a) degrading palsa mound with an adjacent thermokarst pond and floating mats of aquatic *Sphagnum fallax* (b); c) thermokarst pond remaining from a lately collapsed palsa with a dense carpet of submerged *S. fallax* (d); e) hollow as remnant of previously collapsed palsa with terrestrial *S. lindbergii* (f). All depicted palsa successional stages represent examples for sub-sampling sites. Photos by A.Kiss

1.6.4. Kettle Bog Peatlands of Mueritz National Park (MUE)

The Mueritz National Park (53.3° N, 13.2° E) is located in Northern Germany within the temperate zone. The mean annual temperature is 7.8°, the mean annual precipitation is 593 mm. Several kettle bogs are located within the near-natural beech forest (*Fagus sylvatica*) Serrahn (Von Oheimb et al. 2005), of which three bogs were chosen for sampling:

Kiebitzmoor (KIE), a disturbed and rewetted kettle bog with non-typical vegetation like *Drosera rotundifolia*, *Rhynchospora alba*, *Juncus effusus*, *Typha latifolia* and *Carex curta*, influenced by animals such as wild boar (*Sus scrofa*).

Heidbergmoor (HEI), a typical oligotrophic rewetted kettle bog with species-poor *Sphagnum fallax-Eriophorum vaginatum* vegetation.

Klockenbruch (KLO) represents a pristine and intact kettle bog with an oligotrophic centre, which is inhabited by *Sphagnum magellanicum* and *Ledum palustre*, and a surrounding mesotrophic, waterlogged margin with *Sphagnum fallax* (T. Timmermann, personal communication).

Figure 9: Sampling sites of Mueritz National Park. a) Heidbergmoor, a hummock-hollow-complex with emerged and submerged *Sphagnum fallax* (b); c) Klockenbruch, a kettle bog with *S. fallax* at its margin and *S. magellanicum* growing at the elevated centre (d); e) Kiebitzmoor, a kettle bog with *S. magellanicum* (f). Photos by S. Liebner

2. Material and Methods

2.1. Sampling scheme overview

Two main ecosystems (brown moss- and *Sphagnum*-dominated peatlands) were studied, represented by four sites, which are analogous to different stages in the transition from fens to incipient ombrotrophic bogs: 1) High-Arctic lakes with mixed brown moss communities on Svalbard (SV); 2) Arctic polygonal tundra ponds with densely growing brown mosses on Samoylov Island (SA); 3) subarctic *Sphagnum* palsa peatlands in Neiden (NEI), and 4) temperate *Sphagnum* kettle bogs in the Mueritz National Park (MUE). An overview about the study sites and a simplified sampling scheme is given in Figure 10, and a detailed overview of the samples and the corresponding sampling sites, biotic (plant species) variables, environmental variables and geographical coordinates is provided in Tables S1A and S1B.

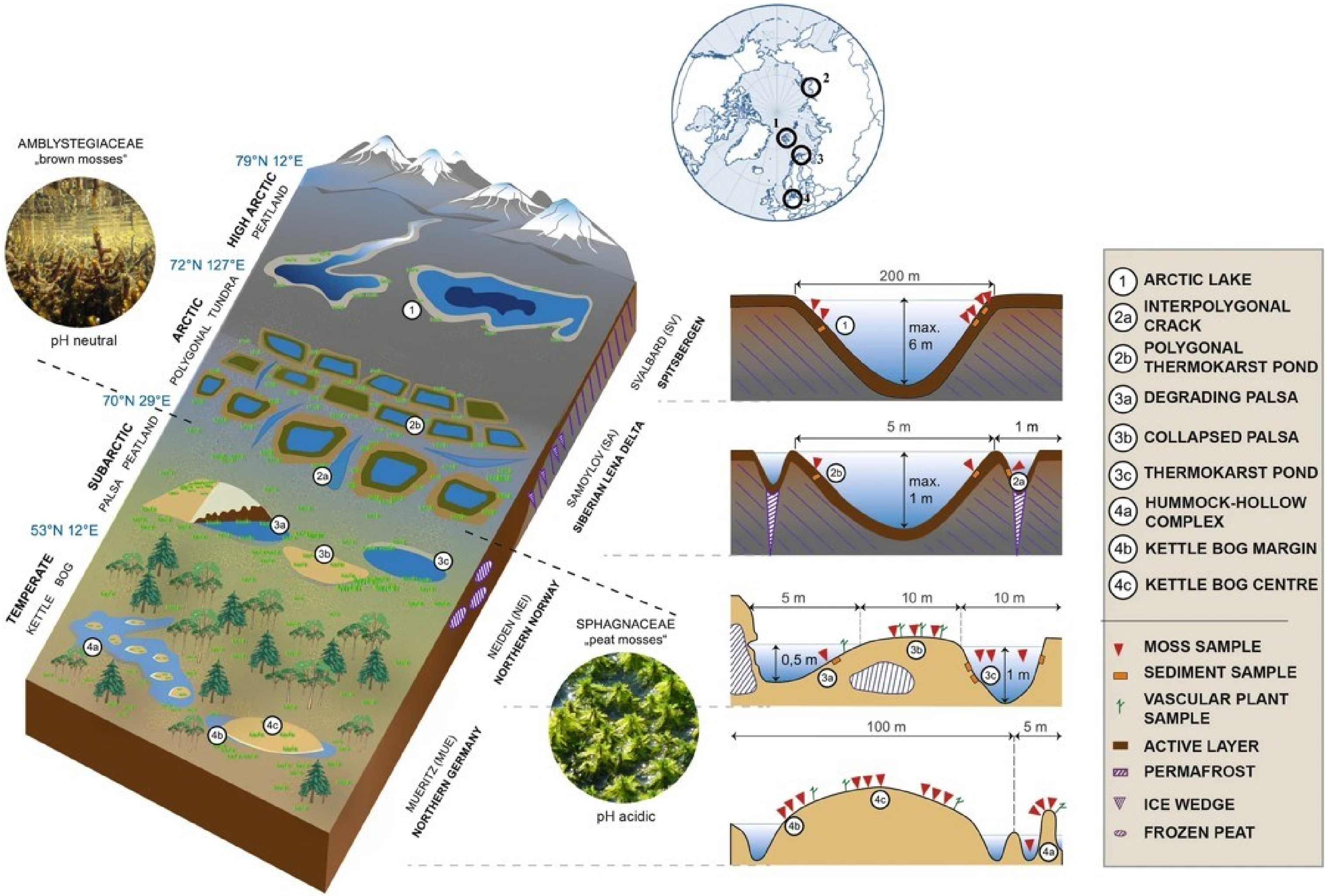


Figure 10: Schematic overview of the investigated sites and the collected sample types. The geographical location of the sampling sites is depicted above. The different peatland types are illustrated on the left, the sampling scheme is depicted on the right. Subsampling sites are not emphasized. Illustration: Grit Schwalbe, GFZ (modified)

2.2. Sampling of pore water

At each site, pore water was retrieved from three depths when possible; slightly above, within and below the moss layer by extracting small samples of pore water with perforated brass tubing according to Liebner et al., 2015. At the hummock sites, pore water was extracted from the shallowest depth possible. Ten-ml plastic syringes equipped with three-way valves were connected to the brass tubes and used to carefully suck out the pore water. Pore water was transferred to gas-tight 20-ml glass serum vials pre-treated with 100 µl 1 M HCl and pre-flushed with N_2 avoiding air bubbles and stored at 4 °C.

2.3. Sampling of moss plantlets

During a field campaign between June and September 2013, mosses for DNA extraction were sampled. On SV, submerged brown mosses from three sub-sites were collected: *Bryum pseudotriquetrum* in Twin Water (TW), *Drepanocladus trichophyllus* and *Scorpidium turgescens* in Knudsenheia (KNU) and *Drepanocladus revolvens* and *S. turgescens* in Gluudneset (GLU), each in duplicates (sample type 1; all sample types are depicted in Figure 10). On SA, a mixture of submerged *Scorpidium scorpioides* and *Meesia triquetra* from an interpolygonal crack (PC; sample type 2a) and *S. scorpioides* from a polygonal pond (three replicate of plants subsumed to PP; sample type 2b) were collected. At both locations, SV and SA, sediment underneath the mosses was sampled as references. In NEI, different successional palsa stages were selected: thermokarst ponds with *Sphagnum riparium* adjacent to degrading palsas (one plant within each of the subsites NEI1, NEI2;

sample type 3a), thermokarst ponds with *S. riparium* as remnants of collapsed palsas (one plant within each of the subsites NEI3, NEI4; sample type 3c) and hollows with *Sphagnum lindbergii*, representing old successional stages of previously collapsed palsas (one plant within each of the subsites NEI5, NEI6, NEI7; sample type 3b). From MUE, three subsites were chosen: Heidbergmoor, a hummock-hollow complex (sample type 4a) with emerged *Sphagnum fallax* (three replicate plants within the subsite called HEI2) and submerged *S. fallax* (one plant within the subsite called HEI1); Klockenbruch, a kettle bog with an oligotrophic, elevated centre (sample type 4c) with *Sphagnum magellanicum* (three replicate plants within KLO1) and a meso-oligotrophic, lower margin (sample type 4b) with *S. fallax* (three replicate plants within KLO2); Kiebitzmoor, a formerly drained and rewetted kettle bog (sample type 4c) with *S. magellanicum* (three replicate plants within KIE). In NEI we collected the sedges *Eriophorum* sp. and *Carex* sp. (NEI1, NEI5, NEI6, NEI7) and sediment underneath the mosses (NEI1, NEI2, NEI3, NEI4) as references, with duplicates for each site and reference type. In MUE, *Eriophorum vaginatum* (HEI2, KLO1 and KLO2) and *Carex* sp. (KIE) were collected as references with duplicates for each site and plant type. Peat or moss batches were sampled using gloves and sterile knifes or spoons. Leaves, stem and upper root material of vascular plants were manually extracted from the peat body, washed with sterilised tap water for removal of organisms from the surrounding environment, cut and used as a bulk reference sample. Complete moss individuals were sampled and also washed with sterilised tap water prior to storage. All samples were stored at − 80 °C immediately after sampling until further processing except for the samples from SA which were continuously stored at − 20 °C.

Mosses for activity measurements were sampled during a field campaign in 2014. Sampling sites corresponded to those in 2013, except for S8 (SA), which represented a dry low-centred polygon with a mixture of emerged brown mosses, containing *Meesia* sp., *Warnstorfia* sp. and *Drepanocladus* sp. Mosses were taken with gloves and a sterile forceps, placed into Ziplock® plastic bags and stored at -20°C for transport and storage until activity measurements.

2.4. Analysis of pore water chemistry

The pore water analysis included determinations of pH, temperature, CH_4, DOC and O_2. Values of pH were measured in the field using a multi parameter probe Multi 350i from WTW (Laboratory and Field Products, Nova Analytics). Air and peat temperatures were measured with a hand-held digital thermometer 2000T (Thermocouple Thermometer, Digitron Instrumentation Ltd, England) equipped with a 50 cm long probe. Pore water methane concentrations were measured in triplicates by gas chromatography shortly after pore water sampling as described elsewhere (Liebner et al. 2015). Briefly, the gas samples within the headspace were taken with a gas-tight syringe (Hamilton Bonaduz AG, Bonaduz, Switzerland), and analysed using a gas chromatograph (7890A GC system, Agilent Technologies, USA), equipped with an HP-PLOT capillary column (Ø 0.53 mm, 30 m in length) and a flame ionisation detector (FID) with helium as carrier gas (injector: 45°C; detector: 250°C), which was calibrated with standard gases prior to measurements. For the determination of DOC values, 20 ml glass vials (Agilent) were flushed with ultrapure water, baked at 550 °C for 2 h, closed with aluminium-sealed PTFE/butyl septa and acidified with 3% HCl Suprapur (VWR). 15 ml of the pore water was filtered with 0.7 µm GF/L filter (Whatman). The samples were sent to 'Potsdamer Wasser- und Umweltlabor GmbH' (PWU) for DOC analysis. Pore water O_2 contents were measured in the field at different depths (above, within and below moss layer, where possible), using an optical oxygen meter (FireStingO_2, PyroScience).

2.5. Cell wall analysis

2.5.1. Cation exchange capacity (CEC)

Up to 45.0 mg of dry moss samples were sealed into labelled polyamide mesh bags. The bags were submerged in 2 l of 20 mM HCl to soak the moss up and to convert all carboxylic cation-exchange sites to undissociated form; free protons were then replaced by repeated thorough wash with distilled water. All the bags were then transferred to 2 l of 0.5 M ammonium acetate ($NH_4CH_3CO_2$) and after pH equilibration the ammonium acetate solution was renewed and adjusted to pH 7.0 using Ammonia Solution (NH_4OH). The bags were repeatedly washed with large amount of distilled water to replace free NH_4^+ and dried.

The bags were individually immersed to 50 ml of 20 mM HCl and shaken for 15 min to elute cell-wall bound NH_4^+ ions. The eluate was sampled and NH_4^+ analysed colorimetrically using Flow Injection Analysis (Foss Tecator AB, Sweden).

2.5.2. Holocellulose (HC)

Dry plant samples were ball-milled for 2 min at 30 Hz to fine dust (MM200, Retsch) and about 40.0 mg of the material was washed with 5 ml of 70% acetone in 15 ml Falcon® tubes and subsequently oven-dried in the tubes at 48 °C. Next, 8 ml of H_2O, 75 µl of glacial acetic acid (CH_3COOH) and 150 µl of 25% sodium chlorite ($NaClO_2$) were added. The tubes were closed shaken and incubated for 1 h in a water bath at 75 °C, being shaken every 10 min. The additions of acetic acid and sodium chlorite and the incubation was repeated three times. Afterwards, samples were cooled and centrifuged at 4000 × g for 15 min, supernatant was discarded. 10 ml H_2O was added, samples were vortexed and centrifuged at 3000 × g, supernatant was discarded. This wash step was repeated twice, followed by drying at 70 °C. The residuum is referred to as holocellulose (structural polysaccharides) and expressed in % of dry mass.

2.5.3. Lignin and Lignin-like polymers (LLP)

To remove phenolic extractives that can interfere with later spectrophotometric determination of acid-soluble Klason lignin (KL), up to 60.0 mg of milled plant material was shaken with 5 ml of 70% acetone ($(CH_3)_2CO$) in 15 ml Falcon® tubes for 1 h. The tubes were then centrifuged, supernatant discarded, and the pellets dried in the tubes at 48 °C. Next, 0.4 ml of 72% sulphuric acid (H_2SO_4) was added to the pellet, the tubes were vortexed and incubated for 1 h at 23 °C, followed by addition of 11.2 ml of H_2O, vortexing and incubation at 100 °C for 2.5 h. The tubes were then centrifuged at 3000 × g for 15 min and the supernatant was sampled for dissolved lignin analysis and discarded. The pellet (Klason lignin, acid-insoluble residuum) was washed three times with 10 ml of water, centrifuged, oven-dried at 70 °C and expressed in % of dry mass. Acid-soluble Klason lignin was measured spectrophotometrically at 205 nm (standard mass attenuation coefficient of 110 l g^{-1} cm^{-1} was applied according to Hatfield and Fukushima 2005) and expressed in % of dry mass. Acid-soluble Klason lignin and Klason-lignin were summed to Total Klason lignin (representing lignin-like phenolics in mosses as they lack true lignin).

2.5.4. Bulk moss litter analysis

Plant samples were dried and milled (Pulverisette, Fritsch). About 5.0 mg of sample was weighed in tin boats (Elementar). Total carbon (TC) and total nitrogen (TN) contents were determined as double measurements with a carbon, nitrogen and sulphur (CNS) analyser (Elementar Vario EL III). For determining C:N ratios (C/N), quotients of TC and TN were calculated.

2.6. Moss surface sterilisation and separation of putative epiphytic and endophytic microbial communities

Between 2.2 and 5.3 g of the moss material pre-treated as described above was thawed and amended with extraction buffer containing ultrapure DEPC water (AppliChem), 0.85% Sodium chlorite (NaCl) (Merck), and 0.01% Tween20 (AppliChem) in a ratio 2:1 (weight percent), modified after (Ikeda et al. 2009). The mixture was shaken horizontally for 1 h at 4 °C prior to ultrasonication (Bandelin Sonoplus HD3100) with pulsation for 2 min (1 s off, 2 s on) at 0.45 W/ml (Morris et al. 1998). Extraction buffer containing the epiphytes was filtered through a 0.2 µm cellulose filter (Sartorius Stedium). The remaining moss was surface-sterilised with 0.15% sodium hypochlorite (NaOCl) (Roth) for 1 min, and rinsed seven times with DEPC water according to a modified protocol by Bay et al., 2013. Filters and sterilised mosses were ground to powder under sterile conditions with liquid nitrogen, transferred to lysis tubes and stored at − 20 °C until DNA extraction. For each moss sample, one filter with wash-off (epiphytes) and two technical replicates of the surface-sterilised moss (putative endophytes) were used for DNA extraction and sequencing.

2.7. DNA extraction and sequencing

For the extraction of genomic DNA, 0.4–0.8 g of each the surface treated mosses, the filters containing the wash-off, the untreated sedges and sediment samples were taken following the CTAB/phenol–chloroform-based method after (Griffiths et al. 2000). The concentrations of the DNA yields were quantified with a Nanophotometer P360 (Implen GmbH, München, Germany) and a Qubit 2.0 Fluorometer (Thermo Fisher Scientific, Darmstadt, Germany) according to the manufacturer's protocols. 16S rRNA genes of bacteria were amplified with the primer combination S-D-Bact-0341-a-S-17 and S-D-Bact-0785-a-A-21 (Herlemann et al. 2011), while the archaeal 16S rRNA genes were amplified with the primer combination S-D-Arch-0349-a-S-17 and S-D-Arch-0786-a-A-20 (Takai and Horikoshi 2000). All primers were labelled with various combinations of barcodes listed together with primer sequences in Table S1B. The PCR mix consisted of 1 × PCR buffer (Tris·Cl, KCl, $(NH_4)_2SO_4$, 15 mM $MgCl_2$; pH 8.7) (QIAGEN, Hilden, Germany), 0.5 µM of each primer (Biomers, Ulm, Germany), 0.2 mM of each desoxynucleoside

(Thermo Fisher Scientific, Darmstadt, Germany), and 0.025 U μl^{-1} hot start polymerase (QIAGEN, Hilden, Germany). The thermocycler was preprogramed to 95 °C for 5 min (denaturation), followed by 40 cycles of 95 °C for 1 min (denaturation), 56 °C for 45 s (annealing) and 72 °C for 1 min and 30 s (elongation); the final elongation step was performed at 72 °C for 10 min. PCR products were purified with a Hi Yield Gel/PCR DNA fragment extraction kit (Süd-Laborbedarf, Gauting, Germany) following the manufacturer's protocol. The PCR products obtained from three individual runs per sample were combined. PCR products of different samples were pooled for sequencing in equimolar concentrations and compressed in a vacuum centrifuge Concentrator Plus (Eppendorf, Hamburg, Germany) to a final volume of 10 µl with a concentration of 200 ng/µl. The sequencing and library preparation was performed by the company GATC (Konstanz, Germany) on an Illumina MiSeq sequencer according to their standard protocols. The library was prepared with the MiSeq Reagent Kit V3 for 2 × 300 bp paired-end reads. To consider for the low-diversity amplicon sampling, 15% PhiX control v3 library was used.

2.8. Sequence analyses and bioinformatics

Raw data was demultiplexed using CutAdapt (Martin 2011); e 0.1; –trim-n; no error in barcodes allowed. Paired-reads were merged using PEAR (Zhang et al. 2014) (Q25; p 10^{-4}; v20), while sequence orientation was standardised using own scripts. All sequences of low quality were filtered and trimmed using Trimmomatic (Bolger et al. 2014) (LEADING:25; TRAILING:25; SLIDINGWINDOW:5:25; MINLEN:200). According to the

QIIME SOP (Caporaso et al. 2011), all chimeras were removed. Reads were finally clustered into Operational Taxonomic Units (OTUs) using QIIME' pick_open_reference.py script with a cutoff value of 97% (Caporaso et al. 2011). Representative sequences of the clusters were annotated with usearch using the curated Greengenes 13.8 taxonomy database (McDonald et al. 2012). OTUs with a small, sample-wise relative abundance (< 0.01%), OTUs assigned to chloroplasts and bacterial OTUs within archaeal samples and *vice versa* were filtered before further exploration.

2.9. Statistical analyses

In order to obtain the differences in microbial community composition between the sites, the inverse Simpson index was calculated and the number of OTUs as measures of the OTU diversity and richness, respectively, were counted. The bubble plot in Figure 15 was generated with the package 'ggplot2' (version 2.2.0) within the statistical software R (version 3.2.2) (R Core Team 2015).16S rRNA gene datasets of either bacteria or archaea as correlation matrices of samples were generated using the R function 'cor', specifying the Spearman rank correlation coefficient. Based on the correlation matrices to generate dendrograms, hierarchical clustering of the samples was calculated using the method 'agnes' within the R package 'cluster', with default settings. All heatmaps were compiled using the R package 'heatmap3' (version 0.3.3). For bacteria, the inverse Simpson index diversity estimates were calculated using the R package 'asbio' (version 1.6-5). For environmental variables, pairwise t-tests were used and carried out using the R function 'pairwise.t.test'. For diversity indices, pairwise Mann–Whitney-Wilcoxon tests were used and carried out using the R function 'pairwise.wilcox.test'. In order to quantify the explanatory power of biotic and environmental variables with respect to the microbial ecology of the peatlands, canonical correspondence analysis (CCA) was carried out (package: vegan (version 2.2.1)). Correspondence analysis (CA) was carried out as described before (Greenacre 2007) and plotted using 'ggplot2'. Due to lacking observations for between 23 and 45% of the samples, eight variables (cation exchange capacity, lignin-like polymers, holocellulose, total nitrogen, total carbon and C:N ratio, DOC, oxygen and water content) were removed from the initial full model. Variation in the microbial communities were constrained to the remaining variables; (1) sites (SV, SA, MUE and NEI), (2) subsite (e.g., KIE1), (3) plant species or reference sediment, (4) location above or below water table, (5) washed and surface-sterilised moss plant (putative endophytes) or wash-off (epiphytes) (6) pH, (7) methane concentration in pore water, and (8) temperature. In order to estimate and account for the spatial autocorrelation that the sites (1) and subsite (2) variables represent, partial CCA was introduced. Running the model without (1) and (2) showed that the constrained inertia was reduced from 72% of total inertia to 40%. Subsequent analysis of variance inflation factors revealed that no remaining variables were redundant. To be considered part of the core microbiota, an OTU had to be present in 80 out of 122 samples and in both system types (brown moss and *Sphagnum*), reflecting a restrictive 66% threshold. Using this threshold, core communities were calculated. moss system core communities (brown moss or *Sphagnum*) were calculated, while moss species communities were calculated with a more restrictive threshold of 75% (Bragina et al. 2015).

2.10. Potential methane production and oxidation assays

After preliminary tests, the following samples were chosen for both, CH_4 production and CH_4 oxidation tests: KNU (mix of submerged *Drepanocladus trichophyllus* and *Scorpidium turgescens),* GLU (mix of submerged *Drepanocladus revolvens* and *S. turgescens*), S0 (submerged *Scorpidium scorpioides*), S8 (mix of emerged *Meesia* sp., *Warnstorfia* sp. and *Drepanocladus* sp.), NEI 1 (submerged *Sphagnum riparium*), NEI 2 (emerged *Sphagnum lindbergii*), KLO mag (emerged *Sphagnum magellanicum*), KLO fall (emerged *Sphagnum fallax*), HEI fall (emerged *Sphagnum fallax*) and HEI fall sub (submerged *S. fallax*). All samples were subdivided into four different series: non-sterile moss ('epiphytes') with and without inhibitor (acetylene) and surface-sterilised moss ('endophytes') with and without inhibitor. Triplicates were prepared from every sample.

2.10.1. Surface sterilisation prior to activity tests

Owing to the large amount of moss material needed, the surface sterilisation protocol used prior to DNA extraction had to be modified: appr. 5.0 g fresh moss material were washed three times with 1000 ml sterile tap water (autoclaved at 120°C for 2h) and soaked in 0.15% NaOCl for 1 min. Then, mosses were rinsed with sterile tap water and placed into 120 ml serum vials, sealed with butyl rubber stoppers and a crimp, except for 1-2 plantlets that were used for sterility check. Therefore, they were pressed onto prepared agar plates, sealed with parafilm® (amcor) and incubated at room temperature for five days.

2.10.2. Methane production

Fresh moss material (5.0 g) was weighed into 120 ml serum vials, sealed with butyl rubber stoppers and a crimp. For CH_4 production, sample vials were flushed with N_2/CO_2 (1,5 bar; 80:20 v/v). Subsequently, all vials were thoroughly vortexed and incubated at room temperature in the absence of light. Prior to measurements, the gas chromatograph (7890A GC system, Agilent Technologies, USA), equipped with an HP-PLOT capillary column (Ø 0.53 mm, 30 m in length) and a flame ionisation detector (FID) with helium as carrier gas (injector: 45°C; detector: 250°C), was calibrated with standard gases. Gas samples were taken with a gas-tight glass syringe. CH_4 production rates were calculated from the linear increase in CH_4 concentration.

2.10.3. Methane oxidation

Fresh moss material (5.0g) was weighed into 120 ml serum vials, sealed with butyl rubber stoppers and a crimp. Sample vials were flushed with synthetic air (20% O_2, 80% N_2) and supplied with 1,5% CH_4 within the headspace. Further, 60 nl acetylene (C_2H_2) per ml headspace was added to samples that were intended as negative controls (Wagner 2017). Subsequently, all vials were thoroughly vortexed and incubated at room temperature in the absence of light. Prior to measurements, the gas chromatograph (7890A GC system, Agilent Technologies, USA), equipped with an HP-PLOT capillary column (Ø 0.53 mm, 30 m in length) and a flame ionisation detector (FID) with helium as carrier gas (injector: 45°C; detector: 250°C), was calibrated with standard gases. Gas samples were taken with a gas-tight glass syringe. CH_4 oxidation rates were calculated from the linear decrease in CH_4 concentration within the headspace.

3. Results

3.1. Peatland bulk and pore water characteristics

The sites Svalbard (SV) and Samoylov (SA) were inhabited by brown mosses and represented minerotrophic fens at the earliest stages of peat formation (‘terrestrialisation’), with circumneutral pH values ranging from 5.8–7.0. The sites Neiden (NEI) and Mueritz (MUE) were dominated by the genus *Sphagnum* and represented later stages of peat formation, (´paludification´) with acidic pH values ranging from 3.3–5.0, thus significantly lower than in SV and SA (Figure 11A). DOC values were significantly higher in *Sphagnum* compared to brown moss-dominated peatlands, with the highest concentrations observed in MUE (42.7–229 mg l^{-1}) and lowest in SV (0.9–6.4 mg l^{-1}) (Figure 11B). Methane concentrations were also significantly higher in the *Sphagnum* compared to the brown moss ecosystems, with the highest range of concentrations in MUE (21.8–948 µM) and the lowest in SV (0–124 µM) (Figure 11C). The average soil temperature at the time of sampling was highest in MUE (16.0 °C, range 14.5–17.6), followed by SA (13.0 °C, range 4.0–19.5), NEI (12.6 °C, range 2.0–20.7 °C) and SV (9.8 °C, range 7.1–12.1 °C) (Figure 11D).

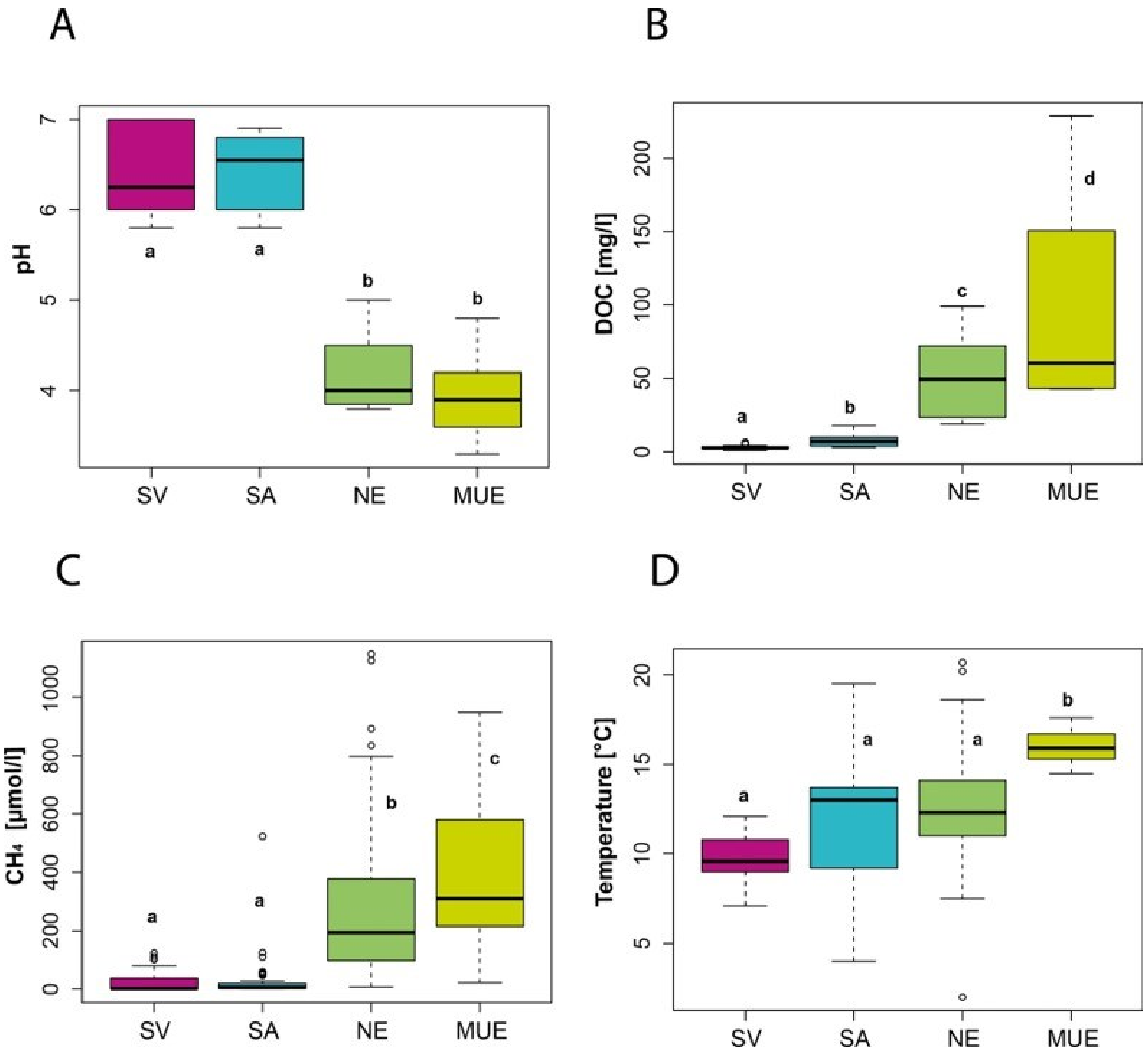


Figure 11: Box plots showing the measurements of selected environmental variables. (A) pH, (B) dissolved organic carbon (DOC), (C) methane and (D) temperature of all subsites in Svalbard (SV, magenta), Samoylov (SA, blue), Neiden (NEI, dark green) and Mueritz (MUE, light green). Pairwise t-tests suggest that samples with different letters show a significant ($p < 0.05$) difference in the mean value between each other. Graphs: Sizhong Yang

Table 1: Cell wall and bulk moss litter analysis. Cation exchange capacity (CEC), total Klason lignin (KL), holocellulose (HC), carbon (C), nitrogen (N), sulphur (S) and C:N ratios (C/N) of brown moss mix samples from Svalbard (SV) and Samoylov (SA) and *Sphagnum* samples from Neiden (NEI) and Mueritz (MUE); n.d. = no data.

Moss species	Site	CEC	total KL	HC	C	N	S	C/N
		[µeq g^{-1}]	[% of dm]	[% of dm]	[% of dm]	[% of dm]	[% of dm]	
Amblystegiaceae								
Drepanocladus revolvens/ Bryum pseudotriquetrum	SV	430,5	49,4	56,4	28,2	1,3	0,3	22,2
Scorpidium turgescens/ Drepanocladus revolvens	SV	668,2 ± 48,7	37,1 ± 0,7	32,9 ± 3,4	30,7 ± 11,0	1,1 ± 0,4	0,1 ± 0,0	28, 3
Scorpidium scorpioides/ Meesia triquetra	SA	565,9	42,7	35,2	64,1	1,2	0,2	52,8
Scorpidium scorpioides	SA	589,3 ± 20,5	40,8 ± 0,8	40,7 ± 4,8	32,7 ± 1,3	0,9 ± 0,0	0,5 ± 0,1	36,7
Sphagnaceae								
Sphagnum lindbergii	NEI	664,5 ± 62,0	16,1 ± 4,6	51,4 ± 5,1	45,5 ± 0,4	0,5 ± 0,0	0,5 ± 0,3	94,5
Sphagnum riparium	NEI	439,0 ± 37,4	12,7 ± 3,3	44,2 ± 0,7	44,0 ± 1,7	1,5 ± 0,6	0,7 ± 0,3	30,3
Sphagnum fallax (emerged)	MUE	625,8 ± 73,4	22,4 ± 6,7	62,3 ± 2,8	46,3 ± 2,9	1,2 ± 0,2	0,2 ± 0,1	39,3
Sphagnum fallax (submerged)	MUE	400,6	n.d.	n.d.	44,5	3,1	0,2	14,3
Sphagnum magellanicum	MUE	773,1 ± 31,0	21,7 ± 7,7	57,4 ± 5,2	45,6 ± 0,7	0,8 ± 0,1	0,3 ± 0,3	55,3

3.2. Diversity and structure of natural peatland microbial communities

Between 2510 and 289.604 sequences (average of 78.933, median of 68.070 and standard deviation of 60.092) were obtained for the 122 bacterial data sets. For the 86 archaeal datasets, between 536 and 83.642 (average 12.626, median of 4892 and standard deviation of 17.424) sequences were obtained. Due to methodological issues (no PCR product obtained or failed sequencing), it was not possible to generate 16S rRNA gene amplicon libraries from 35 samples with bacterial primers and 71 samples with archaeal primers out of the 157 collected samples.

Compared to the *Sphagnum*-dominated NEI and MUE sites, there was a significantly higher bacterial diversity and OTU richness in the moss and reference samples from brown moss-dominated SV and SA sites (Figure 12).

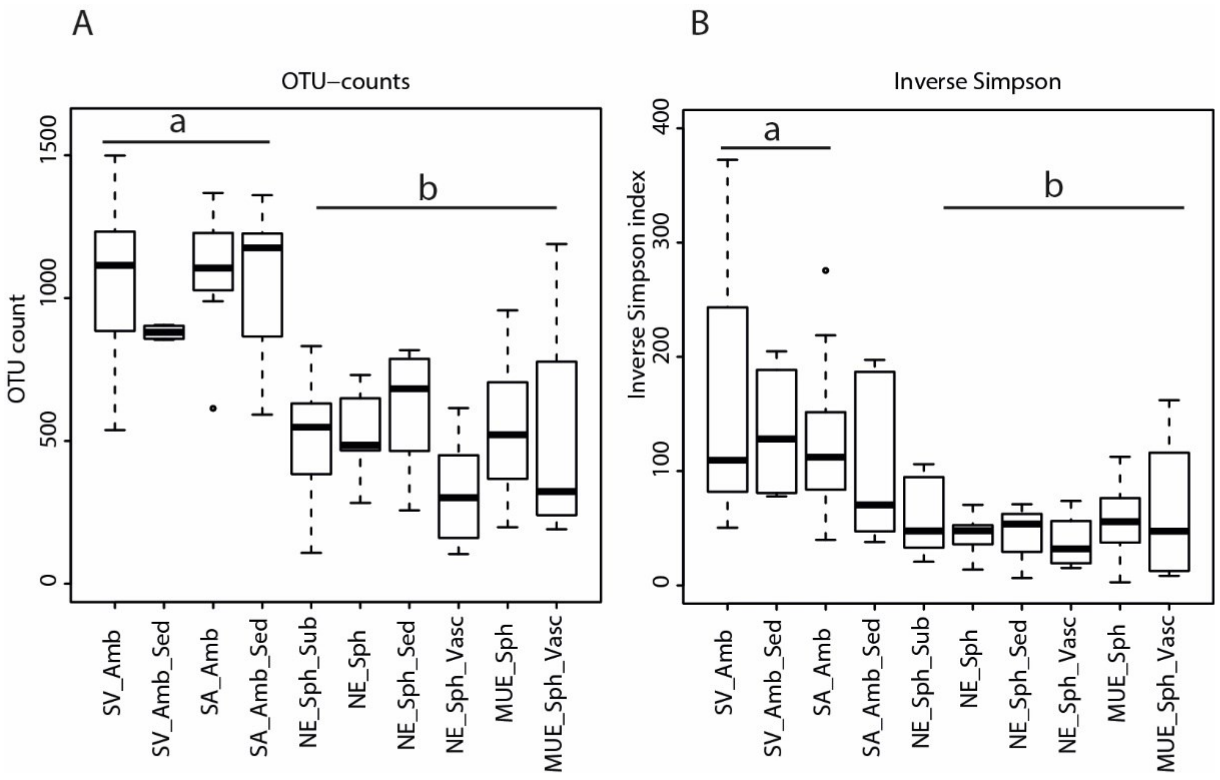


Figure 12: Box plots illustrating bacterial alpha-diversities of all sample types. Panel A: Observed OTU; Panel B: Calculated Inverse Simpson Index; according to a pairwise Mann-Whitney-Wilcoxon test (significance level set to 0.05), mean diversities of samples from brown moss-dominated sites (group a) are overall significantly different to *Sphagnum*-dominated sites (group b). Amb = Amblystegiaceae (brown mosses), Amb_Sed = sediment references to brown mosses, Sph = *Sphagnum*, Sph_Sed = sediment references to *Sphagnum*, Sph_Vasc = vascular plant references to *Sphagnum*. Graphs: Alexander Tveit.

The microbial communities in the brown moss-dominated sites displayed the same level of diversity, independent of the geographical location. Contrarily, the archaeal diversity was similar between the brown moss and *Sphagnum* peatlands with overall little differences between mosses, sediments and vascular plants (Figure S2), except for the sediment samples of brown moss peatland origin, which displayed slightly higher archaeal richness than the other sites within these ecosystems.

3.3. Environmental drivers of moss-associated microbial communities

In order to identify the association between moss taxa, abiotic environmental variables and the bacterial moss microbiota, a canonical correspondence analysis (CCA) was performed. Using variance partitioning, the contribution of the variables to the explanation of total inertia was quantified in the following order from most to least important: (1) plant species and reference sediment: 19.7% (p. value < 0.001), (2) temperature: 4.8% (p. value < 0.001), (3) putative endophytes or epiphytes: 4.6% (p. value < 0.001), (4) methane concentration in pore water: 4.1% (p. value < 0.001), (5) pH: 3.3% (p. value < 0.001) (6) location above or below water table: 3.2% (p. value < 0.001). By repeating the procedure with Hellinger transformed data to control for large effects of low abundant OTUs, the same patterns could be observed at highly similar total and constrained inertia, suggesting a minor impact of rare OTUs on CCA ordination. The initial model included sites and subsites in addition to the six above mentioned variables, which accounted for 32% of the differences between the microbial communities (see materials and methods). By removing site effects due to the correlation with plant species, the influence of latter may be substantially underestimated. However, the removed fraction of the inertia contained in the site variables were considered as ‘environment’, meaning a mix of abiotic and biotic variables that cannot be studied in isolation with the present dataset. Owing to the complexity of the dataset, it was not possible to visualise the major gradients by a single CCA plot. With regard to this, the constraints of the final model above were plotted separately (Figure 13).

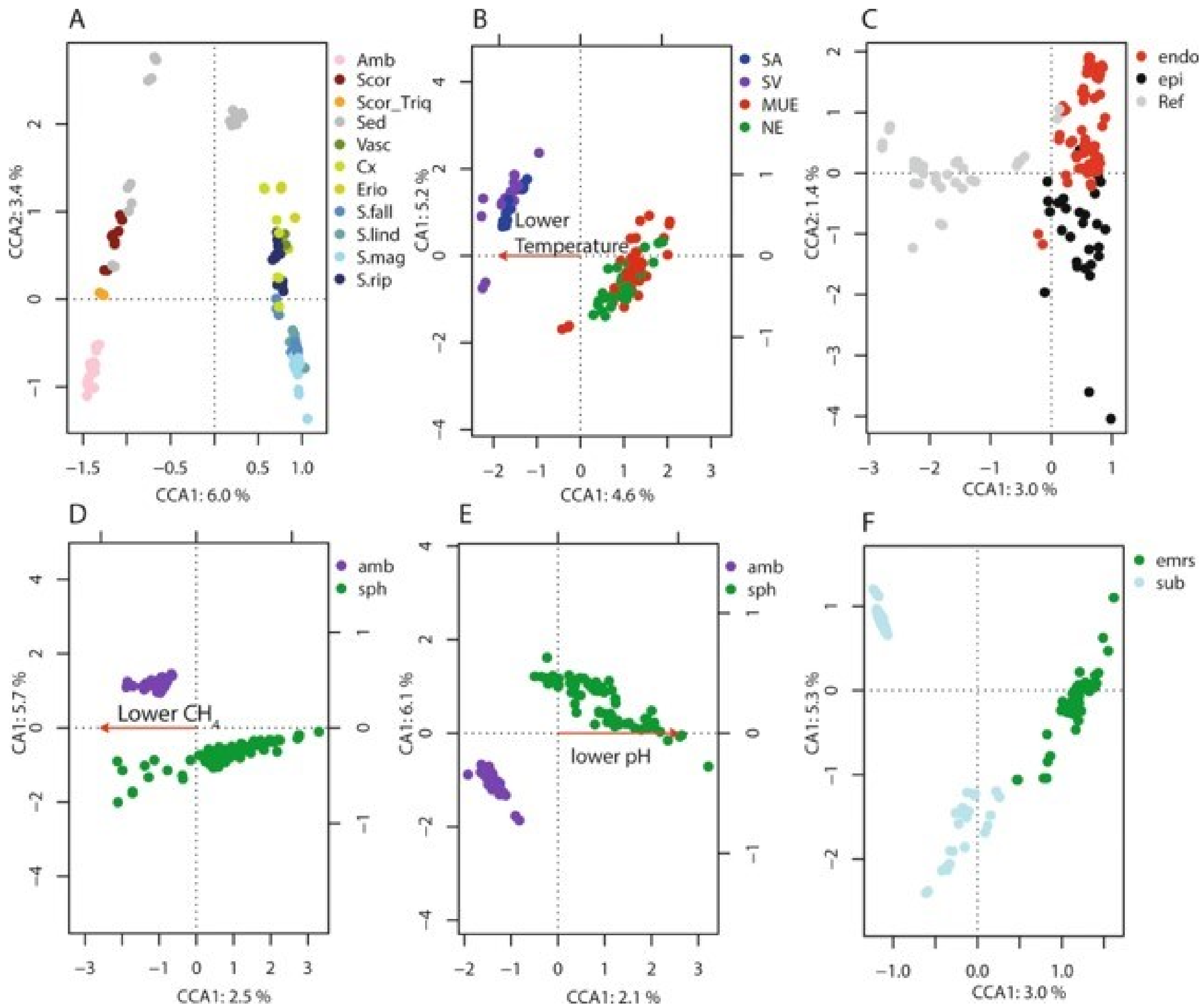


Figure 13: Canonical correspondence analysis of moss-associated bacterial OTUs. In case of categorical variables with more than two factors, the axes represent the first and second CCA dimension (A, C), whereas in case of two factors or continuous variables (B, D, E, F) the first CA dimension is showed on the Y-axis, while the CCA dimension is showed on the X-axis. (A): Restricted by plant species and reference sediment; Amb: Brown moss mix; Cx: Carex; Erio: Eriophorum; S.fall: *Sphagnum fallax;* S.lind: *Sphagnum lindbergii*; S.mag: *Sphagnum magellanicum*; S.rip: *Sphagnum riparium*; Scor: *Scorpidium scorpioides*; Scor_Triq: Mix of *Scorpidium scorpioides* and *Meesia triquetra*; Sed: Sediment; Vasc; Mix of vascular plants. (B) Restricted by location above or below the water table; emrs: Above the water table; sub: Below the water table. (C) Restricted by putative endophytic: endo; putative epiphytic: epi; reference sample: Ref. (D) Restricted by pH samples coloured by System; amb: Brown mosses; sph: *Sphagnum*. (E) Restricted by temperature, samples coloured by sampling sites; MUE: Mueritz; NEI: Neiden; SA: Samoylov; SV: Svalbard. (F) Restricted by CH_4 concentration in pore water, samples coloured by peatland type; amb: Brown moss-dominated; sph: *Sphagnum*-dominated.

The plots show that the bacterial communities correlate substantially with the moss or vascular plant species (Figure 13A), further by submerged or emerged conditions (Figure 13F).

Since both submerged *S. fallax* and *S. riparium* samples clustered together (Figure 13A), the water table had apparently a stronger impact on the microbiota than the host moss species. There were also clear differences between endophytic and epiphytic communities (Figure 13C). Furthermore, considerable differences between the bacterial communities from brown moss- and *Sphagnum*-dominated peatlands were visible (Figure 13B, E), in line with the differences in pH and temperature, whereas the effects of altered CH_4 concentrations on the bacterial communities were similar in brown moss and *Sphagnum* ecosystems (Figure 13D). The CCA explained virtually 40% of the variance in the dataset. Owing to the removal of area and subsite variables which were not considered explanatory variables, the explained variance was small.

A Spearman correlation based dendrogram of the OTU profiles was constructed in order to allow an evaluation of the habitat and site-dependent structure of the microbial communities, along with some of the categorical variables. The analysis revealed a very high level of cumulative clustering in the dataset (0.86), particularly considering the large size of the dataset. The resulting dendrogram verified some previously observed patterns, for example the differences associated with dominating moss vegetation (brown moss vs. *Sphagnum*) and hydrology (Figure 14). However, it also revealed additional data structures. Starting from the top of Figure 14, the dendrogram reveals that the bacterial communities split by (1) the ecosystem and the corresponding dominating moss type (brown moss, resp. *Sphagnum* mosses). (2) Apart from few exceptions, the bacterial communities within the two peat bog types split by areas. (3) In almost all cases, the bacterial communities originating from the same subsites clustered together. (4) Within each subsite, the epiphytic communities and the endophytic communities clustered separately from each other, whereas the endophytic and epiphytic libraries from the same plant clustered consistently together. (5) The bacterial communities associated with the submerged mosses from NEI and MUE clustered together. (6) Within the *Sphagnum*-dominated sites, the majority of the vascular plant communities clustered together with the sediment and submerged moss communities.

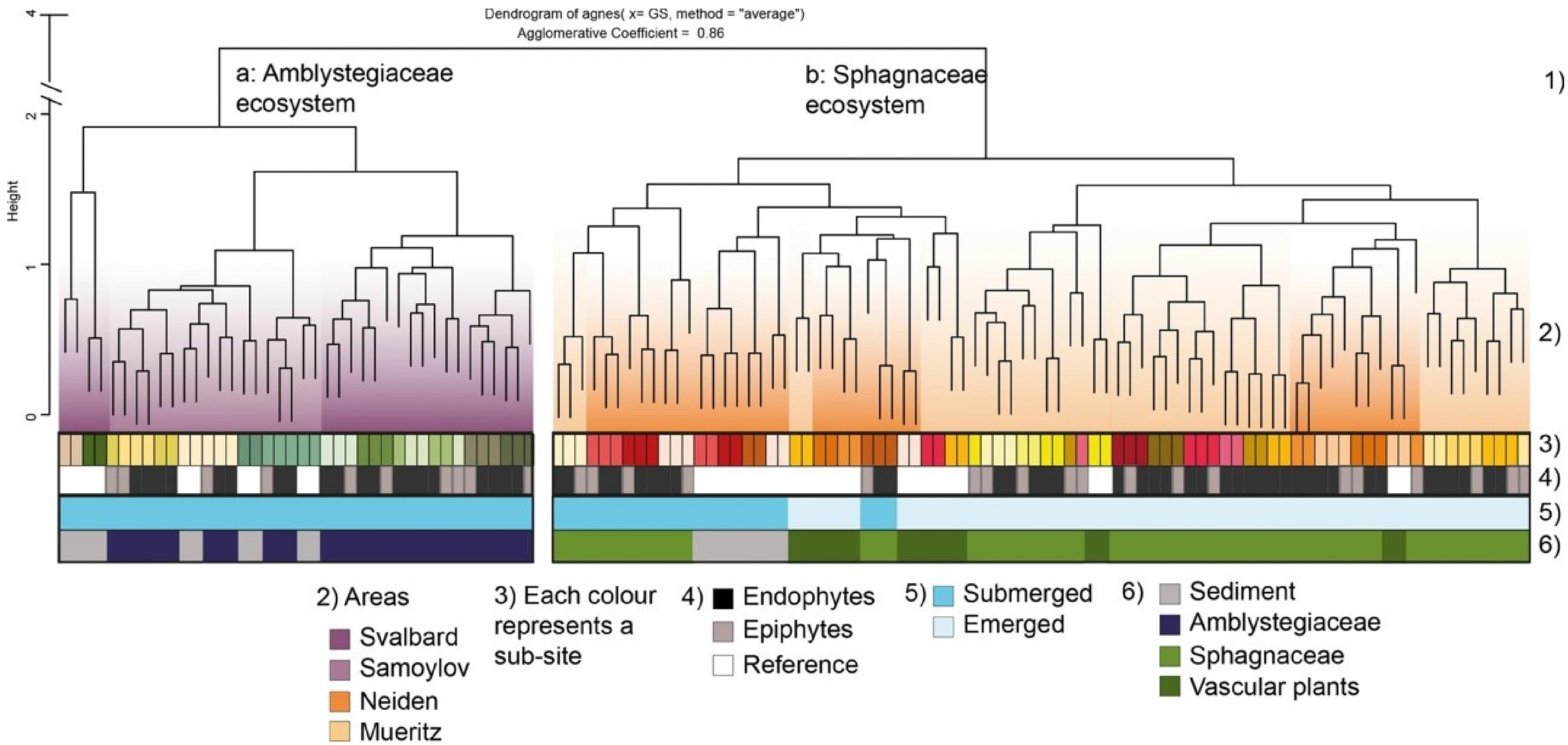


Figure 14: Dendrogram illustrating the clustering of bacterial communities (OTU at 97% sequence similarity) in relation to abiotic and biotic characteristics of the sites. Each top of the dendrogram corresponds to the community profile of a moss, vascular plant or sediment sample. All possible pairwise spearman correlation factors were calculated from the community profiles. The resulting distance matrix was used to cluster the samples applying the agnes hierarchical clustering algorithm. Numbers refer to different levels of clustering. The first level of clustering, (1), illustrates the clustering of the samples according to brown moss- or *Sphagnum*-dominated peatland ecosystems. The second level of clustering, (2), illustrates that the majority of samples from the same sites cluster together, although exceptions related to hydrology and reference samples occur. The third level (3) of clustering illustrates that bacterial communities from the same subsite almost exclusively cluster together. The fourth level (4) illustrates that the putative endophytes cluster almost always with the putative epiphytes from the same moss plantlet. Level (5) illustrates a clear microbial community separation by the hydrology of the site. Level (6) illustrates some clustering of communities according to being associated with a vascular plant, sediment or moss. Graphs: Alexander Tveit.

3.4. Microbial taxa associated with brown mosses and *Sphagnum* mosses

In order to identify which bacterial and archaeal groups accounted for the majority of microbial community variation, the microbial communities were studied at the family level.

3.4.1. Moss-associated bacteria

Within the brown moss-associated bacteria, an evenly high abundance of the following families could be observed: Acidimicrobiales_C111, Pseudoanabaenaceae, Hyphomicrobiaceae, Sphingomonadaceae and Comamonadaceae (Figure 15). Contrarily, only the two bacterial families Acetobacteraceae and Acidobacteriaceae dominated the *Sphagnum* moss microbiota. Sphingomonadaceae was the only family present at similar relative abundances in both, the brown moss and the *Sphagnum* systems. In order to identify the reasons of these large differences, a more detailed investigation of the OTU composition of Acetobacteraceae was conducted (Figure S3).

The relative abundance of Acetobacteraceae was higher in *Sphagnum* than in the brown moss ecosystems, while the majority of the Acetobacteraceae OTUs were present only in *Sphagnum*. However, some OTUs were only present in brown mosses, but only a few OTUs were present in both the brown moss and *Sphagnum* peatlands. The same pattern was observed for other major bacterial taxa such as Acidobacteria (Figure S4), Acidimicrobiales (Figure S5), and Cyanobacteria (Figure S6). These results suggest that distinct bacterial communities of *Sphagnum*- and Amblystegiaceae-dominated peatlands exist, while only individual OTUs occurred in both peatland types. Among the of methane oxidising bacterial (MOB) community, *Methylocystis* was most abundant (Figure S7). Methylocystis occurred in almost all sites, contrarily to most bacterial taxa, but its relative abundance varied and correlated positively with the amount of methane in the pore water. The MOB community contained further members within the genus *Methylomonas*, although primarily in *Sphagnum* sites and preferentially under submerged conditions. Moreover, *Methyloferula*-associated OTUs as part of the MOB community were also detected, but at low relative abundances and besides, only restricted to emerged *Sphagnum* sites. The fasta files of methanotrophic OTUs in Figure S7 is provided as additional supplement (S_methanotrophs_fasta). The complete OTU table for bacteria is online available as supplementary information (Supplementary i: OTU tables).

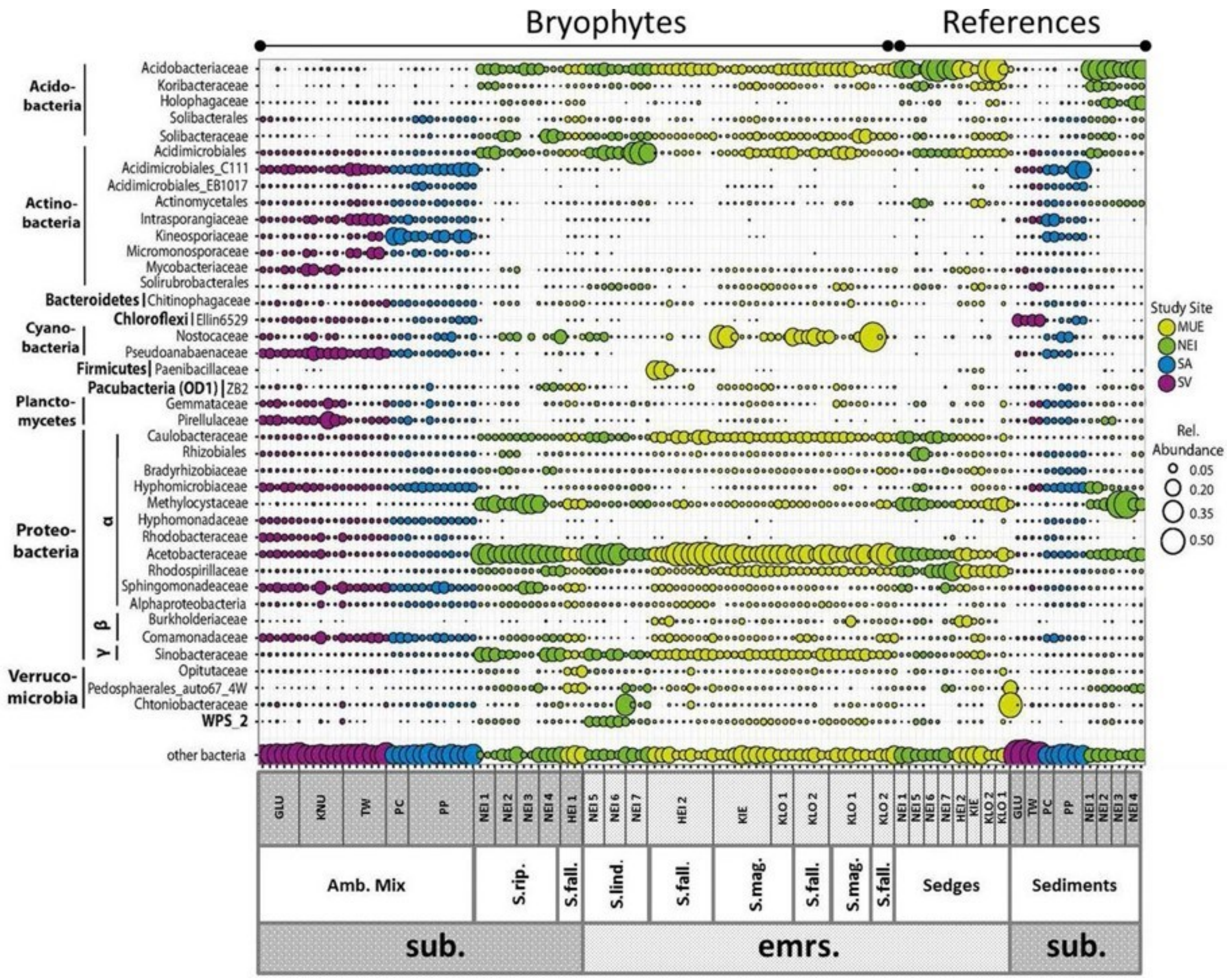


Figure 15: Bubble plot displaying the relative abundances of bacterial families (≥ 0.5% of the total bacterial sequences within the 16S rRNA gene libraries). The sizes of the circles correspond to the relative abundances of the depicted families. MUE: Mueritz, Northern Germany (yellow); NEI: Neiden, Northern Norway (green); SA: Samoylov, Russia (blue); SV: Svalbard, Norway (violet). The samples are sorted by ecosystem types and latitude from left to right. sub. = submerged. emrs. = emerged/above the water table. Amb. Mix. = a mix of brown mosses (Amblystegiaceae). *S. rip.* = *Sphagnum riparium*. *S. fall.* = *Sphagnum fallax*. *S. mag* = *Sphagnum magellanicum*. *S. lind.* = *Sphagnum lindbergii*. Graph: Alexander Tveit.

3.4.2. Moss-associated archaea

Unlike the bacterial communities, the archaeal communities did not reveal any hierarchical clustering patterns related to sample origin (Figure S8). The archaeal community was dominated by OTUs within the phylum Euryarchaeota, majorly OTUs representing methanogenic archaea (Figure 16). The most abundant OTU belonged to the hydrogenotrophic methanogenic family Methanobacteriaceae, which was present in almost all the samples of both, brown moss and *Sphagnum* ecosystems (Figure S9). Methanomassiliicoccaceae, Methanocellales, and Methanosarcinaceae were also widespread, while Methanosaetaceae occurred mainly in the brown moss dominated sites. Besides Euryarchaeota, the phylum Bathyarchaeota was abundant throughout most of the sites, while Woesearchaeota mainly occurred in the brown moss sites. The complete OTU table for archaea is online available as supplementary information (Supplementary i: OTU tables).

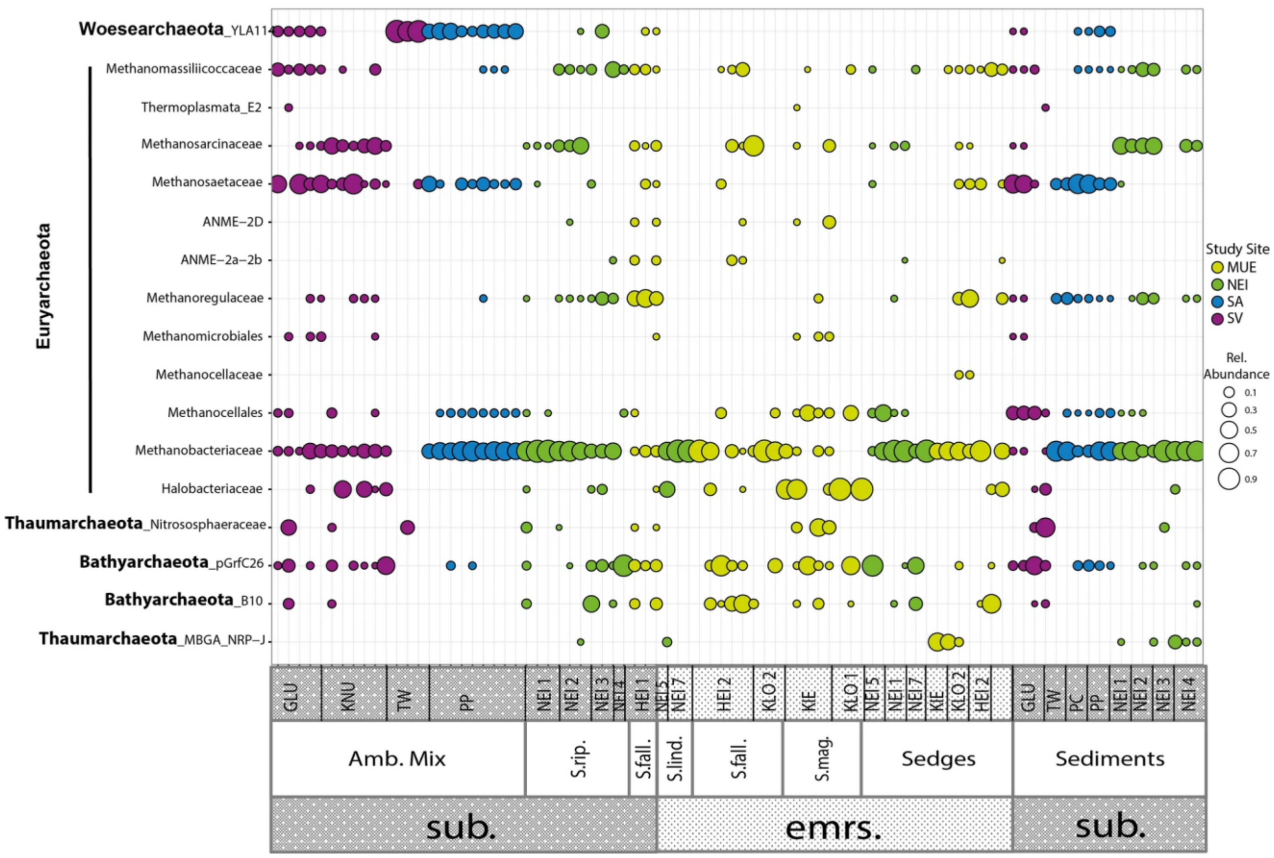


Figure 16: Bubble plot displaying the relative abundances of archaeal families (≥ 0.5% of the total archaeal sequences in the 16S rRNA gene libraries). The sizes of the circles correspond to the relative abundances of the families. MUE: Mueritz, Northern Germany (yellow); NEI: Neiden, Northern Norway (green); SA: Samoylov, Russia (blue); SV: Svalbard, Norway (violet). The samples are sorted by ecosystem types and latitude from left to right. sub. = submerged. emrs. = emerged/above the water table. Amb. Mix. = a mix of brown mosses (Amblystegiaceae). *S. rip.* = *Sphagnum riparium*. *S. fall.* = *Sphagnum fallax*. *S. mag* = *Sphagnum magellanicum*. *S. lind.* = *Sphagnum lindbergii*. Graph: Alexander Tveit.

3.4.3. Bacterial and archaeal core communities

49 out of 13.799 bacterial OTUs (0.4%) were observed in both *Sphagnum* and brown moss ecosystems and designated as the 'core microbiome'. The majority of these OTUs was affiliated to Acetobacteraceae and Acidobacteriaceae, thus reflecting the dominating bacterial families of the *Sphagnum* microbiota. The core microbiome, consisting of these 49 OTUs (52 if only considering mosses) made up 1 – 9% of the total OTU abundance in the brown moss ecosystems and 12 – 65% in the *Sphagnum* ecosystems; interestingly, the OTUs present in both systems are among the most abundant OTUs in *Sphagnum* sites (Table S2A). It was further addressed whether the size of all moss core microbiomes was similar to the individual bacterial core microbiome of brown mosses and *Sphagnum* mosses, respectively. By applying the same threshold as for the total core microbiome (TCM), the core microbiome of brown mosses (Amblystegiaceae) (ACM) comprised 348 OTUs, while the *Sphagnum* core microbiome (SCM) comprised 142 OTUs (Table S2A). Out of these, 20 OTUs were shared between TCM and ACM, and 46 were shared between TCM and SCM. The calculation of the moss species communities of the brown mosses from Svalbard, the brown mosses of Samoylov (only *Scorpidium scorpioides*), *Sphagnum riparium*, *S. fallax*, *S. lindbergii* and *S. magellanicum* showed that the individual core microbiomes were in a similar size range as for the broader core microbiomes at 295, 548, 126, 132, 252 and 154 OTUs, respectively (Table S2B). By calculation of the intersects of these core microbiomes it turned out that the *Sphagnum* mosses share a larger proportion of their core microbiomes with each other than with the Amblystegiaceae (Table S2C). Interestingly, *Scorpidium* mosses shared more OTUs with the *Sphagnum*

species than other brown moss species from Svalbard. Brown mosses from Svalbard and Samoylov shared the highest number of OTUs, thus reflecting the larger overall number of OTUs associated to these mosses and their larger core microbiomes. These few OTUs - compared to the total number of OTUs identified - accounted for a large proportion of the relative abundance in the microbial communities, which was consistent for all core microbiomes calculated.

In order to identify the dominant endophytic communities of brown mosses and *Sphagnum* mosses, the most abundant OTUs of significantly higher abundance in endophytic than epiphytic communities were plotted. This showed that almost none of the most abundant putative endophytes associated with brown mosses was shared with *Sphagnum* (Figure 2.8). For the putative endophytic communities, the taxonomic assignment and list of fasta files are provided as supplementary material (S_endophytes_taxonomy; S_endophytes_fasta). While the brown moss endophytes belonged to Actinobacteria, Proteobacteria, Chloroflexi, Firmicutes and Gemmatimonadetes, the endophytes associated with *Sphagnum* belonged to several families within the Proteobacteria, e.g., the Acetobacteraceae. Interestingly, of the 24 most abundant *Sphagnum* endophyte OTUs, 19 were observed in the total core microbiome, which displayed primarily epiphytes of brown mosses.

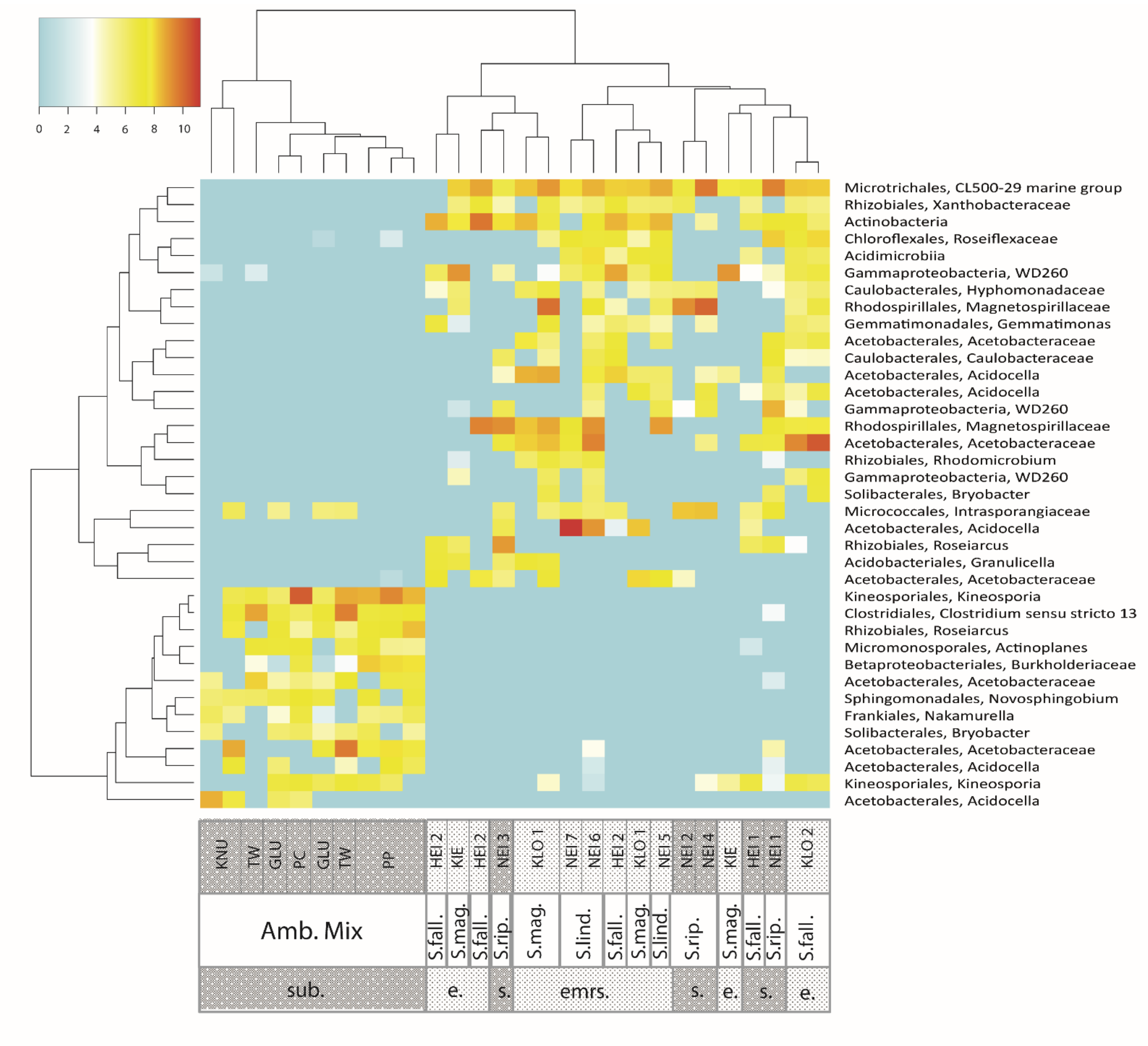


Figure 17: Heatmap displaying the most abundant OTUs present at significantly higher abundance in putative endophytic than epiphytic libraries of the same sample. The heatmap shows that endophytic bacterial communities associated with brown mosses (Amb. mix) from Svalbard and Samoylov form a distinct cluster apart from putative endophytic communities of *Sphagnum* mosses from Neiden and Mueritz. sub. = submerged. emrs. = emerged/above the water table. Amb. Mix. = a mix of Amblystegiaceae. *S. rip.* = *Sphagnum riparium*. *S. fall.* = *Sphagnum fallax*. *S. mag* = *Sphagnum magellanicum*. *S. Lind.* = *Sphagnum lindbergii*. Bacterial communities of brown moss samples from Twin Water (TW), Gluudneset (GLU) and Knudsenheia (KNU) in Svalbard and from polygonal crack (PC) and polygonal pond (PP) in Samoylov. Bacterial communities of *Sphagnum* samples from Klockenbruch (KLO), Kiebitzmoor (KIE), Heidbergmoor (HEI) in Mueritz, and Neiden (NEI) in Northern Norway. Chi-square contingency table tests were applied, where the p-values were calculated for Monte Carlo simulations with 5,000 replicates. The significance threshold was set at 0.001. Of the OTUs present at significantly higher abundance in the putative endophytic than epiphytic libraries, only OTUs at a higher than 0.5% relative abundance (average of the two endophytic libraries of each sample) in four or more samples were plotted in the heat map. The colour intensity corresponds to the binary logarithm of the average relative abundance of the OTU in the two endophytic libraries multiplied by 100,000. Pearson correlation was used as the basis for the hierarchical clustering of samples and OTUs in the heatmap. Graph: Alexander Tveit

3.4.4. Acetobacteraceae as dominant taxon of the bacterial core community

Members of the family Acetobacteraceae made up 4.7 % of the total amount of bacterial OTUs identified (650 vs. 13799) (bacterial OTU table in Supplementary), while their average percentage increased considerably from brown mosses (2.2 +/- 1.1%) towards *Sphagnum* mosses (24.6 +/- 9.8%).

Within the investigated brown mosses, *Bryum pseudotriquetrum* from Twin Water (SV) displayed the lowest percentage of Acetobacteraceae within the total putative endophytic bacteriome (1.03 +/- 0.24 %), while the highest percentage (4.03 +/- 0.70 %) was found epiphytically associated with the brown moss mix containing *Drepanocladus revolvens* and *Scorpidium turgescens* from Gluudneset (TW). The percentage of Acetobacteraceae within the *Sphagnum* bacteriome increased considerably. With 14.84 +/- 7.16%, *Sphagnum lindbergii* mosses originating from hollows in the Palsa peatland (NEI) displayed the lowest portion of Acetobacteraceae within the epiphytic bacteriomes, while the highest percentage (28.08 +/- 12.47%) was found within the endophytic bacteriomes of *Sphagnum fallax* mosses from HEI and KLO (MUE). Notably, the portion of Acetobacteraceae within the *Sphagnum* bacteriomes was constantly higher in the endophytic than in the epiphytic communities (Figure 18).

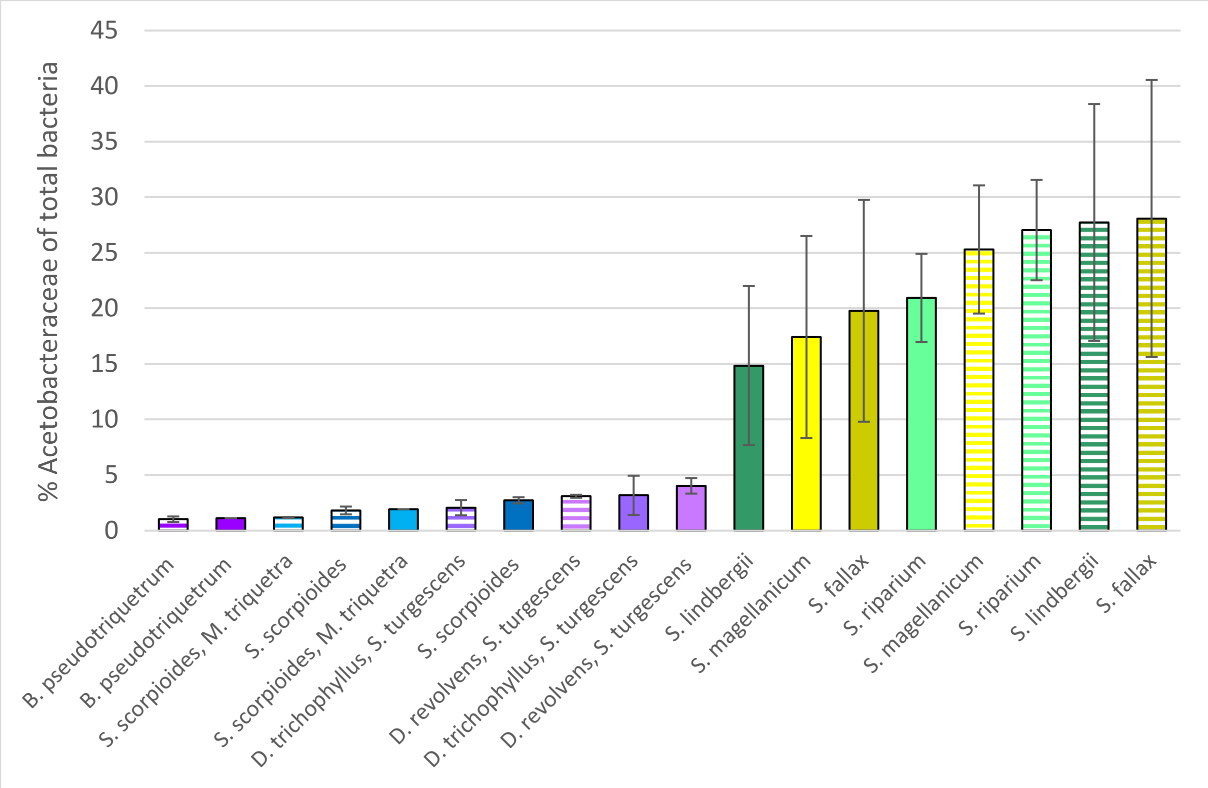


Figure 18: Bar chart displaying the increase of the relative abundance of Acetobacteraceae within total moss bacteriomes of brown mosses towards *Sphagnum* mosses. The colours indicate the sampling site of the moss plantlets: purple = Svalbard (SV); blue = Samoylov (SA); green = Neiden (NEI); yellow = Mueritz National Park (MUE). Ruled bars display putative endophytic Acetobacteraceae, filled bars depict putative epiphytic Acetobacteraceae. From left to right: *B. pseudotriquetrum* = *Bryum pseudotriquetrum* from Twin Water (SV); *S. scorpioides, M. triquetra* = *Scorpidium scorpioides* and *Meesia triquetra* from PC (SA); *S. scorpioides* = *Scorpidium scorpioides* from PP (SA); *D. trichophyllus, S. turgescens* = *Drepanocladus trichophyllus and Scorpidium turgescens* from KNU (SV); *D. revolvens, S. turgescens* = *Drepanocladus revolvens* and *Scorpidium turgescens* from GLU (SV); *S. lindbergii* = *Sphagnum lindbergii* from NEI 5-7 (NEI); *S. magellanicum* = *Sphagnum magellanicum* from KIE and KLO (MUE*); S. fallax* = *Sphagnum fallax* from HEI and KLO (MUE); *S. riparium* = *Sphagnum riparium* from NEI 1-4 (NEI).

When only focussing on the moss samples of a single subsite, *Sphagnum fallax* from Heidbergmoor harboured with 46.1% even the highest relative portion of Acetobacteraceae within the endophytic bacterial community (bacterial OTU table in Supplementary).

The moss-associated Acetobacteraceae remained in large parts unidentified (Figure 19) *Scorpidium scorpioides* mosses from Siberian polygonal ponds harboured the largest group of unidentified Acetobacteraceae (90,2 ± 0,8%), whereas *Sphagnum fallax* mosses from Heidbergmoor exhibited the smallest group of unassigned Acetobacteraceae at genus level (40,8 ± 1%). The genus *Acidocella* was mostly pronounced in association with *Sphagnum fallax* mosses from Heidbergmoor (55,4 ± 1,2%) and less pronounced in association with brown mosses from Gluudneset (4,6 ± 6,4%). Acetobacteraceae of the genus *Roseomonas* (15,9 ± 5%) and *Roseococcus* (6,8 ± 2,5%) were mainly associated with brown mosses from Twin Water, while both genera were negligible in association with *Sphagnum* mosses. The genus *Acidisoma* was mostly pronounced in association with *Sphagnum magellanicum* from Klockenbruch (5,4 ± 2,1%) and less pronounced when associated with brown mosses from Gluudneset (0,1 ± 0,2%). Acetobacteraceae of the genus *Acidiphilium* were mainly associated with *Sphagnum fallax* from Heidbergmoor (0,5 ± 0,3%), but negligible all other samples.

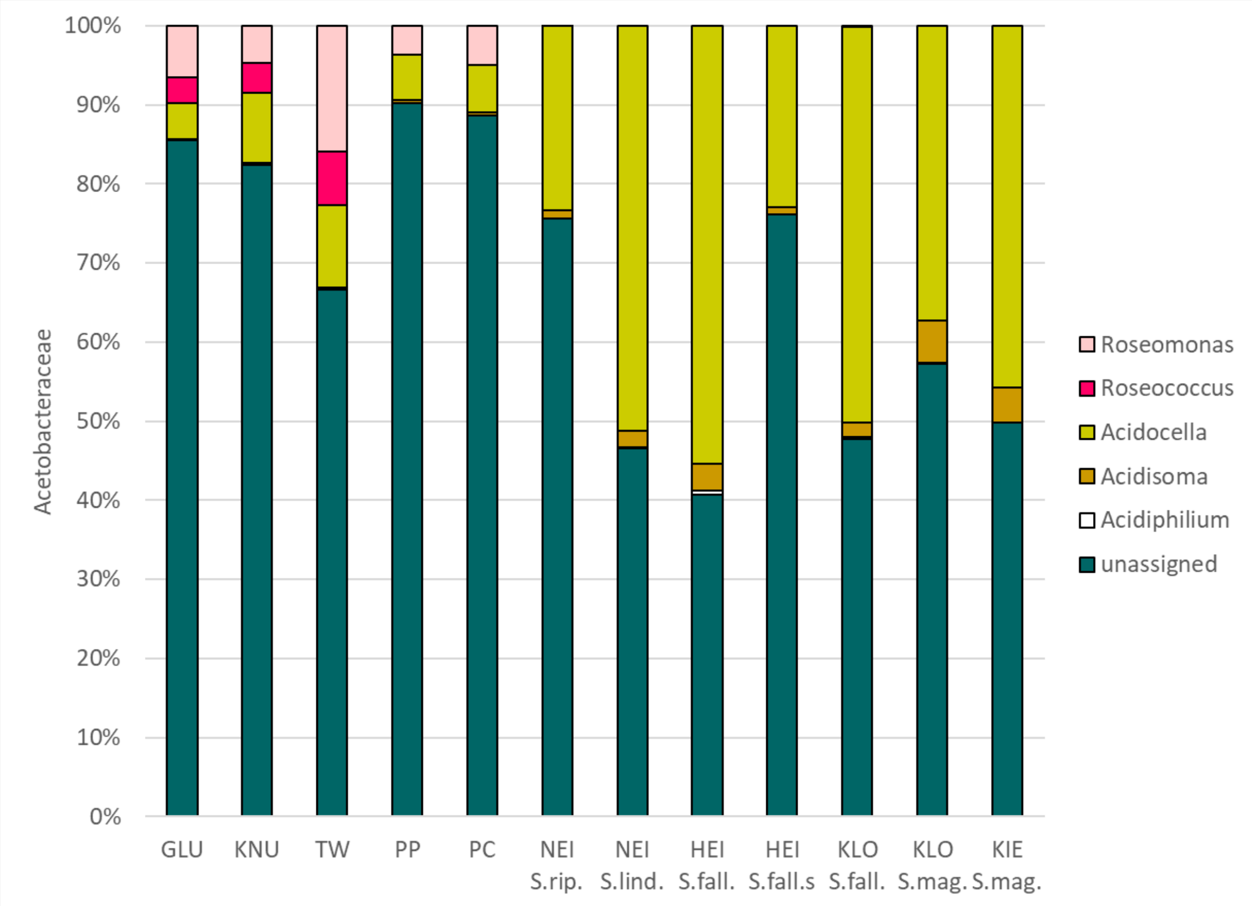


Figure 19: Relative abundance of identified genera within the family Acetobacteraceae. The majority of OTUs remained unassigned at genus level (blue). While the genus *Acidocella* (yellow) was mostly pronounced in *Sphagnum* mosses, *Roseomonas* and *Roseococcus* appeared solely in association with brown mosses. GLU = brown mosses from Gluudneset; KNU = brown mosses from Knudsenheia; TW = brown mosses from Twin Water; PP = *Scorpidium scorpioides* from Siberian polygonal ponds; PC = *Scorpidium scorpioides* and *Meesia triquetra* from a Siberian polygonal crack; NEI *S. rip.* = *Sphagnum riparium* from Neiden; NEI *S. lind.* = *Sphagnum lindbergii* from Neiden; HEI *S. fall.* = *Sphagnum fallax* from Heidbergmoor; HEI *S. fall.s* = submerged *Sphagnum fallax* from Heidbergmoor; KLO *S. fall.* = *Sphagnum fallax* from Klockenbruch; KLO *S. mag.* = *Sphagnum magellanicum* from Klockenbruch; KIE *S. mag.* = *Sphagnum magellanicum* from Kiebitzmoor.

3.5. *Sphagnum* bacteriomes of disturbed, rewetted and pristine temperate kettle bog

Overall, 212 OTUs were associated with mosses and reference vascular plants from MUE (Venn diagram in Supplementary), while 188 OTUs were only associated with *Sphagnum* mosses (Figure 20). Of these, 65 OTUs (34.6%) displayed the core community shared between all *Sphagnum* species from all investigated sites (Figure 20A), including Acetobacteraceae, Methylocystaceae, Nostocaceae and Caulobacteraceae. If considering *S. fallax* and *S. magellanicum* from KLO separately, the core community comprised still 45 common OTUs (Figure 20B).

Altogether 47 OTUs (25%) were solely associated with *S. magellanicum* from KIE, including taxa such as *Streptococcus*, *Ruminococcus*, *Haemophilus* and *Prevotella*. A total of 29 OTUs (15.4%) prevailed only in association with *S. fallax* from HEI, among them taxa such as Methylococcaceae, Methylobacteriaceae, *Geothrix*, *Kaistia*, *Paenibacillus* and *Rhodanobacter*. Among the 13 OTUs (6.9%) that were only associated with *Sphagnum* mosses from KLO were genera like *Agrobacterium*, *Nocardia*, *Accumulibacter* and *Methylobacterium*. Notably, no OTU was shared exclusively between *S. magellanicum* growing in the centre and *S. fallax* growing at the margin of KLO (Figure 20B).

The bacterial diversity was highest in association with mosses, resp. mosses and vascular plants from KIE (Shannon indices: 3.617, resp. 3.74), and lowest in KLO (Shannon indices: 3.072, resp. 3.239), while the relative amount of moss-associated OTUs was appr. 28% higher in KIE compared to HEI and KLO (Table S3).

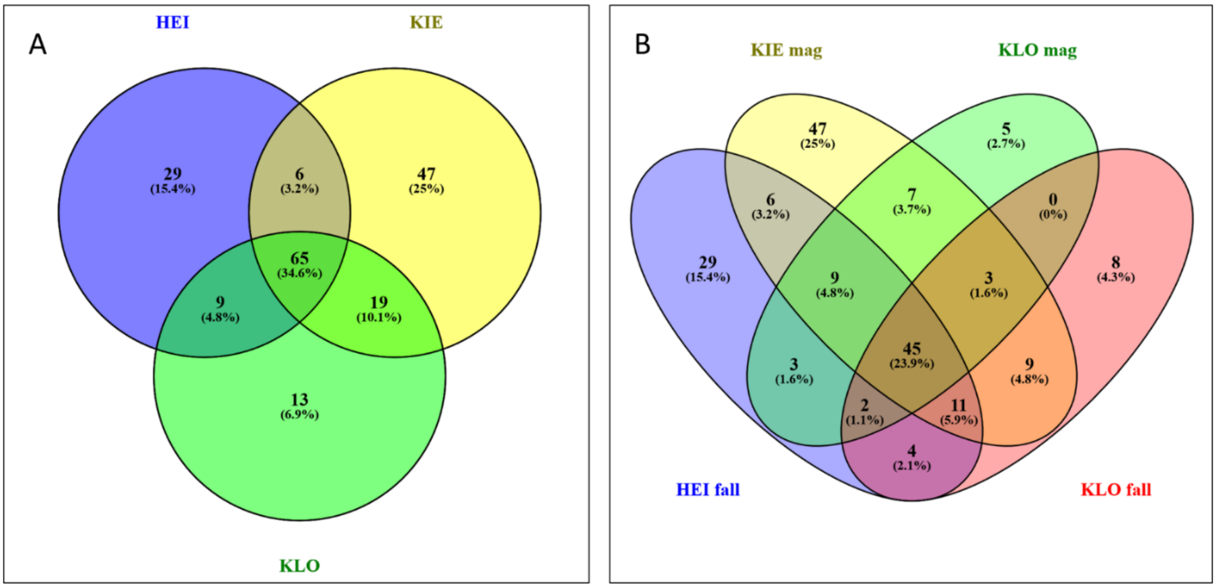


Figure 20: Venn diagrams showing the Sphagnum bacteriomes from all subsites within the Mueritz sampling site. Bacterial OTUs (relative amount and corresponding percentage) associated with *Sphagnum* mosses from Heidbergmoor (HEI), Kiebitzmoor (KIE) and Klockenbruch (KLO) (A); Bacterial OTUs associated with *S. fallax* from Heidbergmoor (HEI fall) and Klockenbruch (KLO fall) and *S. magellanicum* from Kiebitzmoor (KIE mag) and Klockenbruch (KLO mag) (B). Created at: https://bioinfogp.cnb.csic.es/tools/venny/index.html (Oliveros, J.C. (2007-2015) Venny. An interactive tool for comparing lists with Venn's diagrams).

3.6. Potential moss-associated methane production and methane oxidation rates

In general, potential methane oxidation rates exceeded methane production by appr. two orders of magnitude. Moss-associated methanogenesis was slightly more pronounced in submerged mosses, while moss-associated methanotrophy was highest in submerged *Sphagnum*, up to eight times higher compared to all other samples.

3.6.1. Moss-associated methane production

Potential methane production rates for non-sterile ('epiphytic') brown mosses ranged between 2.40 +/- 0.32 nmol CH_4 h^{-1} g dw $^{-1}$ and 0.63 +/-0.33 nmol CH_4 h^{-1} g dw $^{-1}$ (GLU non-sterile, resp. S0 non-sterile). Potential methane production rates for sterile (putative endophytic brown mosses ranged between 2.14 +/- 0.2 – 0 nmol CH_4 h^{-1} g dw $^{-1}$ (GLU sterile, resp. S0, S8). The potential methane production rates for putative epiphytic and endophytic *Sphagnum* mosses were negligible or could not be measured, except for the putative epiphytic methanogenic communities associated with the submerged *Sphagnum fallax* (1.43 +/- 0.2 nmol CH_4 h^{-1} g dw^{-1}).

3.6.2. Moss-associated methane oxidation

Potential methane oxidation (MO) rates for non-sterile ('epiphytic') brown mosses ranged between 33.61 +/- 5.68 nmol CH_4 h^{-1} g dw $^{-1}$ and 10.95 +/-0.91 nmol CH_4 h^{-1} g dw $^{-1}$ (S0 non-sterile, resp. S8 non-sterile). Potential methane oxidation rate for sterile ('endophytic') brown mosses ranged between 15.15 +/- 0.43 and 2.68 +/-0.43 nmol CH_4 h^{-1} g dw $^{-1}$ (S0 sterile, resp. S8 sterile). Potential methane oxidation rates for putative epiphytic *Sphagnum* mosses were with 288.12 +/- 5.51 nmol CH_4 h^{-1} g dw $^{-1}$ highest for *S. fallax* submerged, and ranged between 72.55 +/- 19.12 and 0.9 +/- 0.08 nmol CH_4 h^{-1} g dw $^{-1}$ for other *Sphagnum* species (NEI 2 non-sterile, resp. KLO fall. non-sterile).

Potential methane oxidation rates for putative endophytic methane oxidisers associated with *Sphagnum* were with 12.97 +/- 2.70 nmol CH_4 h^{-1} g dw $^{-1}$ highest in *Sphagnum magellanicum* from Klockenbruch, and lowest in NEI 1 sterile (0.48 +/- 0.19 nmol CH_4 h^{-1} g dw^{-1}); methanotrophic activity was not measurable in two samples, NEI 2 sterile and KLO fall sterile (Table S4).

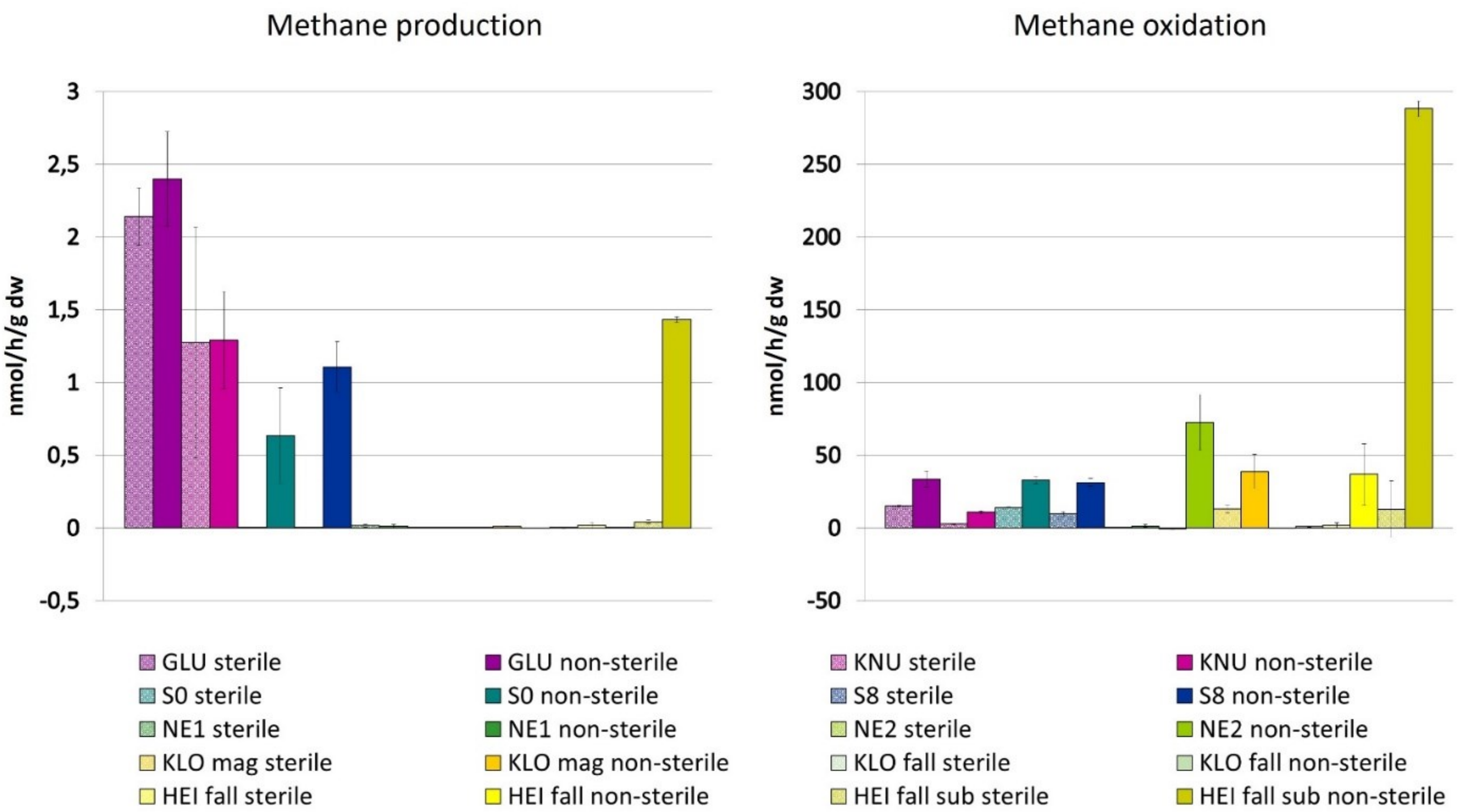


Figure 21: Moss-associated potential methane production (A) and methane oxidation rates (B). The colours indicate the sampling sites. Pale bars display putative endophytic moss-associates ('sterile'), while the rich-coloured bars display the putative epiphytic moss-associates ('non-sterile'). GLU = submerged *Drepanocladus revolvens* and *S. turgescens* from Gluudneset; KNU = submerged *Drepanocladus trichophyllus* and *Scorpidium turgescens* from Knudsenheia; S0 = submerged *Scorpidium scorpioides* from a low-centred polygon on Samoylov; S8 = mix of emerged *Meesia sp., Warnstorfia sp.* and *Drepanocladus sp.* from a high-centred polygon on Samoylov; NE 1 = submerged *Sphagnum riparium* from Neiden; NE 2 = emerged *Sphagnum lindbergii* from Neiden; KLO mag = emerged *Sphagnum magellanicum* from Klockenbruch; KLO fall = emerged *Sphagnum fallax* from Klockenbruch; HEI fall = emerged *Sphagnum fallax* from Heidbergmoor; HEI fall sub = submerged *Sphagnum fallax* from Heidbergmoor.

4. Discussion

4.1. Environmental influences on moss-associated bacterial communities

The results of the present work allowed to rank the influences of certain environmental variables on the microbial community on both, large and small geographical scales. Corresponding to the hierarchical clustering in the bacterial dendrogram, the peatland type (brown moss- or *Sphagnum*-dominated peatlands) had the major impact on bacterial community structure, which corresponds to other studies reporting on characteristic microbial communities that evolved in contrasting peatland ecosystems with different vegetation, water chemistry and hydrology (Andersen et al. 2013, Potter et al. 2017). Interestingly, testate amoebae communities seemed also to differ when associated with either brown mosses or *Sphagnum* mosses (Jassey et al. 2014). Moreover, species richness and diversity were significantly higher in circumneutral brown moss-dominated peatlands compared to acidic *Sphagnum* bogs, which was also reported for soil bacteria from neutral and acidic environments (Fierer and Jackson 2006, Zhalnina et al. 2014). Most bacteria are unable to survive under acidic conditions that prevail in *Sphagnum* peat bogs, owing to a lack of substantial mechanisms to regulate their intracellular pH close to neutral when exposed to low extracellular pH (Slonczewski et al. 2009). At the same time, acidophilic bacteria inhabiting *Sphagnum* peat bogs function optimally at pH 5, but can even survive at higher pH values (Oren 2018), for example in sub-neutral brown moss-dominated peatlands. This could explain the association of core community members such as *Acetobacteraceae* and *Acidobacteriaceae* with both, brown mosses and *Sphagnum* mosses. However, pH values are often mutually dependent from other abiotic factors such as plant-derived tannins and tannin-like compounds (Rousk and Rousk 2020) and leaf litter (Jean et al. 2020), wherefore the role of pH remains ambiguous.

The host moss taxon had a greater influence on the bacterial moss-associates compared to other controlling variables such as pH, hydrology or temperature, which confirms previous findings on distinct bacterial communities of several *Sphagnum* species. It has been stated that *S. magellanicum* and *S. fallax*, two peat moss species with different ecological functions, harbour a suite of highly specific bacteria, independently from the geographic location (Opelt et al. 2007a, 2007b, Bragina et al. 2012a). One possible explanation for high degrees of host specificity even over great distances was given by Bragina and colleagues who reported on haploid sporophytes of *S. fallax* that contained a versatile endophytic bacterial consortia, which was obviously passed vertically to the diploid gametophyte (Bragina et al. 2012a, 2013). Moreover, individual secondary metabolites produced by particular hosts may further influence the assembly of host-specific microbiota (Opelt et al. 2007b, Bragina et al. 2012a). Interestingly, the moss-microbiome composition permits a high predictability of moss species identity, as revealed by a study on bacterial communities being well-correlated with the phylogenetic distances of many boreal and tundra bryophytes (Holland-Moritz *et al.*, unpublished).

The present results extend the knowledge on host moss taxa and their particular bacterial community to other *Sphagnum* species such as *S. riparium* and *S. lindbergii*, but also to brown mosses such as *Scorpidium scorpioides* or *Meesia triquetra*. Furthermore, the present work supports previous findings on distinct sediment and plant microbiomes from the same habitat (Bulgarelli et al. 2012, 2013).

The present results are congruent with Carrell *et al.*, who state a negative correlation between temperature and moss-associated bacterial diversity (Carrell et al. 2017), although temperature had obviously only a minor influence on the moss microbiome (explaining 4.8% of inertia in the partial CCA), despite originating from different climatic zones. One reason could be the relatively similar temperature ranges at the time of sampling during the growing season, compared to the mean annual temperatures of the sites. Besides, other studies reported also on a poor influence of temperature on bacterial assemblages on short and long time-scales (Radujkovic 2016, Oliverio et al. 2018).

The prevailing water regime seemed to be a key environmental factor shaping the microbiomes of aquatic *Sphagnum* and brown mosses and terrestrial *Sphagnum* species, which was in some cases more important than the influence of the host plant. For example, emerged and submerged *S. fallax* growing in the same subsite within the temperate hummock hollow-complex were associated with different microbial communities, while the microbiota of the latter was more similar to submerged *S. riparium* from the subarctic palsa bog. The hydrology of the habitats has been shown previously to affect the microbiomes of *Sphagnum* (Mitchell et al. 2003, Raghoebarsing et al. 2005, Leppänen et al. 2014) and other mosses (Wang et al. 2018), but also to influence the morphology and physiology of the host mosses (Fiala and Winkler 1969, Rice 1995, Rice and Schuepp 1995). Thus, it can be concluded that hydrology affects the moss microbiota both directly and indirectly.

The prevalence of the methanotrophic genus *Methylocystis* in wetlands as reported by several studies (Kip et al. 2011, Putkinen et al. 2012, Knief 2015) was also confirmed within this study. *Methylocystis* was present throughout all sites, and its abundance correlated with pore water methane concentrations (Figure S7), corresponding to related studies (Larmola et al. 2010, Osudar et al. 2016). Based on the assumption that variations in *Methylocystis* communities are rather based on contingent historical events than on evolutionary acquired fitness (Lüke 2010, Lüke et al. 2014), it is suggested that *Methylocystis* is able to adapt to the environmental changes associated with peatland succession, including pH, and rather driven by substrate availability.

Besides *Methylocystis*, other methanotrophic genera such as *Methylomonas* and *Methyloferula* were substantially abundant in the *Sphagnum*-dominated sites, but virtually absent in brown moss-dominated sites. Together with other studies on methanotrophs such as *Methylocystis*, *Methylocella* and *Methylocapsa* in acidic peatlands (Dedysh et al. 1998, 2002, Dedysh 2009, Vorobev et al. 2011) or *Methylobacter* in pH-neutral peatlands (Tveit et al. 2013, 2014), this work underpins the omnipresence of some methanotrophic bacteria across all investigated peatland types and successional stages, presumably mainly driven by the prevailing methane regime, while others are restricted to circumneutral, resp. acidic peatlands.

4.2. Moss-associated archaeal communities and their environmental drivers

The results of the present thesis reveal that archaea, particularly methanogenic Euryarchaeota, are commonly found in bryophytes across High Arctic to temperate peatlands, which has not been reported before. Interestingly, the investigated moss-associated archaea were found to be less influenced by biotic and abiotic parameters, when compared to moss-associated bacteria, but exhibited relatively homogenous communities within their hosts' bryosphere.

Along with various bacteria, methanogenic archaea were found within the hyaline cells of two *Sphagnum* species from an ombrotrophic northern bog, assuming that they gain H_2 for methanogenesis from the adjacent diazotrophic microorganisms. The authors hypothesised that the produced methane is further transferred to CO_2 by methanotrophic moss symbionts (Granhall and Hofsten 1976). It was already stated that methanotrophic archaea in plant spheres are mainly driven by substrate availability and the presence of bacterial competitors (Karlsson et al. 2012, Ma et al. 2013, Taffner et al. 2018, Alori et al. 2020). Recently, a study on the archaeal communities associated with *Sphagnum* mosses and other alpine bog plants has been conducted, in which, so far unclassified archaea were identified that form an ecosystem-specific core archaeome common to all bog plants (Taffner et al. 2018). While archaea associated with *Sphagnum* mosses were already reported (Taffner et al. 2018), brown moss-associated archaeal communities were never investigated so far.

The results of the present thesis reveal new and striking insights into the archaeomes of both, brown mosses and *Sphagnum* species from circumneutral lakes to acidic kettle bogs. Compared to the moss bacteriomes, the moss-associated archaeal communities seemed less influenced by the investigated biotic and abiotic parameters. No distinct archaeal community patterns could be estimated for the peatland type, brown mosses or *Sphagnum* mosses.

The archaeomes of brown mosses and *Sphagnum* mosses were mainly represented by methanogenic Euryarchaeota, but also by Bathyarchaeota and Woesearchaeota. It is known that salinity has an impact on methanogenic archaea on a global scale, while pH and temperature display major controls in non-saline soils and lake environments (Wen et al. 2017). Methanogens are further influenced by ground water level and vegetation dynamics at different temporal and spatial scales (Wen et al. 2017), while methanogenic communities are more diverse in shallower lakes (Milferstedt et al. 2010). The present results support the hypothesis that Woesearchaeota occur as possible syntrophic partners of methanogens in similar habitats (Liu et al. 2018). Bathyarchaeota is a phylum of global generalists that thrive in anoxic sediments (Zhou et al. 2018), and its presence within the bryopshere corresponds to its former observations in peatlands (Xiang et al. 2017, Emsens et al. 2020), where they presumably degrade aromatic compounds such as cellulose and lignin (Yu et al. 2018). Despite the ostensible ubiquitous distribution of the archaeal communities in association with peatland mosses, there was some site-dependent clustering. For example, the genus *Methanosaeta* was only found in association with brown mosses and associated sediments which is in accordance with the biogeography of Methanosaetaceae being most abundant in pH neutral environments (Wen et al. 2017). Contrarily, *Methanobacterium* as the most abundant methanogen was present in all sites and samples, which underpins former reports on the prevalence of the order

Methanobacteriales in northern peat bogs in general (Metje and Frenzel 2005, Rooney-Varga et al. 2007, Tveit et al. 2015) and in circumneutral and acidic soils (Wen et al. 2017). Interestingly, it has been reported that the archaeomes of *S. magellanicum*, which displayed the lowest diversity compared to archaeal communities of other bog plants such as *Eriophorum vaginatum*, were mainly involved in auxin biosynthesis, response to oxidative stress as well as CO_2 fixation and DNA repair (Taffner et al. 2018). Taken together with our results, this may lead to the assumption that moss archaeomes display comparably homogenous communities with plant-promoting features, thriving more or less uninfluenced from environmental parameters within their hosts bryopshere.

4.3. Distinct patterns of endophytic bacteria

Within this study, distinct patterns of putative endophytic bacteria for both *Sphagnum* and brown mosses could be identified. The comparison of endophytic bacterial communities of brown mosses and *Sphagnum* species likely reflects a direct influence of the moss taxa on the microbiota. It has been shown before that bryophytes release species-specific chemo-attractants which guide beneficial bacterial endophytes towards them (Bay et al. 2013), while *Sphagnum* mosses select for beneficial bacteria through secondary metabolites (Opelt et al. 2007b).

In the frame of this study, the cell wall compositions of certain investigated moss species were analysed. Similar cell wall-bound components such as polysaccharides and lignin-like polymers (Table 1) indicate a minor effect of the cell wall composition on the structure of the moss microbiota. Pectin-like polymers represent a small fraction of cell wall polysaccharides and provide the bryophytes with substantial cation exchange capacity (CEC) (Stalheim et al. 2009, Hájek et al. 2011), which is accounted for the extraordinary acidifying capacity of *Sphagnum* mosses (Clymo 1963, Gagnon and Glime 1992). However, the present results reveal similar CEC values in both moss groups, which is in line with previous findings (Soudzilovskaia et al. 2010), assuming that the cation exchange does not reduce and control pH in brown moss-dominated fens due to the substantial neutralisation capacity of the mineral-rich groundwater. Microbial activity in acidic peat bogs is further inhibited by pectin-like polymers which are bound to the *Sphagnum* cell walls and are released to the environment as so-called sphagnan (Stalheim et al. 2009, Hájek et al. 2011). Apart from the selection of beneficial microorganisms, *Sphagnum* mosses protect themselves against pathogens by the release of antimicrobial substances or via close association with antagonistic and antifungal bacteria (Rudolph and Samland 1985, Basile et al. 1999, Stalheim et al. 2009, Hájek et al. 2011).

The present work suggests the existence of a distinct putative endophytic microbiome that differs from the epiphytic communities. It is known that bacterial endophytes can be host plant-specific and promote the growth and health of their hosts (Sturz et al. 2000, Berg et al. 2014). Several OTUs that here represented putative endophytes of brown mosses or *Sphagnum* were previously reported as host plant-specific, e.g., Kineosporiaceae, Hyphomicrobiaceae, Intrasporangiaceae and Acidimicrobiales (Reiter and Sessitsch 2006, Selbmann et al. 2010, Qin et al. 2012, Yu et al. 2015), and some of these might be transferred from one generation to another, similarly to *Sphagnum* endophytes (Bragina et al. 2012a, Putkinen et al. 2012, Bay et al. 2013). Thus, the inheritance and selection of potentially beneficial endophytes on the one hand, and the active prevention of colonisation by pathogens on the other hand, may provide an explanation for distinct endophytic communities of both brown mosses and *Sphagnum* mosses.

4.4. The core microbiota and their possible role for peatland succession

The total core microbiome of brown moss and *Sphagnum*-dominated ecosystems was small compared to the total amount of OTUs identified (49 vs. 13799). However, the *Sphagnum* core microbiome in our study (142 OTUs) was comparable in size to the alpine *Sphagnum* bog core microbiome (260 OTUs) reported elsewhere (Bragina et al. 2015). Interestingly, these few OTUs were highly abundant within the core community, thus representing presumably important members of the moss microbiota. On the other site, the large number of low abundant OTUs outside of the core microbiomes identified in this study might represent local assemblies of microorganisms from the adjacent surroundings. Notably, the largest part of the total core microbiome appeared epiphytically on brown mosses, but were dominant endophytes in *Sphagnum*. This finding is consistent across large distances, many subsites, moss species and environmental conditions, which leads to the assumption that *Sphagnum* recruited parts of the brown moss-microbiota during its establishment. Parts of this recruited microbiota might have adapted to the specific conditions provided by the *Sphagnum* host and became dominant endophytes and part of the core microbiome, which might have been were vertically transferred to the next generation as shown previously (Bragina et al. 2012a). This way, over time, a *Sphagnum* core microbiome might have established that originated at least in part from brown mosses. An alternative explanation could be that the *Sphagnum* mosses recruited their microorganisms independently from peatland succession processes. If so, the presence of dominant endophytes of *Sphagnum* and epiphytes of brown mosses is a coincidence and these bacteria dominate both systems, able to survive in both types of environments. However, considering that brown mosses and *Sphagnum* co-exist during certain stages of peatland succession, which frequently occurred through history (Kuhry et al. 1993, Rydin et al. 2006, Schumann and Joosten 2008), parts of the shared microbiome might been transferred during times of co-existence. However, the existence of an abundant core microbiome throughout brown moss- and *Sphagnum*-dominated peatlands and its role during peat bog succession needs to be addressed in further studies.

4.5. The potential role of Acetobacteraceae for *Sphagnum* host mosses and bog ecosystems

The results of this thesis suggest that a versatile group of Acetobacteraceae is not only part of the peat core microbiome, but associated with both moss types and especially abundant in association with *Sphagnum* species. The submerged brown mosses hosted the genera *Roseomonas*, *Roseococcus* and *Acidocella*, while all investigated *Sphagnum* species harboured mainly *Acidocella* species. A common feature of members within the family Acetobacteraceae is the production of acetic acid (Komagata et al. 2014, Boiştean et al. 2020), and some genera are even able to oxidise acetic acid further to CO_2 and H_2O (Sievers and Swings 2015). While reports on Acetobacteraceae associated with brown mosses remain sparse (Tang et al. 2016), their presence and dominance within the microbiota of *Sphagnum* from northern and sub-alpine peat bogs has been frequently reported (Opelt and Berg 2004, Bragina et al. 2012a, 2012b, 2015, Xiang et al. 2013, Tsitko et al. 2014, Holland-Moritz et al. 2018, Tian et al. 2020), which is also supported by the present work. However, the underlying reasons for the dominance of Acetobacteraceae in acidic peat bogs have not been explained yet.

The genus *Roseomonas* was at first primarily linked to human infections (Rihs et al. 1993), but later isolates were also obtained from freshwater habitats like wetlands (Baik et al. 2012, Lee et al. 2015), ponds (Furuhata et al. 2008), lake sediments, agriculture drainage water (Jiang et al. 2006), drinking water (Gallego et al. 2006) and estuarine habitats (Venkata Ramana et al. 2010). *Roseomonas* species where further detected in cyanobacterial blooms from Swedish, Chinese and Australian lakes (Eiler and Bertilsson 2004, Jiang et al. 2006, Pope 2007, Zhang et al. 2021) and in Arctic tundra soils (Kim et al. 2016). More recently, a strain was also isolated from the phyllospheres of the olive plant *Elaeocarpus hygrophilus* (Damtab et al. 2016).

Members of the genus *Roseococcus* were isolated from sediments of a Siberian soda lake (Boldareva et al. 2009) and represented moreover a highly abundant key prokaryote in a hyper-alkaline, oligotrophic and radioactive fuel storage pond (Ruiz-Lopez et al. 2020). Besides, *Roseococcus* spp. were among the dominant bacteria associated with microalgae from a Chinese artificial lake (Zhang et al. 2021) and part of a bacterial consortia from freshwater environments that colonised preferably microplastic substrates (Miao et al.

2019). Among the identified Acetobacteraceae, only *Roseomonas* and *Roseococcus* represent bacteriochlorophyll *a* (BChl*a*) - containing genera. Moreover, these two genera were solely associated with brown mosses from Svalbard and Samoylov, but virtually absent in *Sphagnum* mosses from Neiden and Mueritz. These findings indicate that potentially photosynthetic Acetobacteraceae are frequently associated with brown mosses from circumneutral peatlands, but do not appear within the microbiome of *Sphagnum* mosses from acidic peat bogs. *Roseomonas* and *Roseococcus* are able to perform anoxygenic (non-evolving O_2) photosynthesis in the presence of oxygen (Yurkov and Beatty 1998, Koblížek 2015), contrarily to the purple non-sulphur bacteria, which require anaerobic conditions (Rathgeber et al. 2004, Yurkov and Elizabeth Hughes 2017). Therefore, these bacteria are referred to as aerobic anoxygenic phototrophic (AAP) bacteria (Komagata et al. 2014, Pankratov et al. 2020, Salama et al. 2020). AAPs such as *Roseomonas* and *Roseobacter* are unable to fix CO_2 (Yurkov and Elizabeth Hughes 2017) and depend therefore on organic compounds as alternative C source, for example dissolved organic matter (DOC) that derive from the litter, leachates and exudates of primary producers (Atamna-Ismaeel et al. 2012, Stiefel et al. 2013, Szabó-Tugyi et al. 2019, Piwosz et al. 2020). Due to relatively low BChl*a* contents and the inability of AAPs to grow photoautotrophically (Yurkov et al. 1993, Koblížek 2015), light seems to provide primarily an additional driving force for incorporating complex organic molecules such as DOC and other coloured dissolved organic matter (CDOM), which leads to a competitive advantage over exclusively heterotrophic microbes (Fauteux et al. 2015, Koblížek 2015, Szabó-Tugyi et al. 2019). Therefore, AAPs can thrive in extreme habitats such as acidic, humic-rich peat bog lakes (Lew et al. 2015), nutrient-depleted, polar environments (George et al. 2020) and oligotrophic glacial lakes, where they represent up to 12% of the total bacterial community (Mašín et al. 2012). In line with this, the brown moss-associated *Roseomonas* and *Roseococcus* in the oligotrophic lakes and ponds of Svalbard, resp. Samoylov may benefit from DOC that is released by the hosts, probably as part of the biofilm on the surface of the moss hosts. Other studies have already reported on *Roseomonas* and *Roseococcus* as common inhabitants of aquatic biofilms (Furuhata et al. 2013, Wagner et al. 2015, Miao et al. 2019) and moreover, as initiators of biofilm formation (Furuhata et al. 2008). To the best of our knowledge, no plant-promoting effect was yet reported neither for *Roseomonas,* nor for *Roseococcus*, contrarily to other plant-associated Acetobacteraceae which are able to fix N_2 (Pedraza 2008, Saravanan et al. 2008, Reis and Teixeira 2015) or produce the growth promoting phytohormone indole-3-acetic acid (IAA) (Kielak et al. 2016, Zhang et al. 2021).

Besides *Roseomonas* and *Roseococcus*, *Acidocella* displayed another distinct genus in association with brown mosses, and its relative abundance increased remarkably when associated with *Sphagnum* mosses (Figure S3). *Acidocella* occurred further as putative endophyte in both, brown mosses and *Sphagnum* and was moreover part of the core community (Figure 17) of all mosses. The name '*Acidocella'* can be translated as 'acid-requiring cell' (Hiraishi 2015) and indicates the need for acid and therefore the preference for acidic habitats. *Acidocella* species inhabit strongly acidic, mineral environments with high loads of heavy metals and aromatic compounds, such as certain shallow lakes

(Servín-Garcidueñas et al. 2013), acidic coal mine drainages (Wichlacz et al. 1986) and freshwater lakes (Okamoto et al. 2017). Members of this genus grow in the range of pH 3.0 – 6.0 and utilise simple sugars such as fructose and glucose, as well as simple alcohols such as ethanol (Hiraishi 2015, Okamoto et al. 2017). Like other acidophilic heterotrophic bacteria, the growth of *Acidocella* is inhibited by high concentrations of organic acids; nonetheless, some *Acidocella* strains have the remarkable capability to grow at low amounts of acetate, lactate and succinate, which they oxidise to CO_2 and H_2 (Jones et al. 2013, Hiraishi 2015). In this way, *Acidocella* may potentially provide additional CO_2 for their *Sphagnum* hosts, which points towards a mutualistic relationship between both and probably explains the frequent findings of the genus *Acidocella* within the *Sphagnum* bryosphere (Opelt and Berg 2004, Lindo and Gonzalez 2010, Bragina et al. 2012b, 2012a, Graham et al. 2017, Dobrovolskaya et al. 2020). Interestingly, *Acidocella* seems to play a major role as plant-promoting symbiont of *Nepenthes* spp. (carnivorous pitcher plants), where it thrives within the plant´s digestive fluid, making up 30% of the total bacteriome (Kanokratana et al. 2016). Here, *Acidocella* produce bioactive compounds and by this contributes to pathogen suppression and the maintenance of a suitable digestive bacterial community (Chan et al. 2020). Analogous to that, *Acidocella* account for 26% of the total endophytic bacterial community of *S. fallax* (data not shown) and may support the self-defence of *Sphagnum* by the release of antimicrobial compounds that prevent the host of microbial and fungal attack, as the host moss does by means of cell wall-bound polysaccharides (Stalheim et al. 2009, Hájek et al. 2011), phenolic compounds (Børsheim et al. 2001) and secondary metabolites (Opelt et al. 2007b). Moreover, the production and release of acetic acid by *Acidocella* and other members of the Acetobacteraceae is a powerful strategy to eliminate microorganisms, as acetic acid diffuses through the cell membrane, acidifies the cytoplasm and finally disrupts the proton gradient of prokaryotic competitors (Vidra and Németh 2018). Acidity is accounted as one of the main control strategies of plants that prevent microbial decomposition (Lewis and Ausubel 2006) and has a profound influence on the composition of the *Sphagnum*-associated microflora (Stalheim et al. 2009). As an ecosystem engineer, *Sphagnum* mosses create, inhabit and maintain at the same time an environment inhospitable for competing plants and degradative prokaryotes (van Breemen 1995, Johnson et al. 2015, Bengtsson et al. 2018). *Acidocella* (and other Acetobacteraceae) seem not only to be extremely well adapted to these harsh conditions, but also seem to contribute to these low pH values and antimicrobial properties of *Sphagnum* peat bogs. This could raise the question if *Sphagnum* mosses would establish and expand in such as successful manner without the associated *Acidocella*. The low pH of acidic peat bogs may also result from acetic acid (and other organic acids) produced by moss-associated Acetobacteraceae in the acrotelm, by fermentative acetogenic bacteria within the catotelm, but also from photochemical formation of acetic acid when UV light degrades bog water DOC (Bertilsson and Tranvik 1998, Brinkmann et al. 2003). As assumed earlier, mainly indirect effects such as peat accumulation and subsequent blocking of alkaline soil water lead to the transition from neutral fens to acidic bogs, since CEC values are similar among brown mosses and Sphagna (Soudzilovskaia et al. 2010), which is also confirmed by the data of this work. Similarly, the increasing percentage of moss-associated

Acetobacteraceae during fen-bog-transition may facilitate the establishment and expansion of *Sphagnum* mosses by enhancing peat bog acidification. *Acidocella* is part of the core microbiome and appears even as putative brown moss-endophyte in early bog succession stages, assuming a key role for both the host mosses as well as the bog ecosystems. *Acidocella* and related AAB may be encountered as 'hub taxa' which have strong effects on host microbiota and the microbial communities of the habitat (Agler et al. 2016), or may even display 'keystone microbes' that influence whole-community dynamics (Herren and McMahon 2018). Thus, *Acidocella* and other Acetobacteraceae seem not only to be highly adapted to the extreme acidic and antibiotic microenvironment created by *Sphagnum*, they rather may contribute to the prevailing harsh conditions and facilitate with this probably the establishment of their host during the early stages of bog development, while supporting host growth and expansion by beneficial effects such as additional CO_2 supply and the suppression of moss pathogens. In turn, Acetobacteraceae such as *Acidocella* may benefit from organic compounds deriving from the host mosses, for example DOC released with *Sphagnum* leachate which is highly labile and therefore easily consumable (Wickland et al. 2007). In addition, *Sphagnum* mosses release ethanol and other volatile organic compounds (VOC) (Vicherová et al. 2020) which could serve as C source for *Acidocella* and related Acetobacteraceae.

4.6. Moss-associated microbial communities of the methane cycle and their potential metabolic activity

The present work for the first time investigates both, brown moss- and *Sphagnum* -associated prokaryotes of the methane cycle and their potential methane production, respectively methane oxidation rates. The results demonstrate that mosses of both, circumneutral and acidic peatlands, are colonised by a versatile methanogenic community composed by the hydrogenotrophic *Methanobacteria*, *Methanoregula*, *Methanomassiliicoccaceae* and *Methanocellales*, as well as the hydrogenotrophic/acetoclastic *Methanosarcina* and the acetoclastic *Methanosaeta*. However, potential methane production rates could only be measured on submerged *S. fallax* and brown mosses, and those rates were low.

The presence of anaerobic methanogenic archaea within the bryosphere is surprising, since they are exposed to photosynthesis-deriving oxygen which is released across the entire moss surface, and even to atmospheric oxygen when associated with emerged *Sphagnum* mosses. Nevertheless, methanogenic archaea were shown to occur in the oxygenated spheres of diverse other primary producers such as algal mats, fluid-filled pitchers and rice rhizospheres (Chakraborty et al. 2000, Erkel et al. 2006, Cadillo-Quiroz et al. 2010, Krieger and Kourtev 2012, Moissl-Eichinger et al. 2018). This indicates a certain degree of aerotolerance as a prerequisite for the survival in microaerated plant habitats (Angel et al. 2012) that probably evolved around the Great Oxygenation Event (Lyu and Lu 2018) and is realised by enzyme-based mechanisms to combat oxidative stress (Erkel et al. 2006, Horne and Lessner 2013).

The discrepancy between the presence of methanogens on all investigated mosses but observed methanogenesis on brown mosses and submerged *S. fallax* only could be explained with methanogens that colonise the mosses from surrounding peat and water, analogous to methanotrophic bacteria (Putkinen et al. 2012), but switch to a metabolically inactive, dormant stage when exposed to atmospheric oxygen, e.g. when the water table drops. Under anoxic conditions and appropriate nutrient supply, methanogenesis may be reactivated, similarly to rewetted peatlands (Emsens et al. 2020, Urbanová and Bárta 2020). While brown mosses and submerged *S. fallax* provided optimal conditions and were therefore already 'inoculated' by metabolically active methanogens from the corresponding sites, the *in situ*-methanogenesis of all other investigated sites was presumably hampered by other factors, for example constantly aerobic conditions provided by emerged moss hosts, or - in the case of submerged *S. riparium* - lower temperatures and DOC availability compared to the submerged *S. fallax*. These methanogens may require a longer lag period before starting methanogenesis. If so, incubation time during activity tests should be prolonged. It has to be mentioned that acetate was not added during the activity measurements, thus excluding potential acetoclastic methanogenesis. While some authors state that hydrogenotrophic methanogenesis prevails in peatlands (Kotsyurbenko et al. 1996, Blodau et al. 2008, St. James et al. 2021), others report on a higher ratio of acetoclastic methanogenesis (Kotsyurbenko et al. 2004, Negandhi et al. 2013). However, the mode of methanogenesis depends also on the pH level (Metje 2006) and on the quality of organic carbon (Hornibrook et al. 1997, Penning and Conrad 2007, Negandhi et al. 2013).

The results of this thesis show for the first time that methanogenic archaea can colonise peatland bryophytes and may be metabolically active under certain conditions. Nevertheless, potential methane production rates remain low compared to sediment and peat samples from the same sites (Kiss 2012, Tveit et al. 2013, Knoblauch et al. 2015, Rey-Sanchez et al. 2019), indicating a minor role of mosses-associated methanogenesis for overall methane production and release from northern peatlands.

Contrarily to moss-associated methanogenesis, potential methanotrophic activity could be measured on almost all investigated mosses, comparable to other studies with partly similar rates (Raghoebarsing et al. 2005, Liebner et al. 2011, Küpfer 2015, Putkinen et al. 2018).

Brown mosses displayed similar potential methane oxidation rates as emerged *Sphagnum* species although brown mosses lack hyaline cells that are typical features of *Sphagnum* mosses and display a suitable spatial niche for methanotrophic bacteria (Basiliko et al. 2004). Together with lower DOC values and mean annual temperatures, which indicate a lower habitat productivity, these factors may hamper moss-associated methanotrophy in Arctic circumneutral peatlands.

Potential methane oxidation rates were most pronounced in submerged *S. fallax*, which is in line with previous reports (Raghoebarsing et al. 2005, Kip et al. 2010, Parmentier et al. 2011, Larmola et al. 2014). A mutualistic relationship characterises the association between methanotrophic bacteria and submerged *Sphagnum* and brown mosses, where the methanotroph benefits from the oxygen produced by photosynthesis, and the moss host from the additional CO2 supplied through methane oxidation (Raghoebarsing et al. 2005, Kip et al. 2010, Larmola et al. 2010, Liebner et al. 2011). Owing to the low distances between methane that is produced in anoxic peat layers and the ambient aerobic bryosphere, floating moss mats within waterlogged peatlands display appropriate locations for methane oxidising bacteria, where significant methane oxidation occur (Basiliko et al. 2004, Blodau et al. 2008). Under such conditions, methane emissions can be reduced by 50 - 99% (Parmentier et al. 2011, Knoblauch et al. 2015, Kox et al. 2021).

Compared to other investigated sites with dense mats of *Sphagnum* spp., the hummock-hollow-complex with emerged and submerged *S. fallax* was characterised by a small-scale heterogeneity, where bryophytes and plants with different habitat preferences coexisted in spatial proximity. Such diverse surface patterns and microforms develop by complex feedback mechanisms and feature increased nutrient availability and greater gross primary production (Harris et al. 2020), which may explain higher methane and DOC concentrations, but also a more versatile methanotrophic community compared to the thermokarst pond. Thus, small-scale heterogeneity and the resulting enhanced productivity may lead, together with higher mean annual temperatures, to remarkable moss-associated methane oxidation in heterogeneous bogs.

Surprisingly, potential methane oxidation rates of submerged *S. riparium* from a thermokarst pond were considerably lower compared to emerged *S. lindbergii* from an adjacent collapsed palsas (Liebner and Svenning 2013), despite higher *in-situ* methane emission rates from the thermokarst pond (Liebner et al. 2015).

Methylocystis (type II methanotrophs) and *Methylomonas* (type I methanotrophs) were the prevailing methanotrophic genera within our study. They have been frequently reported as moss associates in acidic bogs (Kip et al. 2011, Liebner and Svenning 2013, Kox et al. 2021) or as inhabitants of brown moss-dominated ponds (Liebner et al. 2011, Osudar et al. 2016). *Methylocystis* is a facultative methane oxidiser that can utilise acetate in the absence of methane, and was previously described as predominant, but metabolically less active methanotroph in a palsa peat bog (Liebner and Svenning 2013). *Methylomonas* is directly involved in methane oxidation at the peat bog surface as a key bacteria (Esson et al. 2016) and belongs also to the endophytic methanotrophic community of various vascular plants of acidic peat bogs (Stępniewska and Kuźniar 2014).

4.7. Diversity and structure of *Sphagnum* bacteriomes from pristine, disturbed and rewetted kettle bogs

The close proximity of pristine (KLO), disturbed (KIE) and rewetted (HEI) peat bogs within the Mueritz National Park provides a unique opportunity to compare the bacteriomes of the respective *Sphagnum* species on a geographically small but environmentally heterogeneous scale. The aim was to assess whether and to what extent these bacterial moss communities differ from each other. The bacteriomes of *Sphagnum* mosses from pristine and disturbed bogs varied widely. In pristine sites, the bacteriomes were comparably homogenous, with a few but highly abundant bacterial taxa associated with *Sphagnum*. Contrarily, the *Sphagnum* bacteriomes from disturbed sites were more diverse.

Within the Mueritz subsites, 65 OTUs (34.6%) displayed the *Sphagnum*-associated core community. These OTUs were also found to be part of the core microbiota of all investigated peatlands in the study. This core community included several functional groups such as methanotrophs (Methylocystaceae) and diazotrophs (Nostocaceae, *Azospirillum*), as well as potential plant promoters (Sinobacteraceae, Caulobacteraceae). Additionally, members of the Acetobacteraceae, Acidocella and Acidobacteriaceae were also an integral part the core community. These taxa occur even in disturbed (KIE) and rewetted (HEI) sites, indicating a resilient and persistent *Sphagnum* bacteriome.

Among the 47 OTUs (25%) exclusively found in KIE (*S. magellanicum*) were potential intestinal taxa of wild game, e.g. *Streptococcus* (Verkühlen 2005, del Rey et al. 2014), *Ruminococcus* (Peruzy et al. 2019, Wilson et al. 2019), *Haemophilus* (Aguirre et al. 1999, Cuesta Gerveno et al. 2013) and *Prevotella* (Fogarty and Voytek 2005, Li et al. 2015). This underpins the description of KIE as a non-typical, disturbed habitat with unusual vegetation (*Drosera rotundifolia*, *Rhynchospora alba*, *Juncus effusus*, *Typha latifolia*, *Carex curta*) growing on scarified ground, presumably caused by grazing and wallowing deer and wild boar. Additionally, a bank of sand that was supposedly inserted into KIE ca. 100 years ago influences most likely the oscillating behaviour of the bog and leads to frequent overflow and subsequent nutrient enrichment within the bog centre (T. Timmermann, personal communication). The nutrient content of peat bogs depends particularly on the nature of the supplied water, and eutrophication and the subsequent development of eutrophic vegetation forms in bogs with high flow-through and intensive water exchange (Landgraf and Notni 2004).

The mesotrophic to eutrophic character of KIE may also result from the rise of the water table and the subsequent extinction of surrounding tree and shrub layers within the past years. Although this biomass is excluded from humification when the water level is high, organic compounds accumulate continuously due to water-logged conditions at those sites, analogous to growing peat bogs. The resulting interrupted nitrification process leads to an accumulation of nitrogen in the peat. Similarly, the carbon cycle is interrupted (Kopp et al. 1982, *Müritz-National Park. National Parkplan und Bestandsanalyse* 2003). The higher pH compared to HEI and KLO may also point towards an eutrophicated *Sphagnum* bog. These factors, together with a slightly higher pH compared to the other subsites, may be responsible for the higher bacterial diversity and the unusual bacterial composition within KIE. An experimental eutrophication of a *Sphagnum* peatland revealed a modification in the taxonomic composition and functioning of microbial communities and a substantial increase in the bacterial abundance (Mieczan et al. 2015), confirming the present results.

HEI harboured 29 (15.4%) site-specific OTUs and represented a rewetted and stagnating, non-oscillating *Sphagnum* peat bog with oligotrophic to mesotrophic conditions. A species-poor hummock-hollow-complex consisting of *S. fallax* and *Eriophorum vaginatum* established after the extinction of the tree layer (*Betula pubescens*), with submerged *Sphagnum fallax* growing in the water-filled bog margin (T. Timmermann, personal communication). HEI harboured the highest relative amount of obligate and facultative methane oxidisers such as Methylococcaceae (e.g., *Methylomonas*) and Methylobacteriaceae, respectively, most likely due to the sufficient methane supply in the waterlogged sites. The presence of bacteria characteristic for aquatic habitats, e.g. *Geothrix* (Coates et al. 1999, Küsel et al. 2008), *Flavobacterium* (Lew et al. 2018) and *Kaistia* (Weon et al. 2008, Jin et al. 2012) underpins further the strong influence of the hydrology onto the hosts and their microbiomes in HEI. Moreover, numerous plant-associated and potentially host-promoting bacteria genera shaped the HEI-specific community, for example *Paenibacillus* (Selbmann et al. 2010, Hui et al. 2013, Alcaraz et al. 2018), *Flavobacterium* (Kolton et al. 2016), *Pandoraea* (Sickel et al. 2016, Obermeier et al. 2019), Bosea (Safronova et al. 2015, Ma et al. 2017), *Kaistia* (Sickel et al. 2016) and *Rhodanobacter* (De Clercq et al. 2006, Sickel et al. 2016).

Among the 13 OTUs (6.9%) that were solely found in KLO were numerous plant growth-promoting taxa such as *Agrobacterium* (Yu et al. 2015, Zhang et al. 2021), *Nocardia* (Schellenberger et al. 2010, Trujillo et al. 2015), *Accumulibacter* (Santana et al. 2016, Graham et al. 2017) and *Methylobacterium* (Sickel et al. 2016, Graham et al. 2017), while latter was frequently reported as moss symbiont (Hornschuh et al. 2002, Kutschera 2007, Schauer and Kutschera 2011, Tani et al. 2012). This may underpin the important role of these bacterial taxa for the establishment, resilience and persistence of their *Sphagnum* hosts which inhabit extreme narrow ecological niches in ombrotrophic peat bogs.

According to T. Timmermann (personal communication), KLO represents an ideal model of a pristine and apparently intact, oscillating kettle bog which underwent obviously much less disturbance events compared to KIE and HEI. The small number of OTUs that appear exclusively in KLO could represent a mature, homogenous microbial community that may have developed and established over a long time period, analogous to vegetation climax communities (Whittaker and Levin 1977, Fierer et al. 2010). Interestingly, *S. magellanicum* growing in the oligotrophic centre and *S. fallax* growing in the mesotrophic margin of KLO did not share any common, site-specific OTUs, despite the relative spatial proximity to each other, while *S. magellanicum* from KIE and KLO shared 7 OTUs and *S. fallax* from KLO and HEI shared 4 OTUs. Considering the similar pore water chemistry and environmental data of both KLO subsites (S1A), the host species and its habitat preference may influence the moss microbiota. *Sphagnum* mosses simultaneously create and inhabit extreme habitats. Interestingly, different *Sphagnum* genera evolved with variable niche evolution rates (Johnson et al. 2015). While hummock-preferring species are able to exist withing more aquatic environments, hollow-preferring *Sphagnum* species cannot cope with the more stressful hummock environment (Rydin et al. 2006, Johnson et al. 2015). As a characteristic inhabitant of ombrotrophic bogs, *S. magellanicum* occurs within a narrower trophic range with very low pH (< 4.1) and ion concentrations (conductivity), while *S. fallax* growing in lawns has a broad ecological amplitude with higher pH values and ion contents (Wojtuń et al. 2013). Moreover, *S. magellanicum* and *S. fallax* belong to different sections (*Sphagnum*, resp. Cuspidata) with distinct metabolites and litter quality (Bengtsson et al. 2018), which might further affect the associated microbiota.

The present results suggest that disturbed, eutrophicated *Sphagnum* peat bogs display a greater bacterial diversity and different bacterial community composition compared to rewetted and pristine bogs, while low-diversity *Sphagnum* microbiomes may reflect a mature bog and a late successional stage. Intact poor fens and naturally developed ombrotrophic bogs may remain stable for decades regarding their pH and *Sphagnum* coverage, while other bryophyte species and vascular plants decrease (Gunnarsson et al. 2000). Such constant conditions over a long time period promote the establishment of a species-poor, highly specific microbial community that is associated with *Sphagnum* mosses and promotes at the same time growths and resilience of its host. Peat bog disturbance such as nutrient deposition and draining alters in particular the *Sphagnum* vegetation and bog chemistry, with subsequent shifts in the *Sphagnum* microbiome. The disturbance intensity is a crucial factor that leads to changes in bacterial community composition and functional performance, while recovery rates and response of the bacteriomes depend on functional type and character of disturbance (Berga et al. 2012). The eutrophication of *Sphagnum* peat bogs alters microbial processes and parameters, and increasing habitat fertility might modify the taxonomic composition and functioning of microbial communities (Mieczan et al. 2015), as can be observed for KIE. The considerably higher amount of OTUs of *S. magellanicum* from KIE (137 OTUs) compared to *S. magellanicum* growing in KLO (74 OTUs) may be regarded as a further indication of bog eutrophication, analogous to the substantial increase of bacterial abundances in eutrophicated *Sphagnum* bogs (Mieczan et al. 2015). Besides eutrophication, rewetting after drought can cause substantial shifts in peatland microbiomes (Kitson and Bell 2020, Unger et al. 2021) while microbial communities may considerably recover upon rewetting and subsequent re-vegetation of *Sphagnum*, probably along with a concomitant recovery of biogeochemical peatland functioning (Elliott et al. 2015, Emsens et al. 2020). Compared to the *S. magellanicum* bacteriomes from KIE and KLO, the numbers of *S. fallax*-associated OTUs from the rewetted HEI (109 OTUs) and the pristine KLO margin (80 OTUs) differed less. The occurrence of various HEI-specific (potential) methanotrophic moss associates may indicate a gradual recovery state of HEI after rewetting. It has been reported that methanotrophic bacteria re-establish slowly after rewetting, while the methanogenic archaea recover rapidly, resulting in prolonged increased methane emissions following rewetting (Wen et al. 2018). Moreover, the hummock-hollow-complex of HEI provides a pronounced habitat heterogeneity on a relatively small spatial scale, where emerged and submerged *S. fallax* grow side by side. This is also reflected in a versatile *Sphagnum*-associated bacteriome with characteristic aquatic and terrestrial taxa. At long sight, the lacking oscillation capacity and stagnating waterbody with changing water level might favour the establishment of aquatic *Sphagnum*-specific microbiomes with presumably higher diversity compared to the *S. fallax* microbiome of KLO with more stable conditions.

5. Conclusion

This work presents novel and comprehensive insights into the microbial communities associated with peatland bryophytes on a large geographical scale, framed by a systematic analysis of the environmental factors that shape the community structure of these moss microbiomes. Moreover, the results of this thesis indicate key prokaryotic taxa and their potential role for host mosses and peat ecosystems.

Based on the scientific questions raised at the beginning of this thesis, the following key insights can be summarised:

1. Both, *Sphagnum* and brown mosses harbor specific endophytic bacteria. The epiphytic and endophytic bacterial communities of the individual plantlets differ clearly from each other.
2. A core microbiome exists across bryophytes from natural northern peatlands spanning the High Arctic, subarctic and the temperate zone. This core community is small, but made up of many bacterial taxa that are epiphytes of brown mosses and highly abundant endophytes of *Sphagnum* mosses.
3. Brown mosses and *Sphagnum* mosses display an appropriate habitat for archaea and harbor few, but abundant archaeal species, among which most taxa belong to the functional group of methanogenic archaea. Thus, also in peatlands methanogenic archaea are not restricted to anoxic microhabitats such as deep soil layers. Contrarily to the moss-associated bacteria, the archaeal community structure of brown mosses

and *Sphagnum* mosses is similar. Additionally, no clear differences between epiphytic and endophytic moss archaeomes were observed.

4. The impact of the investigated environmental parameters on the moss microbiomes can be ranked, beginning from the host moss species as the main driver, followed by the pH regime and the water level. The prevailing temperature has only a minor impact on the community structure of moss microbiomes.
5. Within peatland ecosystems, microbial methane production is not restricted to waterlogged, anoxic soil and peat layers. It is also associated with both, brown mosses and *Sphagnum* mosses from the Arctic, subarctic and the temperate zone. However, methane production rates associated with mosses are very low. In comparison, potential moss-associated methane oxidation rates are significantly higher. Moreover, brown mosses display similar potential methane oxidation rates as emerged *Sphagnum* species, while submerged *Sphagnum* mosses from a rewetted peat bog site show the highest potential activity rates.
6. The structure of *Sphagnum*-associated bacterial communities from pristine, rewetted and degraded peat bogs differs from each other, while the *Sphagnum*-bacteriome diversity decreases from degraded towards pristine peat bog sites.
7. *Sphagnum* mosses from degraded sites harbour the most versatile bacterial communities with uncommon bacterial taxa such as *Ruminococcus* and *Haemophilus*, whereas members of the Acetobacteraceae, mainly represented by the genus

Acidocella, prevail within the ombrotrophic sites. The *Sphagnum*-associated bacterial community from the rewetted sites differ according to the prevailing water level.

8. Members of the bacterial family Acetobacteraceae are an integral part of the core microbiome and omnipresent in the bryosphere of all investigated mosses, with *Acidocella* as a remarkably abundant genus possibly holding a key role in fen-bog-transition processes. However, a large part within the moss-associated Acetobacteraceae remained unassigned at the genus level.

6. Critical remarks and outlook

6.1. Critical remarks

The results of this thesis contribute to a better comprehension of the taxonomy of *Sphagnum*- and brown moss-associated prokaryotes from northern peatlands and helps to better understand the complex relationships between the moss hosts and their microbial assemblages. The nature of moss-microbe-interactions and the underlying mechanisms depend on a range of physiological, biochemical and ecological processes that cannot be explained by the identity of the moss-associated procaryotes. Although this thesis can, therefore, not disentangle the mechanisms of moss-microbe interaction, it provides valuable information to formulate testable hypothesis on those interactions.

The presented taxonomic results are based on Operational Taxonomic Units (OTUs), while recent publications use the Amplicon Sequence Variants (ASV) approach (Jeske and Gallert 2022, Kolton et al. 2022, Camargo et al. 2023). The use of OTUs in microbial ecology has been a common practice for many years, and also at the time of data collection in the frame of this thesis. Compared to OTUs, ASV offer more precise identification and quantification of microbial taxa by analysing individual sequences without clustering them into OTUs, thus avoiding a loss of information during processing steps such as quality filtering (Callahan et al. 2017).

Furthermore, OTUs are analysis-specific and generated internally, hence the achieved results are not directly comparable with other studies. Each comparison has to be rather made indirectly via cross-referencing with different databases, assumed that both OTUs, i.e., both 97% sequence similarity threshold centroids, accurately represent the organism present in the respective sample (Jeske and Gallert 2022). However, the interpretation of microbial community structure depends also on several other factors, including the choice of sample sequencing, appropriate filtering strategies and the use of taxonomic level for data clustering (Joos et al. 2020).

In order to gain robust and comparable results in the field of environmental microbiology, it is furthermore crucial to adapt established methods to the respective sample material, especially at the initial analysis such as DNA extraction and subsequent amplification. Therefore, comparisons between different environmental studies should be made with caution, as the differences observed can base on different DNA extraction approaches or on the choice of the primers. The fact that certain taxa could not be detected within the samples by the chosen methods does not necessarily imply that those species are absent in the respective habitat. For instance, DNA extraction and subsequent analysis of plant-associated microorganisms can be hampered by plant-deriving phenolic compounds (Hills and Van Staden 2002). One should therefore be aware that the applied methods do never cover the entire diversity of microorganisms contained in a sample. In addition to the influence of the underlying extraction method, the revealed moss-associated microbial assemblages and their metabolic activity are also influenced by various factors such as the sampling time, e.g., the growing season. Hence, the outcomes of this thesis can only display a current snapshot of the plant microbiomes and does not illustrate dynamics in community structures and metabolic activity rates. Most of the here investigated microbial taxa are well adapted to the prevailing low temperatures within their habitat, with temperature optima lower than those of microorganisms from warmer climates, but at the same time, these microbiota exhibit higher temperature optima when in culture (Carson 2018). Therefore, one should be aware that the assessed methane oxidation and methane production rates display only artificial potential activity rates that do not reflect microbial metabolic activities under natural conditions.

6.2. Outlook

In this study the microbiomes of brown mosses and *Sphagnum* mosses from four different pristine northern bogs have been investigated to assess the community structure of the bacterial and archaeal associates. Based on the examination of the prokaryotic core community of northern peat bogs, future work should focus on the question whether this core microbiome is a result of transfers of epiphytic bacteria from brown mosses to *Sphagnum* during natural peatland succession from fens to bogs. For this purpose, experimental set-ups with axenic moss cultures are conceivable, as described already elsewhere (Sastad et al. 1998, Hohe and Reski 2005).

In that regard, further studies should investigate the role of endophytic taxa to gain more insights on the nature of moss host-microbe-interactions, with a special focus on Acetobacteraceae. This could be accomplished by the use of metagenomic and metatranscriptomic techniques which provide a complete description of the genomic composition and diversity of the moss-associated Acetobacteraceae, possibly complemented by a 'multiomics' approach which combines metagenomic, metatranscriptomic, metaproteomic and metabolomic data. Such techniques have already been utilised in multiple studies to investigate soil microbiomes and to unravel the molecular changes that occur at the community level due to environmental disturbances (Gamalero et al. 2022).

Based on this work, cultivation and subsequent analysis of yet unknown *Acidocella* species and other Acetobacteraceae associated with peatland mosses is suggested. Connected to this, functional and molecular characterisation of previously isolated *Acidocella* should be conducted, i.e. the investigation of *in vitro* plant growth promoting traits such as IAA production or phosphate solubilisation (Kalam et al. 2020). This could lead to a better understanding of the beneficial role of *Acidocella* for their *Sphagnum* hosts and enhance current nature conservation measures such as paludiculture, which have the capacity to significantly reduce carbon dioxide emissions (Tanneberger et al. 2021).

Moreover, several studies demonstrated the biodegradation capabilities of *Acidocella* strains towards toxic industrial pollutants (Okibe et al. 2016, Eze 2021, Eze et al. 2021). This suggests that *Acidocella* could play a significant role in the bioremediation of former coal mining sites, which is of particular interest regarding the current energy transformation and subsequent phase-out of fossil fuels in Germany. Therefore, it is suggested to investigate the bioremediation potential of *Sphagnum*-associated *Acidocella* by conducting tolerance tests against various toxic contaminants present in wastewater from abandoned coal mining sites.

In order to assess the microbial core community of peatlands on a global scale, it is further recommended to examine also peat bogs of the Southern hemisphere, for instance within the Antarctic zone, where both brown mosses and *Sphagnum* species thrive (Whinam and Copson 2006, Hedenäs 2012, Oloo et al. 2016).

In the course of this thesis, a new technique was successfully established to estimate the moss-associated methane oxidation and methane production of both, the epiphytic and the endophytic communities. The experimental set-up should be further developed, for instance by applying varying temperature regimes or controlled light exposure to take photosynthetic activities of the host mosses in account.

Finally, the studied system of moos-microbe associations in pristine, northern peatlands are currently facing substantial environmental pressure caused by rising surface temperatures. The impact of these changing conditions on the studied associations remains unknown, but alterations in vegetation patterns, temperature and precipitation may profoundly alter the composition and function of moss-microbe communities.

Bibliography

Aerts, R., B. Wallen, and N. Malmer. 1992. Growth-Limiting Nutrients in Sphagnum-Dominated Bogs Subject to Low and High Atmospheric Nitrogen Supply. The Journal of Ecology 80:131.

Agler, M. T., J. Ruhe, S. Kroll, C. Morhenn, S. T. Kim, D. Weigel, and E. M. Kemen. 2016. Microbial Hub Taxa Link Host and Abiotic Factors to Plant Microbiome Variation. PLoS Biology 14:1–31.

Aguirre, A. A., C. Bröjer, and T. Mörner. 1999. Descriptive epidemiology of roe deer mortality in Sweden. Journal of Wildlife Diseases 35:753–762.

Åkerman, J., and J. Boardman. 1987. Periglacial forms of Svalbard: a review. Periglacial Processes and Landforms in Britain and Ireland. Cambridge University Press, Cambridge.:9–25.

Alcaraz, L. D., M. Peimbert, H. R. Barajas, A. E. Dorantes-Acosta, J. L. Bowman, and M. A. Arteaga-Vázquez. 2018. Marchantia liverworts as a proxy to plants' basal microbiomes. Scientific Reports 8:1–12.

Alori, E. T., O. C. Emmanuel, B. R. Glick, and O. O. Babalola. 2020. Plant–archaea relationships: a potential means to improve crop production in arid and semi-arid regions. World Journal of Microbiology and Biotechnology 36:1–10.

Alves, R. J. E. 2011. Ammonia-oxidizing Archaea from High Arctic Soils.

Andersen, R., S. J. Chapman, and R. R. E. Artz. 2013. Microbial communities in natural and disturbed peatlands: A review. Soil Biology and Biochemistry 57:979–994.

Andreas, B. K., and G. R. Bryan. 1990. The Vegetation of Three Sphagnum-dominated Basin-type Bogs in Northeastern Ohio. The Ohio Journal of Science 90:54–66.

Angel, R., P. Claus, and R. Conrad. 2012. Methanogenic archaea are globally ubiquitous in aerated soils and become active under wet anoxic conditions. ISME Journal 6:847–862.

Arlen-Pouliot, Y., and N. Bhiry. 2005. Palaeoecology of a palsa and a filled thermokarst pond in a permafrost peatland, subarctic Québec, Canada. The Holocene 15:408–419.

Atamna-Ismaeel, N., O. Finkel, F. Glaser, C. von Mering, J. A. Vorholt, M. Koblížek, S. Belkin, and O. Béjà. 2012. Bacterial anoxygenic photosynthesis on plant leaf surfaces. Environmental Microbiology Reports 4:209–216.

Baik, K. S., S. C. Park, H. N. Choe, S. N. Kim, J. H. Moon, and C. N. Seong. 2012. Roseomonas riguiloci sp. nov., isolated from wetland freshwater. International Journal of Systematic and Evolutionary Microbiology 62:3024–3029.

Barbier, B. A., I. Dziduch, S. Liebner, L. Ganzert, H. Lantuit, W. Pollard, and D. Wagner. 2012. Methane-cycling communities in a permafrost-affected soil on Herschel Island, Western Canadian Arctic: active layer profiling of mcrA and pmoA genes. FEMS Microbiology Ecology 82:287–302.

Basile, A., S. Giordano, J. A. Lopez-Saez, and R. C. Cobianchi. 1999. Antibacterial activity of pure flavonoids isolated from mosses. Phytochemistry 52:1479–1482.

Basilier, K. 1979. Moss-associated nitrogen fixation in some mire and coniferous forest environments around Uppsala, Sweden. Lindbergia 5:84–88.

Basilier, K., and U. Granhall. 1978. Nitrogen Fixation in Wet Minerotrophic Moss Communities of a Subarctic Mire. Oikos 31:236–246.

Basiliko, N., R. Knowles, and T. R. Moore. 2004. Roles of moss species and habitat in methane consumption potential in a northern peatland. Wetlands 24:178–185.

Bay, G., N. Nahar, M. Oubre, M. J. Whitehouse, D. A. Wardle, O. Zackrisson, M. C. Nilsson, and U. Rasmussen. 2013. Boreal feather mosses secrete chemical signals to gain nitrogen. New Phytologist 200:54–60.

Belkina, O. A., and A. A. Vilnet. 2015. Some aspects of the moss population development on the Svalbard glaciers. Czech Polar Reports 5:160–175.

Bengtson, S.-A., A. Fjellberg, and T. Solhöy. 1974. Abundance of Tundra Arthropoda in Spitsbergen. Journal Entomologica scandinavica 5:137–142.

Bengtsson, F., H. Rydin, and T. Hájek. 2018. Biochemical determinants of litter quality in 15 species of Sphagnum. Plant and Soil 425:161–176.

Berg, A., Å. Danielsson, and B. H. Svensson. 2013. Transfer of fixed-N from N2-fixing cyanobacteria associated with the moss Sphagnum riparium results in enhanced growth of the moss. Plant and Soil 362:271–278.

Berg, G., M. Grube, M. Schloter, and K. Smalla. 2014. Unraveling the plant microbiome: Looking back and future perspectives. Frontiers in Microbiology 5:1–7.

Berga, M., A. J. Székely, and S. Langenheder. 2012. Effects of disturbance intensity and frequency on bacterial community composition and function. PLoS ONE 7.

Bergamini, A., and D. Pauli. 2001. Effects of increased nutrient supply on bryophytes in montane calcareous fens. Journal of Bryology 23:331–339.

Bertilsson, S., and L. J. Tranvik. 1998. Photochemically produced carboxylic acids as substrates for freshwater bacterioplankton. Limnology and Oceanography 43:885–895.

Bhiry, N., and É. C. Robert. 2006. Reconstruction of changes in vegetation and trophic conditions of a palsa in a permafrost peatland, subarctic Québec, Canada. Ecoscience 13:56–65.

Bjorck, S. 1991. Stratigraphic and paleoclimatic studies of a 5500-year-old moss bank on Elephant Island, Antarctica. Arctic & Alpine Research 23:361–374.

Blodau, C., R. Rees, H. Flessa, A. Rodionov, G. Guggenberger, K. H. Knorr, O. Shibistova, G. Zrazhevskaya, N. Mikheeva, and O. A. Kasansky. 2008. A snapshot of CO2 and CH4 evolution in a thermokarst pond near Igarka, northern Siberia. Journal of Geophysical Research: Biogeosciences 113:1–8.

Bobbink, R., M. Hornung, and J. G. Roelofs. 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. Journal of ecology 86:717–738.

Boiştean, A., A. Chirsanova, D. Zgardan, I. Mitina, and B. Gaina. 2020. Methodological aspects of real-time PCR usage in acetobacter detection. Journal of Engineering Sciences XXVII:232–238.

Boldareva, E. N., T. P. Tourova, T. V. Kolganova, A. A. Moskalenko, Z. K. Makhneva, and V. M. Gorlenko. 2009. Roseococcus suduntuyensis sp. nov., a new aerobic bacteriochlorophyll a-containing bacterium isolated from a low-mineralized soda lake of Eastern Siberia. Microbiology 78:92–101.

Bolger, A. M., M. Lohse, and B. Usadel. 2014. Trimmomatic: A flexible trimmer for Illumina sequence data. Bioinformatics 30:2114–2120.

Borga, P. 1994. Bacterial Communities in Peat in Relation Botanical Composition As Revealed By Fatty Acid Analysis. Science 26.

Borrel, G., J. F. Brugère, S. Gribaldo, R. A. Schmitz, and C. Moissl-Eichinger. 2020. The host-associated archaeome. Nature Reviews Microbiology 18:622–636.

Børsheim, K. Y., B. E. Christensen, and T. J. Painter. 2001. Preservation of fish by embedment in Sphagnum moss, peat or holocellulose: Experimental proof of the oxopolysaccharidic nature of the preservative substance and of its antimicrobial and tanning action. Innovative Food Science and Emerging Technologies 2:63–74.

Bouchard, R., G. Peñaloza-Bojacá, S. Toupin, Y. Guadalupe, J. Gudiño, N. Salazar Allen, F. W. Li, and J. C. Villarreal A. 2020. Contrasting bacteriome of the hornwort Leiosporoceros dussii in two nearby sites with emphasis on the hornwort-cyanobacterial symbiosis. Symbiosis 81:39–52.

Bragazza, L., C. Freeman, T. Jones, H. Rydin, J. Limpens, N. Fenner, T. Ellis, R. Gerdol, M. Hajek, T. Hajek, P. Lacumin, L. Kutnar, T. Tahvanainen, and H. Toberman. 2006. Atmospheric nitrogen deposition promotes carbon loss from peat bogs. Proceedings of the National Academy of Sciences of the United States of America 103:19386–19389.

Bragina, A., C. Berg, and G. Berg. 2015. The core microbiome bonds the Alpine bog vegetation to a transkingdom metacommunity. Molecular Ecology 24:4795–4807.

Bragina, A., C. Berg, M. Cardinale, A. Shcherbakov, V. Chebotar, and G. Berg. 2012a. Sphagnum mosses harbour highly specific bacterial diversity during their whole lifecycle. The ISME journal 6:802–13.

Bragina, A., M. Cardinale, C. Berg, and G. Berg. 2013. Vertical transmission explains the specific Burkholderia pattern in Sphagnum mosses at multi-geographic scale. Frontiers in Microbiology 4:1–10.

Bragina, A., S. Maier, C. Berg, H. Müller, V. Chobot, F. Hadacek, and G. Berg. 2012b. Similar diversity of Alphaproteobacteria and nitrogenase gene amplicons on two related Sphagnum mosses. Frontiers in Microbiology 2:1–10.

van Breemen, N. 1995. How Sphagnum bogs down other plants. Trends in ecology & evolution 10:270–275.

Bridgham, S. D., H. Cadillo-Quiroz, J. K. Keller, and Q. Zhuang. 2013. Methane emissions from wetlands: Biogeochemical, microbial, and modeling perspectives from local to global scales. Global Change Biology.

Brinkmann, T., P. Hörsch, D. Sartorius, and F. H. Frimmel. 2003. Photoformation of low-molecular-weight organic acids from brown water dissolved organic matter. Environmental Science and Technology 37:4190–4198.

Buée, M., W. de Boer, F. Martin, L. van Overbeek, and E. Jurkevitch. 2009. The rhizosphere zoo: An overview of plant-associated communities of microorganisms, including phages, bacteria, archaea, and fungi, and of some of their structuring factors. Plant and Soil 321:189–212.

Bulgarelli, D., M. Rott, K. Schlaeppi, E. Ver Loren van Themaat, N. Ahmadinejad, F. Assenza, P. Rauf, B. Huettel, R. Reinhardt, E. Schmelzer, J. Peplies, F. O. Gloeckner, R. Amann, T. Eickhorst, and P. Schulze-Lefert. 2012. Revealing structure and assembly cues for Arabidopsis root-inhabiting bacterial microbiota. Nature 488:91–5.

Bulgarelli, D., K. Schlaeppi, S. Spaepen, E. V. L. van Themaat, and P. Schulze-Lefert. 2013. Structure and Functions of the Bacterial Microbiota of Plants. Annual Review of Plant Biology 64:807–838.

Cabrera, M. Á., and J. M. Blamey. 2018. Biotechnological applications of archaeal enzymes from extreme environments. Biological Research 51:1–15.

Cadillo-Quiroz, H., E. Yashiro, J. B. Yavitt, and S. H. Zinder. 2008. Characterization of the archaeal community in a minerotrophic fen and terminal restriction fragment length polymorphism-directed isolation of a novel hydrogenotrophic methanogen. Applied and Environmental Microbiology 74:2059–2068.

Cadillo-Quiroz, H., J. B. Yavitt, S. H. Zinder, and J. E. Thies. 2010. Diversity and community structure of Archaea inhabiting the rhizoplane of two contrasting plants from an acidic bog. Microbial Ecology 59:757–767.

Cai, S., and Z. Yu. 2011. Response of a warm temperate peatland to Holocene climate change in northeastern Pennsylvania. Quaternary Research 75:531–540.

Callahan, B. J., P. J. McMurdie, and S. P. Holmes. 2017. Exact sequence variants should replace operational taxonomic units in marker-gene data analysis. ISME Journal 11:2639–2643.

Camargo, A. P., R. S. C. de Souza, J. Jose, I. R. Gerhardt, R. A. Dante, S. Mukherjee, M. Huntemann, N. C. Kyrpides, M. F. Carazzolle, and P. Arruda. 2023. Plant microbiomes harbor potential to promote nutrient turnover in impoverished substrates of a Brazilian biodiversity hotspot. ISME Journal 17:354–370.

Cao, W., Y. Xiong, D. Zhao, H. Tan, and J. Qu. 2020. Bryophytes and the symbiotic microorganisms, the pioneers of vegetation restoration in karst rocky desertification areas in southwestern China. Applied Microbiology and Biotechnology 104:873–891.

Caporaso, J. G., J. Kuczynski, J. Stombaugh, K. Bittinger, F. D. Bushman, E. K. Costello, N. Fierer, A. G. Peña, K. Goodrich, J. I. Gordon, G. a Huttley, S. T. Kelley, D. Knights, E. Jeremy, R. E. Ley, C. a Lozupone, D. Mcdonald, B. D. Muegge, J. Reeder, J. R. Sevinsky, P. J. Turnbaugh, and W. a Walters. 2011. QIIME allows analysis of high-throughput community sequencing data. Natural Methods 7:335–336.

Carrell, A. A., M. Kolton, M. J. Warren, D. A. Pelletier, J. B. Glass, J. E. Kostka, P. J. Hanson, and D. J. Weston. 2017. Experimental warming reduces the diversity and functional potential of the

Sphagnum microbiome. bioRxiv:194761.

Carrell, A. A., T. J. Lawrence, K. G. M. Cabugao, D. L. Carper, D. A. Pelletier, S. Jawdy, and D. J. Weston. 2020. Sphagnum peat moss thermotolerance is modulated by the microbiome. bioRxiv.

Carson, M. A. 2018. Methane Production in Peatlands. Laurentian University, Sudbury, Ontario, Canada.

Chakraborty, N., G. M. Sarkar, and S. C. Lahiri. 2000. Methane emission from rice paddy soils, aerotolerance of methanogens and global thermal warming. Environmentalist 20:343–350.

Chan, E. W. L., M. Y. Chin, Y. H. Low, H. Y. Tan, Y. S. Ooi, and C. W. Chong. 2020. The Antibacterial Agent Identified from Acidocella spp. in the Fluid of Nepenthes gracilis Against Multidrug-Resistant Klebsiella pneumoniae: A Functional Metagenomic Approach. Microbial Drug Resistance.

Chapman, H., R. Van Beek, B. Gearey, B. Jennings, D. Smith, N. H. Nielsen, and Z. Z. Elabdin. 2020. Bog Bodies in Context: Developing a Best Practice Approach. European Journal of Archaeology 23:227–249.

Chapman, S., A. Buttler, A.-J. Francez, F. Laggoun-Défarge, H. Vasander, M. Schloter, J. Combe, P. Grosvernier, H. Harms, D. Epron, D. Gilbert, and E. Mitchell. 2003. Exploitation of northern peatlands and biodiversity maintenance: a conflict between economy and ecology. Frontiers in Ecology and the Environment 1:525–532.

Christen, J. A., R. S. Clymo, and C. D. Litton. 1995. A Bayesian Approach to the Use of 14 C dates in the Estimation of the Age of Peat. Radiocarbon 37:431–441.

De Clercq, D., S. Van Trappen, I. Cleenwerck, A. Ceustermans, J. Swings, J. Coosemans, and J. Ryckeboer. 2006. Rhodanobacter spathiphylli sp. nov., a gammaproteobacterium isolated from the roots of Spathiphyllum plants grown in a compost-amended potting mix. International Journal of Systematic and Evolutionary Microbiology 56:1755–1759.

Clymo, R. S. 1963. Ion exchange in Sphagnum and its relation to bog ecology. Annals of Botany 27:309–324.

Coates, J. D., D. J. Ellis, C. V. Gaw, and D. R. Lovley. 1999. Geothrix fermentans gen. nov., sp. nov., a novel Fe(III)-reducing bacterium from a hydrocarbon-contaminated aquifer. International Journal of Systematic Bacteriology 49:1615–1622.

Cornelissen, J. H. C., S. I. Lang, N. A. Soudzilovskaia, and H. J. During. 2007. Comparative cryptogam ecology: A review of bryophyte and lichen traits that drive biogeochemistry. Annals of Botany 99:987–1001.

Cuesta Gerveno, J. M., D. Risco Pérez, P. Gonçalves Blanco, W. L. García Jiménez, M. Gil Molino, P. Fernandez-Llario, J. Hermoso de Mendoza Salcedo, and L. J. Gómez Gordo. 2013. Fatal infection due to Haemophilus parasuis in a young wild boar (Sus scrofa). Journal of Veterinary Diagnostic Investigation 25:297–300.

Damtab, J., P. Nutaratat, W. Boontham, N. Srisuk, K. Duangmal, H. Yurimoto, Y. Sakai, Y. Muramatsu, and Y. Nakagawa. 2016. Roseomonas elaeocarpi sp . nov ., isolated from olive (Elaeocarpus hygrophilus Kurz.) phyllosphere. International Journal of Systematic and

Evolutionary Microbiology 66:474–480.

Daniels, R. E., and A. Eddy. 1990. Handbook of European Sphagna.

Dedysh, S. N. 2009. Exploring methanotroph diversity in acidic northern wetlands: Molecular and cultivation-based studies. Microbiology 78:655–669.

Dedysh, S. N., V. N. Khmelenina, N. E. Suzina, Y. A. Trotsenko, J. D. Semrau, W. Liesack, and J. M. Tiedje. 2002. Methylocapsa acidiphila gen. nov., sp. nov., a novel methane-oxidizing and dinitrogen-fixing acidophilic bacterium from Sphagnum bog. International Journal of Systematic and Evolutionary Microbiology 52:251–261.

Dedysh, S. N., N. S. Panikov, and J. M. Tiedje. 1998. Acidophilic methanotrophic communities from Sphagnum peat bogs. Applied and Environmental Microbiology 64:922–929.

Dickson, J. H., and R. E. Johnson. 2014. Mosses and the beginning of plant succession on the Walker Glacier, southeastern Alaska. Lindbergia 2:60–65.

Dise, N. B. 2009. PERSPECTIVES : Peatland Response to Global Change. Science 326:810–811.

Dobrovolskaya, T. G., A. V. Golovchenko, E. N. Yurchenko, A. V. Yakushev, N. A. Manucharova, L. V. Lysak, and N. V. Kostina. 2020. Bacterial Communities of Regressive Spots in Ombrotrophic Bogs: Structure and Functions. Microbiology (Russian Federation) 89:107–114.

Drobnik, J., and A. Stebel. 2017. Tangled history of the European uses of Sphagnum moss and sphagnol. Journal of Ethnopharmacology:41–49.

Eiler, A., and S. Bertilsson. 2004. Composition of freshwater bacterial communities associated with cyanobacterial blooms in four Swedish lakes. Environmental Microbiology 6:1228–1243.

Elliott, D. R., S. J. M. Caporn, F. Nwaishi, R. H. Nilsson, and R. Sen. 2015. Bacterial and fungal communities in a degraded ombrotrophic peatland undergoing natural and managed re-vegetation. PLoS ONE 10:1–20.

Emsens, W. J., R. van Diggelen, C. J. S. Aggenbach, T. Cajthaml, J. Frouz, A. Klimkowska, W. Kotowski, L. Kozub, Y. Liczner, E. Seeber, H. Silvennoinen, F. Tanneberger, J. Vicena, M. Wilk, and E. Verbruggen. 2020. Recovery of fen peatland microbiomes and predicted functional profiles after rewetting. ISME Journal 14:1701–1712.

Erkel, C., M. Kube, R. Reinhardt, and W. Liesack. 2006. Genome of Rice Cluster I archaea—the key methane producers in the rice rhizosphere. Science 313:370–372.

Esson, K. C., X. Lin, D. Kumaresan, J. P. Chanton, J. C. Murrell, and J. E. Kostka. 2016. Alpha-and gammaproteobacterial methanotrophs codominate the active methane-oxidizing communities in an acidic boreal peat bog. Applied and Environmental Microbiology 82:2363–2371.

Eze, M. O. 2021. Metagenome analysis of a hydrocarbon-degrading bacterial consortium reveals the specific roles of btex biodegraders. Genes 12:1–14.

Eze, M. O., G. C. Hose, S. C. George, and R. Daniel. 2021. Diversity and metagenome analysis of a hydrocarbon-degrading bacterial consortium from asphalt lakes located in Wietze , Germany:1–24.

La Farge, C., K. H. Williams, and J. H. England. 2013. Regeneration of Little Ice Age bryophytes emerging from a polar glacier with implications of totipotency in extreme environments. Proceedings of the National Academy of Sciences of the United States of America 110:9839–9844.

Fauteux, L., M. T. Cottrell, D. L. Kirchman, C. M. Borrego, M. C. Garcia-Chaves, and P. A. Del Giorgio. 2015. Patterns in abundance, cell size and pigment content of aerobic anoxygenic phototrophic bacteria along environmental gradients in northern lakes. PLoS ONE 10:1–17.

Fenton, N. J., and Y. Bergeron. 2006. Facilitative succession in a boreal bryophyte community driven by changes in available moisture and light. Journal of Vegetation Science 17:65–76.

Fiala, I., and S. Winkler. 1969. Entwicklungsgeschichtliche Untersuchungen an Sphagnum centrale Jens. Flora oder Allgemeine botanische Zeitung. Abt. B, Morphologie und Geobotanik 158:390–401.

Fierer, N., and R. B. Jackson. 2006. The diversity and biogeography of soil bacterial communities. Proc Natl Acad Sci U S A 103:626–31.

Fierer, N., D. Nemergut, R. Knight, and J. M. Craine. 2010. Changes through time: Integrating microorganisms into the study of succession. Research in Microbiology 161:635–642.

Flatberg, K. I. ., and A. A. Frisvoll. 1984a. Sphagnum arcticum sp. nov. The Bryologist 87:143–148.

Flatberg, K. I. ., and A. A. Frisvoll. 1984b. Revision of Svalbard bryophytes.-3-The genus Sphagnum. Journal of the Hattori Botanical Laboratory 56:287–319.

Fogarty, L. R., and M. A. Voytek. 2005. Comparison of Bacteroides-Prevotella 16S rRNA genetic markers for fecal samples from different animal species. Applied and Environmental Microbiology 71:5999–6007.

Frahm, J.-P. 2007. Diversity, dispersal and biogeography of bryophytes (mosses). Pages 43–50 Protist diversity and geographical distribution. Springer, Dordrecht.

Franz, D., F. Koebsch, E. Larmanou, J. Augustin, and T. Sachs. 2016. High net CO2and CH4release at a eutrophic shallow lake on a formerly drained fen. Biogeosciences 13:3051–3070.

Freeman, C., N. Ostle, and H. Kang. 2001. An enzymic “latch” on a global carbon store. Nature 409:149.

Furuhata, K., N. Ishizaki, A. Edagawa, and M. Fukuyama. 2013. Roseomonas tokyonensis sp. nov. isolated from a biofilm sample obtained from a cooling tower in Tokyo, Japan. Biocontrol Science 18:205–209.

Furuhata, K., Y. Kato, K. Goto, K. Saitou, J. I. Sugiyama, M. Hara, and M. Fukuyama. 2008. Identification of pink-pigmented bacteria isolated from environmental water samples and their biofilm formation abilities. Biocontrol Science 13:33–39.

Gagnon, Z. E., and J. M. Glime. 1992. The pH-lowering ability of Sphagnum magellanicum Brid. Journal of bryology 17:47–57.

Galand, P. E., H. Fritze, R. Conrad, and K. Yrjälä. 2005. Pathways for methanogenesis and diversity of methanogenic archaea in three boreal peatland ecosystems. Applied and

Environmental Microbiology 71:2195–2198.

Gałka, M., and M. Lamentowicz. 2014. Sphagnum succession in a Baltic bog in central-eastern Europe over the last 6200 years and paleoecology of Sphagnum contortum. The Bryologist 117:22–36.

Gallego, V., C. Sánchez-Porro, M. T. García, and A. Ventosa. 2006. Roseomonas aquatica sp. nov., isolated from drinking water. International Journal of Systematic and Evolutionary Microbiology 56:2291–2295.

Gamalero, E., E. Bona, and B. R. Glick. 2022. Current Techniques to Study Beneficial Plant-Microbe Interactions. Microorganisms 10:1–40.

Ganzert, L., G. Jurgens, U. Münster, and D. Wagner. 2007. Methanogenic communities in permafrost-affected soils of the Laptev Sea coast, Siberian Arctic, characterized by 16S rRNA gene fingerprints. FEMS Microbiology Ecology 59:476–488.

Gaudig, G., J. Couwenberg, and H. Joosten. 2006. Peat accumulation in kettle holes: bottom up or top down? Mires and Peat 1:1–16.

Gavazov, K. S., N. A. Soudzilovskaia, R. S. P. van Logtestijn, M. Braster, and J. H. C. Cornelissen. 2010. Isotopic analysis of cyanobacterial nitrogen fixation associated with subarctic lichen and bryophyte species. Plant and Soil 333:507–517.

Genderjahn, S., M. Alawi, K. Mangelsdorf, F. Horn, and D. Wagner. 2018. Desiccation-and saline-tolerant bacteria and archaea in kalahari pan sediments. Frontiers in Microbiology 9:1–15.

George, D. M., A. S. Vincent, and H. R. Mackey. 2020. An overview of anoxygenic phototrophic bacteria and their applications in environmental biotechnology for sustainable Resource recovery. Biotechnology Reports 28:e00563.

Gorham, E. 2014. Northern Peatlands : Role in the Carbon Cycle and Probable Responses To Climatic Warming1 1:182–195.

Gorham, E., and J. A. Janssens. 1992. The paleorecord of geochemistry and hydrology in northern peatlands and its relation to global change. Suo 43:117–126.

Graham, L. E., J. M. Graham, J. J. Knack, M. T. Trest, M. J. Piotrowski, and P. Arancibia-Avila. 2017. A Sub-Antarctic peat moss metagenome indicates microbiome resilience to stress and biogeochemical functions of early paleozoic terrestrial ecosystems. International Journal of Plant Sciences 178:618–628.

Granhall, U., and A. V. Hofsten. 1976. Nitrogenase Activity in Relation to Intracellular Organisms in Sphagnum Mosses. Pages 88–94 Physiologia Plantarum.

Greenacre, M. 2007. Computation of correspondence analysis. Pages 213–259 *in* N. Keiding, editor. Correspondance Analysis in Practice. Chapman and Hall/CRC.

Greilhuber, J., S. M. Såstad, and K. I. Flatberg. 2003. Ploidy determination in Spagnum samples from Svalbard, Arctic Norway, by DNA image cytometry. Journal of Bryology 25:235–239.

Griffiths, R. I., A. S. Whiteley, G. Anthony, O. Donnell, M. J. Bailey, and A. G. O. Donnell. 2000. Rapid Method for Coextraction of DNA and RNA from Natural Environments for Analysis of Ribosomal DNA- and rRNA-Based Microbial Community Composition. Applied and

Environmental Microbiology 66:5488–5491.

Gunnarsson, U. 2005. Global patterns of Sphagnum productivity. Journal of Bryology 27:269–279.

Gunnarsson, U., H. Rydin, and H. Sjörs. 2000. Diversity and pH changes after 50 years on the boreal mire Skattlösbergs Stormosse , Central Sweden. Journal of Ecology 11:277–286.

Günther, A., A. Barthelmes, V. Huth, H. Joosten, G. Jurasinski, F. Koebsch, and J. Couwenberg. 2020. Prompt rewetting of drained peatlands reduces climate warming despite methane emissions. Nature Communications 11:1–5.

Hájek, T., and L. Adamec. 2009. Mineral nutrient economy in competing species of Sphagnum mosses. Ecological Research 24:291–302.

Hájek, T., S. Ballance, J. Limpens, M. Zijlstra, and J. T. A. Verhoeven. 2011. Cell-wall polysaccharides play an important role in decay resistance of Sphagnum and actively depressed decomposition in vitro. Biogeochemistry 103:45–57.

Haldorsen, S., M. Heim, B. Lefauconnier, L. Pettersson, M. Røros, and K. Sandsbråten. 2010. Norsk Geografisk Tidsskrift - Norwegian Journal of Geography The water balance of an arctic lake and its dependence on climate change : Tvillingvatnet in Ny-Ålesund , Svalbard The water balance of an arctic lake and its dependence on climate Ê lesund , Sv. Journal of Geography 1951:37–41.

Hansen, J., H. C. Petersen, K. M. Frei, P. Courtaud, A. Tillier, A. Fischer, and M. E. Allentoft. 2017. The Maglemosian skeleton from Koelbjerg, Denmark revisited: identifying sex and provenance. Danish Journal of Archaeology 6:50–66.

Harholt, J., Ø. Moestrup, and P. Ulvskov. 2016. Why plants were terrestrial from the beginning. Trends in Plant Science:96–101.

Harris, L. I., N. T. Roulet, and T. R. Moore. 2020. Mechanisms for the Development of Microform Patterns in Peatlands of the Hudson Bay Lowland. Ecosystems 23:741–767.

Heckman, D. S., D. M. Geiser, B. R. Eidell, R. L. Stauffer, N. L. Kardos, and S. B. Hedges. 2001. Molecular evidence for the early colonization of land by fungi and plants. Science 293:1129–1133.

Hedenäs, L. 2012. Global phylogeography in Sanionia uncinata (Amblystegiaceae: Bryophyta). Botanical Journal of the Linnean Society 168:19–42.

Hedenäs, L., and A. Vanderpoorten. 2007. The Amblystegiaceae and Calliergonaceae. Pages 163–176 Pleurocarpous mosses: systematics and evolution.

Herlemann, D. P., M. Labrenz, K. Jürgens, S. Bertilsson, J. J. Waniek, and A. F. Andersson. 2011. Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. The ISME journal 5:1571–9.

Herren, C. M., and K. D. McMahon. 2018. Keystone taxa predict compositional change in microbial communities. Environmental Microbiology 20:2207–2217.

Heusser, C. J. 1972. Polsters of the moss Drepanocladus berggrenii on Gilkey Glacier, Alaska. Bulletin of the Torrey Botanical Club:34–36.

Hills, P. N., and J. Van Staden. 2002. An improved DNA extraction procedure for plant tissues with a high phenolic content. South African Journal of Botany 68:549–550.

Hiraishi, A. 2015. Acidocella . Bergey's Manual of Systematics of Archaea and Bacteria 362:1–6.

Ho, A., and P. L. E. Bodelier. 2015. Diazotrophic methanotrophs in peatlands: the missing link? Plant and Soil:419–423.

Hofgaard, A. 2003. Effects of climate change on the distribution and development of palsa peatlands: background and suggestions for a national monitoring project. Page NINA Project report .

Hohe, A., and R. Reski. 2005. From axenic spore germination to molecular farming One century of bryophyte in vitro culture. Plant Cell Reports 23:513–521.

Holden, J. 2005. Peatland hydrology and carbon release: why small-scale process matters. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 363:2891–2913.

Holden, J., P. J. Chapman, and J. C. Labadz. 2004. Artificial drainage of peatlands:hydrological and hydrochemical processes and wetland restoration. Progress in Physical Geogrpahy 28 (1):95–123.

Holland-Moritz, H. E., J. E. M. Stuart, L. R. Lewis, S. N. Miller, C. Michelle, J. M. Ponciano, S. F. Mcdaniel, and N. Fierer. 2020. The bacterial communities of Alaskan mosses and their contributions to N2-fixation.

Holland-Moritz, H., J. Stuart, L. R. Lewis, S. Miller, M. C. Mack, S. F. McDaniel, and N. Fierer. 2018. Novel bacterial lineages associated with boreal moss species. Environmental Microbiology 20:2625–2638.

Hopple, A. M., R. M. Wilson, M. Kolton, C. A. Zalman, J. P. Chanton, J. Kostka, P. J. Hanson, J. K. Keller, and S. D. Bridgham. 2020. Massive peatland carbon banks vulnerable to rising temperatures. Nature Communications 11:4–10.

Horne, A. J., and D. J. Lessner. 2013. Assessment of the oxidant tolerance of Methanosarcina acetivorans. FEMS Microbiology Letters 343:13–19.

Hornibrook, E. R. C., F. J. Longstaffe, and W. S. Fyfe. 1997. Spatial distribution of microbial methane production pathways in temperate zone wetland soils: Stable carbon and hydrogen isotope evidence. Geochimica et Cosmochimica Acta 61:745–753.

Hornschuh, M., R. Grotha, and U. Kutschera. 2002. Epiphytic bacteria associated with the bryophyte Funaria hygrometrica: Effects of Methylobacterium strains on protonema development. Plant Biology 4:682–687.

Hough, M., A. McClure, B. Bolduc, E. Dorrepaal, S. Saleska, V. Klepac-Ceraj, and V. Rich. 2020. Biotic and Environmental Drivers of Plant Microbiomes Across a Permafrost Thaw Gradient. Frontiers in Microbiology 11:1–18.

Hubberten, H. W., D. Wagner, E. M. Pfeiffer, J. Boike, and A. Y. Gukov. 2003. The Russian-German research station Samoylov, Lena Delta - A key site for polar research in the Siberian Arctic. Polarforschung 73:111–116.

Hughes, P. D. M., and L. Dumayne-Peaty. 2002. Testing theories of mire development using multiple successions at Crymlyn Bog, West Glamorgan, South Wales, UK. Journal of Ecology:456–471.

Hui, S., H. Yan, X. Qing, Y. Renyuan, and T. Yongqiang. 2013. Isolation, characterization, and antimicrobial activity of endophytic bacteria from Polygonum cuspidatum. African Journal of Microbiology Research 7:1496–1504.

Ikeda, S., T. Kaneko, T. Okubo, L. E. E. Rallos, S. Eda, H. Mitsui, S. Sato, Y. Nakamura, S. Tabata, and K. Minamisawa. 2009. Development of a Bacterial Cell Enrichment Method and its Application to the Community Analysis in Soybean Stems. Microbial Ecology 58:703–714.

St. James, A. R., J. B. Yavitt, S. H. Zinder, and R. E. Richardson. 2021. Linking microbial Sphagnum degradation and acetate mineralization in acidic peat bogs: from global insights to a genome-centric case study. ISME Journal 15:293–303.

Jassey, V. E. J., L. Lamentowicz, B. J. M. Robroek, M. Gabka, A. Rusińska, and M. Lamentowicz. 2014. Plant functional diversity drives niche-size-structure of dominant microbial consumers along a poor to extremely rich fen gradient. Journal of Ecology 102:1150–1162.

Jassey, V. E. J., and C. Signarbieux. 2019. Effects of climate warming on Sphagnum photosynthesis in peatlands depend on peat moisture and species-specific anatomical traits. Global Change Biology 25:3859–3870.

Jaworski, T. 2017. The morphology of peat bog surfaces on Hermansenøya, NW Svalbard. Polar Science 11:83–95.

Jean, M., H. Holland-Moritz, A. M. Melvin, J. F. Johnstone, and M. C. Mack. 2020. Experimental assessment of tree canopy and leaf litter controls on the microbiome and nitrogen fixation rates of two boreal mosses. New Phytologist 227:1335–1349.

Jeske, J. T., and C. Gallert. 2022. Microbiome Analysis via OTU and ASV-Based Pipelines—A Comparative Interpretation of Ecological Data in WWTP Systems. Bioengineering 9.

Jiang, C. Y., X. Dai, B. J. Wang, Y. G. Zhou, and S. J. Liu. 2006. Roseomonas lacus sp. nov., isolated from freshwater lake sediment. International Journal of Systematic and Evolutionary Microbiology 56:25–28.

Jin, L., K. K. Kim, H. G. Lee, C. Y. Ahn, and H. M. Oh. 2012. Kaistia defluvii sp. nov., isolated from river sediment. International Journal of Systematic and Evolutionary Microbiology 62:2878–2882.

Johansen, B. E., S. R. Karlsen, and H. Tømmervik. 2012. Vegetation mapping of Svalbard utilising Landsat TM/ETM+ data. Polar Record 48:47–63.

Johnsen, L. K. 2012. Adsorption of dissolved organic carbon (DOC) by a poorly podzolized high latitude soil. Norwegian University of Life Sciences, Ås.

Johnson, M. G., G. Granath, T. Tahvanainen, R. Pouliot, H. K. Stenøien, L. Rochefort, H. Rydin, and A. J. Shaw. 2015. Evolution of niche preference in Sphagnum peat mosses. Evolution 69:90–103.

Jones, R. M., S. Hedrich, and D. B. Johnson. 2013. Acidocella aromatica sp. nov.: An acidophilic heterotrophic alphaproteobacterium with unusual phenotypic traits. Extremophiles 17:841–

850.

Joos, L., S. Beirinckx, A. Haegeman, J. Debode, B. Vandecasteele, S. Baeyen, S. Goormachtig, L. Clement, and C. De Tender. 2020. Daring to be differential: metabarcoding analysis of soil and plant-related microbial communities using amplicon sequence variants and operational taxonomical units. BMC Genomics 21:1–17.

Joosten, H. 2012. Zustand und Perspektiven der Moore weltweit. Natur und Landschaft 87:50–55.

Joosten, H., and D. Clarke. 2002. Wise Use of Mires and Peatlands. International Mire Conversation Group and International Peat Society.

Jung, J., J. S. Kim, J. Taffner, G. Berg, and C. M. Ryu. 2020. Archaea, tiny helpers of land plants. Computational and Structural Biotechnology Journal 18:2494–2500.

Kaiser, K., S. Lorenz, S. Germer, O. Juschus, M. Küster, J. Libra, O. Bens, and R. F. Hüttl. 2012. Late Quaternary evolution of rivers, lakes and peatlands in northeast Germany reflecting past climatic and human impact – an overview. E&G Quaternary Science Journal 61:103–132.

Kalam, S., A. Basu, and A. R. Podile. 2020. Functional and molecular characterization of plant growth promoting Bacillus isolates from tomato rhizosphere. Heliyon 6:e04734.

Kanokratana, P., W. Mhuanthong, T. Laothanachareon, S. Tangphatsornruang, L. Eurwilaichitr, T. Kruetreepradit, S. Mayes, and V. Champreda. 2016. Comparative Study of Bacterial Communities in Nepenthes Pitchers and Their Correlation to Species and Fluid Acidity. Microbial Ecology 72:381–393.

Karlsson, A. E., T. Johansson, and P. Bengtson. 2012. Archaeal abundance in relation to root and fungal exudation rates. FEMS Microbiology Ecology 80:305–311.

Kielak, A. M., M. A. P. Cipriano, and E. E. Kuramae. 2016. Acidobacteria strains from subdivision 1 act as plant growth-promoting bacteria. Archives of Microbiology 198:987–993.

Kim, M. C., S. Rim, S. Pak, L. Ren, Y. Zhang, X. Chang, X. Li, C. Fang, C. Zheng, and F. Peng. 2016. Roseomonas arcticisoli sp. Nov., isolated from Arctic tundra soil. International Journal of Systematic and Evolutionary Microbiology 66:4057–4064.

Kip, N., W. Ouyang, J. van Winden, A. Raghoebarsing, L. van Niftrik, A. Pol, Y. Pan, L. Bodrossy, E. G. van Donselaar, G.-J. Reichart, M. S. M. Jetten, J. S. Sinninghe Damsté, and H. J. M. Op den Camp. 2011. Detection, Isolation, and Characterization of Acidophilic Methanotrophs from Sphagnum Mosses. Applied and Environmental Microbiology 77:5643–5654.

Kip, N., J. F. van Winden, Y. Pan, L. Bodrossy, G.-J. Reichart, A. J. P. Smolders, M. S. M. Jetten, J. S. S. Damsté, and H. J. M. Op den Camp. 2010. Global prevalence of methane oxidation by symbiotic bacteria in peat-moss ecosystems. Nature Geoscience 3:617–621.

Kirkinen, J., K. Minkkinen, T. Penttilä, S. Kojola, R. Sievänen, J. Alm, S. Saarnio, N. Silvan, J. Laine, and I. Savolainen. 2007. Greenhouse impact due to different peat fuel utilisation chains in Finland - A life-cycle approach. Boreal Environment Research 12:211–223.

Kiss, A. 2012. Vergleich von methanogenen Gemeinschaften in drei unterschiedlich entwickelten Palsas in der Finnmark , Nordnorwegen. Universität Potsdam.

Kitson, E., and N. G. A. Bell. 2020. The Response of Microbial Communities to Peatland Drainage and Rewetting. A Review. Frontiers in Microbiology 11.

Kjellman, S. E., P. E. Axelsson, B. Etzelmüller, S. Westermann, and A. B. K. Sannel. 2018. Holocene development of subarctic permafrost peatlands in Finnmark, northern Norway. Holocene 28:1855–1869.

Klinger, L. F. 1996. The myth of the classic hydrosere model of bog succession. Arctic and Alpine Research 28:1–9.

Knack, J. J., L. W. Wilcox, P. M. Delaux, J. M. AnÉ, M. J. Piotrowski, M. E. Cook, J. M. Graham, and L. E. Graham. 2015. Microbiomes of streptophyte algae and bryophytes suggest that a functional suite of microbiota fostered plant colonization of land. International Journal of Plant Sciences 176:405–420.

Knief, C. 2015. Diversity and habitat preferences of cultivated and uncultivated aerobic methanotrophic bacteria evaluated based on pmoA as molecular marker. Frontiers in Microbiology 6.

Knoblauch, C., O. Spott, S. Evgrafova, L. Kutzbach, and E. M. Pfeiffer. 2015. Regulation of methane production, oxidation, and emission by vascular plants and bryophytes in ponds of the northeast Siberian polygonal tundra. Journal of Geophysical Research: Biogeosciences 120:2525–2541.

Koblížek, M. 2015. Ecology of aerobic anoxygenic phototrophs in aquatic environments. FEMS Microbiology Reviews 39:854–870.

Koebsch, F., P. Gottschalk, F. Beyer, C. Wille, G. Jurasinski, and T. Sachs. 2020. The impact of occasional drought periods on vegetation spread and greenhouse gas exchange in rewetted fens: Drought effects on vegetation and C loss. Philosophical Transactions of the Royal Society B: Biological Sciences 375:2–7.

Kolton, M., A. Erlacher, and G. Berg. 2016. Microbial Models: From Environmental to Industrial Sustainability. Microbial Models: From Environmental to Industrial Sustainability.

Kolton, M., D. J. Weston, X. Mayali, P. K. Weber, K. J. McFarlane, J. Pett-Ridge, M. M. Somoza, J. Lietard, J. B. Glass, E. A. Lilleskov, A. Jonathan Shaw, S. Tringe, P. J. Hanson, and J. E. Kostka. 2022. Defining the Sphagnum Core Microbiome across the North American Continent Reveals a Central Role for Diazotrophic Methanotrophs in the Nitrogen and Carbon Cycles of Boreal Peatland Ecosystems. mBio 13.

Komagata, K., T. Iino, and Y. Yamada. 2014. The family Acetobacteraceae.

Von Konrat, M., A. J. Shaw, and K. S. Renzaglia. 2014. A special issue of Phytotaxa dedicated to Bryophytes: The closest living relatives of early land plants. Phytotaxa 9:5.

Kooijman, A. 2012. “Poor rich fen mosses”: atmospheric N-deposition and P-eutrophication in base-rich fens. Lindbergia:42–52.

Kooijman, A. M. 1992. The decrease of rich-fen bryophytes in the Netherlands. Biological Conservation 35:143–193.

Kopp, D., K.-D. Jäger, and M. Succow. 1982. Naturräumliche Grundlagen der Landnutzung am Beispiel des Tieflandes der DDR.:1982.

Kostka, J. E., D. J. Weston, J. B. Glass, E. A. Lilleskov, A. J. Shaw, and M. R. Turetsky. 2016. Tansley insight The Sphagnum microbiome : new insights from an ancient plant lineage.

Kotsyurbenko, O. R., K. J. Chin, M. V. Glagolev, S. Stubner, M. V. Simankova, A. N. Nozhevnikova, and R. Conrad. 2004. Acetoclastic and hydrogenotrophic methane production and methanogenic populations in an acidic West-Siberian peat bog. Environmental Microbiology 6:1159–1173.

Kotsyurbenko, O. R., A. N. Nozhevnikova, T. I. Soloviova, and G. A. Zavarzin. 1996. Methanogenesis at low temperatures by microflora of tundra wetland soil. Antonie van Leeuwenhoek, International Journal of General and Molecular Microbiology 69:75–86.

Kox, M. A. R., E. van den Elzen, L. P. M. Lamers, M. S. M. Jetten, and M. A. H. J. van Kessel. 2020a. Microbial nitrogen fixation and methane oxidation are strongly enhanced by light in Sphagnum mosses. AMB Express 10.

Kox, M. A. R., L. F. M. Kop, E. Van Den Elzen, and T. A. Van Alen. 2020b. Functional redundancy of the methane-oxidising and nitrogen-fixing microbial community associated with Sphagnum fallax and Sphagnum palustre in two Dutch fens.

Kox, M. A. R., A. J. P. Smolders, D. R. Speth, L. P. M. Lamers, H. J. M. Op den Camp, M. S. M. Jetten, and M. A. H. J. van Kessel. 2021. A Novel Laboratory-Scale Mesocosm Setup to Study Methane Emission Mitigation by Sphagnum Mosses and Associated Methanotrophs. Frontiers in Microbiology 12:1–11.

Krieger, J. R., and P. S. Kourtev. 2012. Detection of methanogenic archaea in the pitchers of the Northern pitcher plant (Sarracenia purpurea). Canadian Journal of Microbiology 58:189–194.

Krumholz, L. R., J. L. Hollenback, S. J. Roskes, and D. B. Ringelberg. 1995. Methanogenesis and methanotrophy within a Sphagnum peatland. FEMS Microbiology Ecology 18:215–224.

Kühnel, R., C. P. Vega, A. Hodson, E. Isaksson, M. P. Bjo, and J. Stro. 2013. Reactive nitrogen and sulphate wet deposition at Zeppelin Station, Ny-Alesund , Svalbard 1:1–14.

Kuhry, P., B. Nicholson, L. D. Gignac, D. H. Vitt, and S. Bayley. 1993. Development of Sphagnum-dominated peatlands in boreal continental Canada. Canadian Journal of Botany 71:10–22.

Kuhry, P., and J. Turunen. 2006. The Postglacial Development of Boreal and Subarctic Peatlands. Page Boreal Peatland Ecosystems. 188th edition.

Küpfer, V. 2015. Biodiversity and activity of methane oxidizing bacteria associated with Arctic plants. École Polytechnique Fédérale de Lausanne.

Küsel, K., M. Blöthe, D. Schulz, M. Reiche, and H. L. Drake. 2008. Microbial reduction of iron and porewater biogeochemistry in acidic peatlands. Biogeosciences 5:1537–1549.

Kutschera, U. 2007. Plant-associated methylobacteria as co-evolved phytosymbionts: A hypothesis. Plant Signaling and Behavior 2:74–78.

Kutzbach, L., D. Wagner, and E. M. Pfeiffer. 2004. Effect of microrelief and vegetation on methane emission from wet polygonal tundra, Lena Delta, Northern Siberia. Biogeochemistry 69:341–362.

Lakka, H.-K. 2013. The ecology of a freshwater crustacean: lepidurus arcticus (branchiopoda; notostraca) in a high arctic region:151.

Lamentowicz, M., M. Obremska, and E. A. D. Mitchell. 2008. Holocene development of a kettle-hole mire in Northern Poland. Review of Palaeobotany and Palynology:1–17.

Landgraf, L. 2010. Wo steht der Moorschutz in Brandenburg? Moore in Brandenburg - Naturschutz und Landschaftspflege in Brandenburg 19.

Landgraf, L., and P. Notni. 2004. Das Moosfenn bei Potsdam - Langzeitstudie zu Vegetation und Nährstoffhaushalt eines brandenburgischen Kesselmoores. Telma:123–154.

Larmola, T., S. M. Leppänen, E.-S. Tuittila, M. Aarva, P. Merilä, H. Fritze, and M. Tiirola. 2014. Methanotrophy induces nitrogen fixation during peatland development. Proceedings of the National Academy of Sciences 111:734–739.

Larmola, T., E. S. Tuittila, M. Tiirola, H. Nykänen, P. J. Martikainen, K. Yrjälä, T. Tuomivirta, and H. Fritze. 2010. The role of Sphagnum mosses in the methane cycling of a boreal mire. Ecology 91:2356–2365.

Lee, J. H., M. S. Kim, K. S. Baik, H. M. Kim, K. H. Lee, and C. N. Seong. 2015. Roseomonas wooponensis sp. Nov., Isolated from wetland freshwater. International Journal of Systematic and Evolutionary Microbiology 65:4049–4054.

Leppänen, S. M., A. J. Rissanen, and M. Tiirola. 2014. Nitrogen fixation in Sphagnum mosses is affected by moss species and water table level. Plant and Soil:185–196.

Lew, S., K. Glińska-Lewczuk, and A. Ziembińska-Buczyńska. 2018. Prokaryotic community composition affected by seasonal changes in physicochemical properties of water in peat bog lakes. Water (Switzerland) 10:1–20.

Lew, S., M. Koblížek, M. Lew, H. Medová, K. Glińska-Lewczuk, and P. M. Owsianny. 2015. Seasonal changes of microbial communities in two shallow peat bog lakes. Folia Microbiologica 60:165–175.

Lewis, K., and F. M. Ausubel. 2006. Prospects for plant-derived antibacterials 24:1504–1507.

Li, Z., A. D. G. Wright, H. Liu, K. Bao, T. Zhang, K. Wang, X. Cui, F. Yang, Z. Zhang, and G. Li. 2015. Bacterial Community Composition and Fermentation Patterns in the Rumen of Sika Deer (Cervus nippon) Fed Three Different Diets. Microbial Ecology 69:307–318.

Liebner, S., L. Ganzert, A. Kiss, S. Yang, D. Wagner, and M. M. Svenning. 2015. Shifts in methanogenic community composition and methane fluxes along the degradation of discontinuous permafrost. Frontiers in Microbiology 6:1–10.

Liebner, S., and M. M. Svenning. 2013. Environmental transcription of mmoX by methane-oxidizing Proteobacteria in a subarctic palsa peatland. Applied and Environmental Microbiology 79:701–706.

Liebner, S., J. Zeyer, D. Wagner, C. Schubert, E.-M. Pfeiffer, and C. Knoblauch. 2011. Methane oxidation associated with submerged brown mosses reduces methane emissions from Siberian polygonal tundra. Journal of Ecology 99:914–922.

Ligrone, R., J. G. Duckett, and K. S. Renzaglia. 2012. Major transitions in the evolution of early land plants: A bryological perspective. Annals of Botany 109:851–871.

Lindo, Z., and A. Gonzalez. 2010. The bryosphere: An integral and influential component of the Earth's biosphere. Ecosystems 13:612–627.

Liu, X., M. Li, C. J. Castelle, A. J. Probst, Z. Zhou, J. Pan, Y. Liu, J. F. Banfield, and J. D. Gu. 2018. Insights into the ecology, evolution, and metabolism of the widespread Woesearchaeotal lineages. Microbiome 6:1–16.

Lüke, C. 2010. Molecular ecology and biogeography of methanotrophic bacteria in wetland rice fields.

Lüke, C., P. Frenzel, A. Ho, D. Fiantis, P. Schad, B. Schneider, L. Schwark, and S. R. Utami. 2014. Macroecology of methane-oxidizing bacteria: The β-diversity of pmoA genotypes in tropical and subtropical rice paddies. Environmental Microbiology 16:72–83.

Lyu, Z., and Y. Lu. 2018. Metabolic shift at the class level sheds light on adaptation of methanogens to oxidative environments. ISME Journal 12:411–423.

Ma, B., X. Lv, A. Warren, and J. Gong. 2013. Shifts in diversity and community structure of endophytic bacteria and archaea across root, stem and leaf tissues in the common reed, Phragmites australis, along a salinity gradient in a marine tidal wetland of northern China. Antonie van Leeuwenhoek, International Journal of General and Molecular Microbiology 104:759–768.

Ma, J., J. Y. Tang, S. Wang, Z. L. Chen, X. D. Li, and Y. H. Li. 2017. Illumina sequencing of bacterial 16S rDNA and 16S rRNA reveals seasonal and species-specific variation in bacterial communities in four moss species. Applied Microbiology and Biotechnology 101:6739–6753.

MacDonald, G. M., D. W. Beilman, K. V. Kremenetski, Y. Sheng, L. C. Smith, and A. A. Velichko. 2006. Rapid Early Development of Circumarctic Peatlands and Atmospheric CH4 and CO2 Variations. Science 314:285–288.

MacKay, J. R. 2000. Thermally induced movements in ice-wedge polygons, western Arctic coast: a long-term study. Géographie physique et Quaternaire 54:41–68.

Markham, J. H. 2009. Variation in moss-associated nitrogen fixation in boreal forest stands. Oecologia 161:353–359.

Marks, R. A., J. J. Smith, Q. Cronk, and D. N. McLetchie. 2018. Variation in the bacteriome of the tropical liverwort, Marchantia inflexa, between the sexes and across habitats. Symbiosis 75:93–101.

Martí, M., H. Juottonen, B. J. M. Robroek, K. Yrjälä, Å. Danielsson, P. E. Lindgren, and B. H. Svensson. 2015. Nitrogen and methanogen community composition within and among three Sphagnum dominated peatlands in Scandinavia. Soil Biology and Biochemistry 81:204–211.

Martin, M. 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. EMBnet.journal [Online]:10–12.

Mašín, M., Z. Čuperová, E. Hojerová, I. Salka, H. Grossart, and M. Koblížek. 2012. Distribution of aerobic anoxygenic phototrophic bacteria in glacial lakes of northern Europe. Aquatic

Microbial Ecology 66:77–86.

Maturilli, M., A. Herber, and G. König-Langlo. 2013. Climatology and time series of surface meteorology in Ny-Ålesund, Svalbard. Earth System Science Data 5:155–163.

Maus, D., J. Heinz, J. Schirmack, A. Airo, S. P. Kounaves, D. Wagner, and D. Schulze-Makuch. 2020. Methanogenic Archaea Can Produce Methane in Deliquescence-Driven Mars Analog Environments. Scientific Reports 10:1–7.

McDonald, D., M. N. Price, J. Goodrich, E. P. Nawrocki, T. Z. Desantis, A. Probst, G. L. Andersen, R. Knight, and P. Hugenholtz. 2012. An improved Greengenes taxonomy with explicit ranks for ecological and evolutionary analyses of bacteria and archaea. ISME Journal 6:610–618.

Mcqueen, C. B., and R. E. Andrus. 2007. Sphagnaceae Dumortier. Pages 45–101 Flora of North America.

Merilä, P., P. E. Galand, H. Fritze, E. S. Tuittila, K. Kukko-Oja, J. Laine, and K. Yrjälä. 2006. Methanogen communities along a primary succession transect of mire ecosystems. FEMS Microbiology Ecology 55:221–229.

Metje, M. 2006. Terminale Prozesse des anaeroben Abbaus in sauren Torfmooren der Subarktis und des südlichen Boreals. Philipps-Universität Marburg/Lahn.

Metje, M., and P. Frenzel. 2005. Effect of temperature on anaerobic ethanol oxidation and methanogenesis in acidic peat from a Northern Wetland. Applied and Environmental Microbiology 71:8191–8200.

Miao, L., P. Wang, J. Hou, Y. Yao, Z. Liu, S. Liu, and T. Li. 2019. Distinct community structure and microbial functions of biofilms colonizing microplastics. Science of the Total Environment 650:2395–2402.

Mieczan, T., M. Adamczuk, B. Pawlik-Skowrońska, and M. Toporowska. 2015. Eutrophication of peatbogs: Consequences of P and N enrichment for microbial and metazoan communities in mesocosm experiments. Aquatic Microbial Ecology 74:121–141.

Milferstedt, K., N. D. Youngblut, and R. J. Whitaker. 2010. Spatial structure and persistence of methanogen populations in humic bog lakes. ISME Journal 4:764–776.

Milner, A. M., A. J. Baird, S. M. Green, G. T. Swindles, D. M. Young, N. K. Sanderson, M. S. I. Timmins, and M. Gałka. 2020. A regime shift from erosion to carbon accumulation in a temperate northern peatland. Journal of Ecology:1–14.

Minke, M., N. Donner, N. S. Karpov, P. de Klerk, and H. Joosten. 2007. Distribution, diversity, development and dynamics of polygon mires: examples from Northeast Yakutia (Siberia). Peatlands International 1:36–40.

Mitchell, E. A. D., D. Gilbert, A. Buttler, C. Amblard, P. Grosvernier, and J. M. Gobat. 2003. Structure of microbial communities in Sphagnum peatlands and effect of atmospheric carbon dioxide enrichment. Microbial Ecology 46:187–199.

Moissl-Eichinger, C., M. Pausan, J. Taffner, G. Berg, C. Bang, and R. A. Schmitz. 2018. Archaea Are Interactive Components of Complex Microbiomes. Trends in Microbiology 26:70–85.

Moore, P. D. 1989. The ecology of peat-forming processes: a review. International Journal of

Coal Geology 12:89–103.

Morozova, D., and D. Wagner. 2007. Stress response of methanogenic archaea from Siberian permafrost compared with methanogens from nonpermafrost habitats. FEMS Microbiology Ecology 61:16–25.

Morris, C. E., J. Monier, S. Jacques, M. E. T. Al, and A. P. P. L. E. N. M. Icrobiol. 1998. A Technique To Quantify the Population Size and Composition of the Biofilm Component in Communities of Bacteria in the Phyllosphere. Applied and Environmental Microbiology 64:4789–4795.

Müller, C. A., M. M. Obermeier, and G. Berg. 2016. Bioprospecting plant-associated microbiomes. Journal of Biotechnology 235:171–180.

Muraoka, H., M. Uchida, M. Mishio, T. Nakatsubo, H. Kanda, and H. Koizumi. 2002. Leaf photosynthetic characteristics and net primary production of the polar willow (Salix polaris) in a high arctic polar semi-desert , Ny-Ålesund , Svalbard. Canadian Journal of Botany 80:1193–1202.

Müritz-National Park. National Parkplan und Bestandsanalyse. 2003. .

Myers-Smith, I. H., and D. S. Hik. 2018. Climate warming as a driver of tundra shrubline advance. Journal of Ecology 106:547–560.

Nakai, R., T. Abe, T. Baba, S. Imura, H. Kagoshima, H. Kanda, A. Kanekiyo, Y. Kohara, A. Koi, K. Nakamura, T. Narita, H. Niki, K. Yanagihara, and T. Naganuma. 2012. Microflorae of aquatic moss pillars in a freshwater lake, East Antarctica, based on fatty acid and 16S rRNA gene analyses. Polar Biology 35:425–433.

Negandhi, K., I. Laurion, M. J. Whiticar, P. E. Galand, X. Xu, and C. Lovejoy. 2013. Small thaw ponds: An unaccounted source of methane in the Canadian high Arctic. PLoS ONE 8.

Neukom, R., L. A. Barboza, M. P. Erb, F. Shi, J. Emile-Geay, M. N. Evans, J. Franke, D. S. Kaufman, L. Lücke, K. Rehfeld, A. Schurer, F. Zhu, S. Brönnimann, G. J. Hakim, B. J. Henley, F. C. Ljungqvist, N. McKay, V. Valler, and L. von Gunten. 2019. Consistent multidecadal variability in global temperature reconstructions and simulations over the Common Era. Nature Geoscience 12:643–649.

Obermeier, M.-M., J. Taffner, A. Bergna, A. Poehlein, T. Cernava, C. A. Müller, and G. Berg. 2019. Unravelling native plant resistomes – The Sphagnum microbiome harbours versatile and novel antimicrobial resistance genes.

Von Oheimb, G., C. Westphal, H. Tempel, and W. Härdtle. 2005. Structural pattern of a near-natural beech forest (Fagus sylvatica) (Serrahn, North-east Germany). Forest Ecology and Management 212:253–263.

Okamoto, R., H. Kojima, and M. Fukui. 2017. Acidocella aquatica sp. nov., a novel acidophilic heterotrophic bacterium isolated from a freshwater lake. International Journal of Systematic and Evolutionary Microbiology 67:4773–4776.

Okibe, N., M. Maki, D. Nakayama, and K. Sasaki. 2016. Microbial recovery of vanadium by the acidophilic bacterium, Acidocella aromatica. Biotechnology Letters 38:1475–1481.

Oksanen, P. O. 2005. Development of palsa mires on the northern European continent in relation to Holocene climatic and environmental changes. Page Faculty of Science, Department of Biology.

Oksanen, P. O. 2006. Holocene development of the Vaisjeäggi palsa mire, Finnish Lapland. Boreas 35:81–95.

Oliverio, A. M., J. F. Power, A. Washburne, S. C. Cary, M. B. Stott, and N. Fierer. 2018. The ecology and diversity of microbial eukaryotes in geothermal springs. ISME Journal:1–11.

Oloo, F., A. Valverde, M. V. Quiroga, S. Vikram, D. Cowan, and G. Mataloni. 2016. Habitat heterogeneity and connectivity shape microbial communities in South American peatlands. Scientific Reports 6:1–8.

Opelt, K., C. Berg, S. Schönmann, L. Eberl, and G. Berg. 2007a. High specificity but contrasting biodiversity of Sphagnum-associated bacterial and plant communities in bog ecosystems independent of the geographical region. The ISME journal 1:502–16.

Opelt, K., and G. Berg. 2004. Diversity and Antagonistic Potential of Bacteria Associated with Bryophytes from Nutrient-Poor Habitats of the Baltic Sea Coast. Applied and environmental microbiology 70:6569–6579.

Opelt, K., V. Chobot, F. Hadacek, S. Schönmann, L. Eberl, and G. Berg. 2007b. Investigations of the structure and function of bacterial communities associated with Sphagnum mosses. Environmental Microbiology 9:2795–2809.

Oren, A. 2018. Acidophiles. eLS:1–14.

Osudar, R., S. Liebner, M. Alawi, S. Yang, I. Bussmann, and D. Wagner. 2016. Methane turnover and methanotrophic communities in arctic aquatic ecosystems of the Lena Delta, Northeast Siberia. FEMS Microbiology Ecology 92:1–13.

Overland, J., E. Dunlea, J. E. Box, R. Corell, M. Forsius, V. Kattsov, M. S. Olsen, J. Pawlak, L. O. Reiersen, and M. Wang. 2019. The urgency of Arctic change. Polar Science 21:6–13.

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. Carbohydrate Polymers 15:123–142.

Pankratov, T. A., D. S. Grouzdev, E. O. Patutina, T. V. Kolganova, J. J. Berestovskaya, and A. A. Ashikhmin. 2020. Lichenicoccus roseus gen. Nov., sp. nov., the first bacteriochlorophyll a-containing, psychrophilic and acidophilic acetobacteraceae bacteriobiont of lichen cladonia species. International Journal of Systematic and Evolutionary Microbiology 70:4591–4601.

Parmentier, F. J. W., J. Van Huissteden, N. Kip, H. J. M. Op Den Camp, M. S. M. Jetten, T. C. Maximov, and A. J. Dolman. 2011. The role of endophytic methane-oxidizing bacteria in submerged Sphagnum in determining methane emissions of Northeastern Siberian tundra. Biogeosciences 8:1267–1278.

Pastukhov, A., T. Marchenko-Vagapova, S. Loiko, and D. Kaverin. 2021. Vulnerability of the ancient peat plateaus in western Siberia. Plants 10:1–18.

Pedraza, R. O. 2008. Recent advances in nitrogen-fixing acetic acid bacteria. International Journal of Food Microbiology 125:25–35.

Penning, H., and R. Conrad. 2007. Quantification of carbon flow from stable isotope fractionation in rice field soils with different organic matter content. Organic Geochemistry 38:2058–2069.

Peruzy, M. F., N. Murru, Z. Yu, P. J. Kerkhof, B. Neola, M. Joossens, Y. T. R. Proroga, and K. Houf. 2019. Assessment of microbial communities on freshly killed wild boar meat by MALDI-TOF MS and 16S rRNA amplicon sequencing. International Journal of Food Microbiology 301:51–60.

Piwosz, K., A. Vrdoljak, T. Frenken, J. M. González-Olalla, D. Šantić, R. M. McKay, K. Spilling, L. Guttman, P. Znachor, I. Mujakić, L. K. Fecskeová, L. Zoccarato, M. Hanusová, A. Pessina, T. Reich, H.-P. Grossart, and M. Koblížek. 2020. Light and Primary Production Shape Bacterial Activity and Community Composition of Aerobic Anoxygenic Phototrophic Bacteria in a Microcosm Experiment. mSphere 5:1–17.

Pope, P. B. 2007. Metagenomics of Cyanobacterial Blooms. Griffith University.

Potter, C., C. Freeman, P. N. Golyshin, G. Ackermann, N. Fenner, J. E. McDonald, A. Ehbair, T. G. Jones, L. M. Murphy, and S. Creer. 2017. Subtle shifts in microbial communities occur alongside the release of carbon induced by drought and rewetting in contrasting peatland ecosystems. Scientific Reports 7:1–14.

Putkinen, A., T. Larmola, T. Tuomivirta, H. M. P. Siljanen, L. Bodrossy, E. S. Tuittila, and H. Fritze. 2012. Water dispersal of methanotrophic bacteria maintains functional methane oxidation in Sphagnum mosses. Frontiers in Microbiology 3:1–10.

Putkinen, A., T. Larmola, T. Tuomivirta, H. M. P. Siljanen, L. Bodrossy, E. S. Tuittila, and H. Fritze. 2014. Peatland succession induces a shift in the community composition of Sphagnum-associated active methanotrophs. FEMS Microbiology Ecology 88:596–611.

Putkinen, A., E. S. Tuittila, H. M. P. Siljanen, L. Bodrossy, and H. Fritze. 2018. Recovery of methane turnover and the associated microbial communities in restored cutover peatlands is strongly linked with increasing Sphagnum abundance.

Qin, S., H. H. Chen, G. Z. Zhao, J. Li, W. Y. Zhu, L. H. Xu, J. H. Jiang, and W. J. Li. 2012. Abundant and diverse endophytic actinobacteria associated with medicinal plant Maytenus austroyunnanensis in Xishuangbanna tropical rainforest revealed by culture-dependent and culture-independent methods. Environmental Microbiology Reports 4:522–531.

R Core Team. 2015. R: A language and environment for statistical computing.

Radujkovic, D. 2016. Structure of soil microbial communities along a geothermal gradient in Iceland. Universitait Antwerpen.

Raghoebarsing, A. a, A. J. P. Smolders, M. C. Schmid, W. I. C. Rijpstra, M. Wolters-Arts, J. Derksen, M. S. M. Jetten, S. Schouten, J. S. Sinninghe Damsté, L. P. M. Lamers, J. G. M. Roelofs, H. J. M. Op den Camp, and M. Strous. 2005. Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. Nature 436:1153–1156.

Rathgeber, C., J. T. Beatty, and V. Yurkov. 2004. Aerobic phototrophic bacteria: New evidence for the diversity, ecological importance and applied potential of this previously overlooked group. Photosynthesis Research 81:113–128.

Raven, J. a, and D. Edwards. 2014. Photosynthesis in Bryophytes and Early Land Plants. Diversification in evolving enviroments 37:29–58.

Raymond, J. A. 2016. Dependence on epiphytic bacteria for freezing protection in an Antarctic moss, Bryum argenteum. Environmental Microbiology Reports 8:14–19.

Reis, V. M., and K. R. dos S. Teixeira. 2015. Nitrogen fixing bacteria in the family Acetobacteraceae and their role in agriculture. Journal of Basic Microbiology 55:931–949.

Reiter, B., and A. Sessitsch. 2006. Bacterial endophytes of the wildflower Crocus albiflorus analyzed by characterization of isolates and by a cultivation-independent approach. Canadian journal of microbiology 52:140–149.

Renaudin, M., I. Laforest-Lapointe, and J.-P. Bellenger. 2022. Unraveling global and diazotrophic bacteriomes of boreal forest floor feather mosses and their environmental drivers at the ecosystem and at the plant scale in North America. Science of the Total Environment 837.

Reumer, M., M. Harnisz, H. J. Lee, A. Reim, O. Grunert, A. Putkinen, H. Fritze, P. L. E. Bodelier, and A. Ho. 2018. Impact of peat mining and restoration on methane turnover potential and methane-cycling microorganisms in a northern bog. Applied and Environmental Microbiology 84:1–17.

Rey-Sanchez, C., G. Bohrer, J. Slater, Y.-F. Li, R. Grau-Andrés, Y. Hao, V. I. Rich, and G. M. Davies. 2019. The ratio of methanogens to methanotrophs and water-level dynamics drive methane exchange velocity in a temperate kettle-hole peat bog. Biogeosciences Discussions:1–48.

del Rey, V. S., J. F. Fernández-Garayzábal, G. Mentaberre, V. Briones, S. Lavín, ... & Domínguez, L., and A. I. Vela. 2014. Characterisation of Streptococcus suis isolates from wild boars (Sus scrofa). The Veterinary Journal 200:464–467.

Rice, S. K. 1995. Patterns of Allocation and Growth in Aquatic Sphagnum Species. Canadian Journal of Botany-Revue Canadienne De Botanique 73:349-359 ST-Patterns of Allocation and Growth in.

Rice, S. K., and P. H. Schuepp. 1995. On the ecological and evolutionary significance of branch and leaf morphology in aquatic Sphagnum (Sphagnaceae). American Journal of Botany 82:833–846.

Rihs, J. D., D. J. Brenner, R. E. Weaver, A. G. Steigerwalt, D. G. Hollis, and V. L. Yu. 1993. Roseomonas, a new genus associated with bacteremia and other human infections. Journal of Clinical Microbiology 31:3275–3283.

Roads, E., R. E. Longton, and P. Convey. 2014. Millennial timescale regeneration in a moss from Antarctica. Current Biology 24:222–223.

Rooney-Varga, J. N., M. W. Giewat, K. N. Duddleston, J. P. Chanton, and M. E. Hines. 2007. Links between archaeal community structure, vegetation type and methanogenic pathway in Alaskan peatlands. FEMS Microbiology Ecology 60:240–251.

Rousk, K., and J. Rousk. 2020. The responses of moss-associated nitrogen fixation and belowground microbial community to chronic Mo and P supplements in subarctic dry heaths. Plant and Soil 451:261–276.

Rozema, J., P. Boelen, M. Doorenbosch, S. Bohncke, P. Blokker, C. Boekel, R. A. Broekman, and M. Konert. 2006. A vegetation, climate and environment reconstruction based on palynological analyses of high arctic tundra peat cores (5000-6000 years BP) from Svalbard. Plant Ecology 182:155–173.

Rudolph, H., and J. Samland. 1985. Occurrence and Metabolism of Sphagnum Acid in the Cell Walls of Bryophytes 24.

Ruiz-Lopez, S., L. Foster, C. Boothman, N. Cole, K. Morris, and J. R. Lloyd. 2020. Identification of a Stable Hydrogen-Driven Microbiome in a Highly Radioactive Storage Facility on the Sellafield Site. Frontiers in Microbiology 11:1–15.

Rydin, H., U. Gunnarsson, and S. Sundberg. 2006. The role of Sphagnum in peatland development and persistence. Boreal peatland ecosystems 188:47–65.

Rydin, H., and J. K. Jeglum. 2006. Peatland habitats. Page The biology of Peatlands. Oxford university press.

Sachs, T., F. Koebsch, D. Franz, E. Larmanou, A. Serafimovich, K. Kohnert, G. Jurasinski, and J. Augustin. 2015. Mehr Moor?: Zur Treibhausgasdynamik wiedervernässter Feuchtgebiete. System Erde 5:22–27.

Safronova, V. I., I. G. Kuznetsova, A. L. Sazanova, A. K. Kimeklis, A. A. Belimov, E. E. Andronov, A. G. Pinaev, E. P. Chizhevskaya, A. R. Pukhaev, K. P. Popov, A. Willems, and I. A. Tikhonovich. 2015. Bosea vaviloviae sp. nov., a new species of slow-growing rhizobia isolated from nodules of the relict species Vavilovia formosa (Stev.) Fed. Antonie van Leeuwenhoek, International Journal of General and Molecular Microbiology 107:911–920.

Salama, D. M., T. E. Meyer, and J. A. Kyndt. 2020. Genome Sequence of the Acidophilic Nonsulfur Purple Photosynthetic Alphaproteobacterium Rhodovastum atsumiense, a Divergent Member of the Acetobacteraceae Family. Microbiology resource announcements 9.

Sand-Jensen, K., T. Riis, S. Markager, and W. F. Vincent. 1999. Slow growth and decomposition of mosses in Arctic lakes. Canadian Journal of Fisheries and Aquatic Sciences 56:388–393.

Santana, R. S. M., G. W. Fernandes, M. P. Ávila, M. P. Reis, M. Flávio, G. de Araújo, A. C. M. Salim, G. Oliveira, E. Chartone-Souza, and A. M. A. Nascimento. 2016. Endophytic Microbiota Associated with the Root Tips and Leaves of Baccharis dracunculifolia. Brazilian Archives of Biology and Technology 59:1–11.

Saravanan, V. S., M. Madhaiyan, J. Osborne, M. Thangaraju, and T. M. Sa. 2008. Ecological occurrence of Gluconacetobacter diazotrophicus and nitrogen-fixing Acetobacteraceae members: Their possible role in plant growth promotion. Microbial Ecology 55:130–140.

Sastad, S., S. Bakken, and B. Pedersen. 1998. Propagation of Sphagnum in axenic culture - a method for obtaing large numbers of cloned gametophores. Lindbergia 23:65–73.

Schauer, S., and U. Kutschera. 2011. A novel growth-promoting microbe, Methylobacterium funariae sp. nov., isolated from the leaf surface of a common moss. Plant signaling & behavior 6:510–5.

Schellenberger, S., S. Kolb, and H. L. Drake. 2010. Metabolic responses of novel cellulolytic and saccharolytic agricultural soil Bacteria to oxygen. Environmental Microbiology 12:845–861.

Schirmack, J., M. Alawi, and D. Wagner. 2015. Influence of Martian regolith analogs on the activity and growth of methanogenic archaea, with special regard to long-term desiccation. Frontiers in Microbiology 6:1–12.

Schumann, M., and H. Joosten. 2008. A Global Peatland Restoration Manual:357–385.

Selbmann, L., L. Zucconi, S. Ruisi, M. Grube, M. Cardinale, and S. Onofri. 2010. Culturable bacteria associated with Antarctic lichens: Affiliation and psychrotolerance. Polar Biology 33:71–83.

Sellappan, R., S. Dhandapani, A. Selvaraj, and K. Thangavel. 2020. Archaeal Symbiosis for Plant Health and Soil Fertility. Pages 221–228 Symbiotic Soil Microorganisms.

Seppala, M. 2006. Palsa mires in Finland. The Finnish Environment 23:155–162.

Serrano, P., M. Alawi, J. P. De Vera, and D. Wagner. 2019. Response of Methanogenic Archaea from Siberian Permafrost and Non-permafrost Environments to Simulated Mars-like Desiccation and the Presence of Perchlorate. Astrobiology 19:197–208.

Servín-Garcidueñas, L. E., R. A. Garrett, R. Amils, and E. Martínez-Romero. 2013. Genome sequence of the acidophilic bacterium Acidocella sp. strain MX-AZ02. Genome Announcements 1:2–3.

Shacklette, H. T. . 1966. Unattached Moss Polsters on Amchitka Island , Alaska. The Bryologist 69:346–352.

Shaw, A. J., C. J. Cox, and S. B. Boles. 2003. Global patterns in peatmoss biodiversity. Molecular Ecology 12:2553–2570.

Shaw, J. A., P. Szövényi, and B. Shaw. 2011. Bryophyte diversity and evolution: Windows into the early evolution of land plants. American Journal of Botany 98:352–369.

Shcherbakov, a. V., a. V. Bragina, E. Y. Kuzmina, C. Berg, a. N. Muntyan, N. M. Makarova, N. V. Malfanova, M. Cardinale, G. Berg, V. K. Chebotar, and I. a. Tikhonovich. 2013. Endophytic bacteria of Sphagnum mosses as promising objects of agricultural microbiology. Microbiology 82:306–315.

Sickel, W., T. U. Grafe, I. Meuche, I. Steffan-Dewenter, and A. Keller. 2016. Bacterial Diversity and Community Structure in Two Bornean Nepenthes Species with Differences in Nitrogen Acquisition Strategies. Microbial Ecology 71:938–953.

Sievers, M., and J. Swings. 2015. Acetobacteraceae . Bergey's Manual of Systematics of Archaea and Bacteria:1–20.

Skelton, Tracey,Valentine, G. 2013. Cool Places - Geographies of youth subcultures. Page Journal of Chemical Information and Modeling.

Slonczewski, J. L., M. Fujisawa, M. Dopson, and T. A. Krulwich. 2009. Cytoplasmic pH Measurement and Homeostasis in Bacteria and Archaea. Advances in Microbial Physiology 55:1–79.

Solheim, B., a. Endal, and H. Vigstad. 1996. Nitrogen fixation in Arctic vegetation and soils from Svalbard, Norway. Polar Biology 16:35–40.

Sommerkorn, M., M. Bölter, and L. Kappen. 1999. Carbon dioxide fluxes of soils and mosses in wet tundra of Taimyr Peninsula, Siberia: Controlling factors and contribution to net system fluxes. Polar Research 18:253–260.

Soudzilovskaia, N. A., J. H. C. Cornelissen, H. J. During, R. S. P. Van Logtestun, S. I. Lang, and R. Aerts. 2010. Similar cation exchange capacities among bryophyte species refute a presumed mechanism of peatland acidification. Ecology 91:2716–2726.

Stalheim, T., S. Ballance, B. E. Christensen, and P. E. Granum. 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. Journal of Applied Microbiology 106:967–976.

Stępniewska, Z., W. Goraj, A. Kuźniar, A. Szafranek-Nakonieczna, A. Banach, A. Górski, A. Pytlak, and D. Urban. 2018. Methane Oxidation by Endophytic Bacteria Inhabiting Sphagnum sp. and Some Vascular Plants. Wetlands 38:411–422.

Stępniewska, Z., and A. Kuźniar. 2014. Cultivation and detection of endophytic aerobic methanotrophs isolated from Sphagnum species as a perspective for environmental biotechnology. AMB Express 4:58.

Stiefel, P., T. Zambelli, and J. A. Vorholta. 2013. Isolation of optically targeted single bacteria by application of fluidic force microscopy to aerobic anoxygenic phototrophs from the phyllosphere. Applied and Environmental Microbiology 79:4895–4905.

Stobbe, A. H., and M. J. Roossinck. 2014. Plant virus metagenomics: What we know and why we need to know more. Frontiers in Plant Science 5:1–4.

Strack, M., J. M. Waddington, M. Turetsky, N. T. Roulet, and K. a Byrne. 2008. Section 7.4. Greenhouse gas fluxes from restored peatlands formerly under forest, agricultural use or drained fallow land. Page Peatlands and Climate Change.

Strobel, G., and B. Daisy. 2003. Bioprospecting for Microbial Endophytes and Their Natural Products. Microbiology and Molecular Biology Reviews 67:491–502.

Strobel, G., B. Daisy, U. Castillo, and J. Harper. 2004. Natural Products from Endophytic Microorganisms. Journal of Natural Products 67:257–268.

Sturz, A. V., B. R. Christie, and J. Nowak. 2000. Bacterial Endophytes: Potential Role in Developing Sustainable Systems of Crop Production. Critical Reviews in Plant Sciences 19:1–30.

Succow, M., and H. Joosten. 2012. Landschaftsökologische Moorkunde. Second edition. Schweizerbart'sche Verlagsbuchhandlung Nägele u. Obermiller.

Szabó-Tugyi, N., L. Vörös, K. Balogh, Z. Botta-Dukát, G. Bernát, D. Schmera, and B. Somogyi. 2019. Aerobic anoxygenic phototrophs are highly abundant in hypertrophic and polyhumic waters. FEMS Microbiology Ecology 95:1–9.

Taffner, J., A. Erlacher, A. Bragina, C. Berg, C. Moissl-Eichinger, and G. Berg. 2018. What Is the Role of Archaea in Plants? New Insights from the Vegetation of Alpine Bogs . mSphere 3:1–14.

Takai, K., and K. Horikoshi. 2000. Rapid detection and quantification of members of the archael community by quantitative PCR using fluorogenic probes. Appl. Environ. Microbiol. 66:5066–5072.

Tang, J. Y., J. Ma, X. D. Li, and Y. H. Li. 2016. Illumina sequencing-based community analysis of bacteria associated with different bryophytes collected from Tibet, China. BMC Microbiology 16:276.

Tani, A., Y. Takai, I. Suzukawa, M. Akita, H. Murase, and K. Kimbara. 2012. Practical application of methanol-mediated mutualistic symbiosis between methylobacterium species and a roof greening moss, racomitrium japonicum. PLoS ONE 7:2–10.

Tanneberger, F., L. Appulo, S. Ewert, S. Lakner, N. Ó Brolcháin, J. Peters, and W. Wichtmann. 2021. The Power of Nature-Based Solutions: How Peatlands Can Help Us to Achieve Key EU Sustainability Objectives. Advanced Sustainable Systems 5:1–10.

Tarnocai, C., D. G. Adams, V. Glooschenko, W. A. Glooschenko, P. Grondin, H. E. Hirvonen, and C. D. A. Rubec. 1988. The Canadian wetland classification system. Pages 413–427 The Canadian wetland classification system.

Thormann, J., and L. Landgraf. 2010. Neue Chancen für Basen-und Kalk-Zwischenmoore in Brandenburg. Naturschutz und Landschaftspflege in Brandenburg 19:4.

Tian, W., X. Xiang, L. Ma, S. Evers, R. Wang, X. Qiu, and H. Wang. 2020. Rare Species Shift the Structure of Bacterial Communities Across Sphagnum Compartments in a Subalpine Peatland. Frontiers in Microbiology 10:1–13.

Timonen, S., and M. Bomberg. 2009. Archaea in dry soil environments. Phytochemistry Reviews 8:505–518.

Trivedi, P., J. E. Leach, S. G. Tringe, T. Sa, and B. K. Singh. 2020. Plant–microbiome interactions: from community assembly to plant health. Nature Reviews Microbiology 18:607–621.

Trujillo, M. E., R. Riesco, P. Benito, and L. Carro. 2015. Endophytic actinobacteria and the interaction of Micromonospora and nitrogen fixing plants. Frontiers in Microbiology 6:1–15.

Tsitko, I., M. Lusa, J. Lehto, L. Parviainen, A. Ikonen, A. Lahdenperä, and M. Bomberg. 2014. The Variation of Microbial Communities in a Depth Profile of an Acidic, Nutrient-Poor Boreal Bog in Southwestern Finland. Open Journal of Ecology 4:832–859.

Tsujino, R., N. Fujita, M. Katayama, D. Kawase, K. Matsui, A. Seo, T. Shimamura, Y. Takemon, N. Tsujimura, T. Yumoto, and A. Ushimaru. 2010. Restoration of floating mat bog vegetation after eutrophication damages by improving water quality in a small pond. Limnology 11:289–297.

Tuittila, E. S., S. Juutinen, S. Frolking, M. Väliranta, A. M. Laine, A. Miettinen, M. L. Seväkivi, A. Quillet, and P. Merilä. 2013. Wetland chronosequence as a model of peatland development: Vegetation succession, peat and carbon accumulation. Holocene 23:25–35.

Turetsky, M. R. 2003. The Role of Bryophytes in Carbon and Nitrogen Cycling New Frontiers in Bryology and Lichenology. The Bryologist 106:395–409.

Turunen, J., N. T. Roulet, T. R. Moore, and P. J. H. Richard. 2004. Nitrogen deposition and increased carbon accumulation in ombrotrophic peatlands in eastern Canada. Global Biogeochemical Cycles 18:1–12.

Tveit, A., R. Schwacke, M. M. Svenning, and T. Urich. 2013. Organic carbon transformations in high-Arctic peat soils: key functions and microorganisms. The ISME Journal 7:299–311.

Tveit, A. T., T. Urich, P. Frenzel, and M. M. Svenning. 2015. Metabolic and trophic interactions modulate methane production by Arctic peat microbiota in response to warming. Proceedings of the National Academy of Sciences of the United States of America 112:E2507-16.

Tveit, A. T., T. Urich, and M. M. Svenning. 2014. Metatranscriptomic analysis of arctic peat soil microbiota. Applied and Environmental Microbiology 80:5761–5772.

Unger, V., S. Liebner, F. Koebsch, S. Yang, F. Horn, T. Sachs, J. Kallmeyer, K. H. Knorr, G. Rehder, P. Gottschalk, and G. Jurasinski. 2021. Congruent changes in microbial community dynamics and ecosystem methane fluxes following natural drought in two restored fens. Soil Biology and Biochemistry 160:108348.

Urbanová, Z., and J. Bárta. 2020. Recovery of methanogenic community and its activity in long-term drained peatlands after rewetting. Ecological Engineering 150.

Vandamme, P., K. Opelt, N. Knöchel, C. Berg, S. Schönmann, E. De Brandt, L. Eberl, E. Falsen, and G. Berg. 2007. Burkholderia bryophila sp. nov. and Burkholderia megapolitana sp. nov., moss-associated species with antifungal and plant-growth-promoting properties. International Journal of Systematic and Evolutionary Microbiology 57:2228–2235.

Vanderpoorten, A., L. Hedenäs, C. J. Cox, and A. J. Shaw. 2002. Phylogeny and morphological evolution of the Amblystegiaceae (Bryopsida). Molecular Phylogenetics and Evolution 23:1–21.

Venkata Ramana, V., C. Sasikala, S. Takaichi, and C. V. Ramana. 2010. Roseomonas aestuarii sp. nov., a bacteriochlorophyll-a containing alphaproteobacterium isolated from an estuarine habitat of India. Systematic and Applied Microbiology 33:198–203.

Verkühlen, G.-J. 2005. Vorkommen und medizinische Bedeutung von Steptococcus suis beim Wildschwein (Sus scrofa scrofa).

Vicherová, E., R. Glinwood, T. Hájek, P. Šmilauer, and V. Ninkovic. 2020. Bryophytes can recognize their neighbours through volatile organic compounds. Scientific Reports 10:1–11.

Vicherová, E., M. Hájek, P. Šmilauer, and T. Hájek. 2017. Sphagnum establishment in alkaline fens: Importance of weather and water chemistry. Science of the Total Environment 580:1429–1438.

Vidra, A., and Á. Németh. 2018. Bio-produced acetic acid: A review. Periodica Polytechnica Chemical Engineering 62:245–256.

Vigneron, A., P. Cruaud, N. Bhiry, and C. Lovejoy. 2019. Microbial Community Structure and Methane Cycling Potential along a Thermokarst Pond-Peatland Continuum. Microorganisms 7:486.

Vile, M. A., R. Kelman Wieder, T. Živković, K. D. Scott, D. H. Vitt, J. A. Hartsock, C. L. Iosue, J. C. Quinn, M. Petix, H. M. Fillingim, J. M. A. Popma, K. A. Dynarski, T. R. Jackman, C. M. Albright, and D. D. Wykoff. 2014. N2-fixation by methanotrophs sustains carbon and nitrogen accumulation in pristine peatlands. Biogeochemistry 121:317–328.

Vitt, D. H., and N. G. Slack. 1975. An analysis of the vegetation of Sphagnum -dominated kettle-hole bogs in relation to environmental gradients . Canadian Journal of Botany 53:332–359.

Vorobev, A. V., M. Baani, N. V. Doronina, A. L. Brady, W. Liesack, P. F. Dunfield, and S. N. Dedysh. 2011. Methyloferula stellata gen. nov., sp. nov., an acidophilic, obligately methanotrophic bacterium that possesses only a soluble methane monooxygenase. International Journal of Systematic and Evolutionary Microbiology 61:2456–2463.

Wagner, B., and R. Seppelt. 2006. Deep-water occurrence of the moss Bryum pseudotriquetrum in Radok Lake, Amery Oasis, East Antarctica. Polar Biology 29:791–795.

Wagner, D. 2017. Effect of varying soil water potentials on methanogenesis in aerated marshland soils. Scientific Reports 7:1–9.

Wagner, D., E. Spieck, E. Bock, and E.-M. Pfeiffer. 2002. Microbial Life in Terrestrial Permafrost: Methanogenesis and Nitrification in Gelisols as Potentials for Exobiological Process. Pages 143–159 *in* H. G. and B.-K. C, editors. Astrobiology.

Wagner, K., K. Besemer, N. R. Burns, T. J. Battin, and M. M. Bengtsson. 2015. Light availability affects stream biofilm bacterial community composition and function, but not diversity. Environmental Microbiology 17:5036–5047.

Wang, S., L. Li, H. Li, S. K. Sahu, H. Wang, Y. Xu, W. Xian, B. Song, H. Liang, S. Cheng, Y. Chang, Y. Song, Z. Çebi, S. Wittek, T. Reder, M. Peterson, H. Yang, J. Wang, B. Melkonian, Y. Van de Peer, X. Xu, G. K. S. Wong, M. Melkonian, H. Liu, and X. Liu. 2020. Genomes of early-diverging streptophyte algae shed light on plant terrestrialization. Nature Plants 6:95–106.

Wang, S., J. Y. Tang, J. Ma, X. D. Li, and Y. H. Li. 2018. Moss habitats distinctly affect their associated bacterial community structures as revealed by the high-throughput sequencing method. World Journal of Microbiology and Biotechnology 34:1–13.

Wassermann, B., T. Cernava, H. Müller, C. Berg, and G. Berg. 2019. Seeds of native alpine plants host unique microbial communities embedded in cross-kingdom networks. Microbiome 7:108.

Welsh, H. E., and J. Kalff. 1974. Benthic photosynthesis and respiration in Char Lake. Journal of the Fisheries Board of Canada 31:609–620.

Wen, X., V. Unger, G. Jurasinski, F. Koebsch, F. Horn, G. Rehder, T. Sachs, D. Zak, G. Lischeid, K. H. Knorr, M. E. Böttcher, M. Winkel, P. L. E. Bodelier, and S. Liebner. 2018. Predominance of methanogens over methanotrophs in rewetted fens characterized by high methane emissions. Biogeosciences 15:6519–6536.

Wen, X., S. Yang, F. Horn, M. Winkel, D. Wagner, and S. Liebner. 2017. Global biogeographic analysis of methanogenic archaea identifies community-shaping environmental factors of natural environments. Frontiers in Microbiology 8:1–13.

Weon, H. Y., C. M. Lee, S. B. Hong, B. Y. Kim, S. H. Yoo, S. W. Kwon, and S. J. Go. 2008. Kaistia soli sp. nov., isolated from a wetland in Korea. International Journal of Systematic and Evolutionary Microbiology 58:1522–1524.

Whinam, J., and G. Copson. 2006. Sphagnum moss: An indicator of climate change in the sub-Antarctic. Polar Record 42:43–49.

Whittaker, R. H., and S. A. Levin. 1977. The role of mosaic phenomena in natural communities. Theoretical Population Biology 12:117–139.

Wichlacz, P. L., R. F. Unz, and T. A. Langworthy. 1986. Acidiphilium angustum sp. nov., Acidiphilium facilis sp. nov., and Acidiphilium rubrum sp. nov.: acidophilic heterotrophic bacteria isolated from acidic coal mine drainage. International Journal of Systematic and Evolutionary Microbiology 36:197–201.

Wickland, K. P., J. C. Neff, and G. R. Aiken. 2007. Dissolved organic carbon in Alaskan boreal forest: Sources, chemical characteristics, and biodegradability. Ecosystems 10:1323–1340.

Wieder, R. K., and D. H. Vitt. 2006. Boreal Peatland Ecosystems. Page (R. K. Wieder and D. H. Vitt, Eds.). Springer Science & Business Media.

Wilson, R., K. Østbye, I. L. Angell, and K. Rudi. 2019. Association between diet and rumen microbiota in wild roe deer. FEMS Microbiology Letters 366:1–5.

van Winden, J. F., G. J. Reichart, N. P. McNamara, A. Benthien, and J. S. S. Damsté. 2012. Temperature-induced increase in methane release from peat bogs: A mesocosm experiment. PLoS ONE 7:4–8.

van Winden, J., N. Kip, H. M. Talbot, G.-J. Reichart, N. P. McNamara, A. Bentien, M. S. M. Jetten, H. J. M. den Camp, and J. S. Sinninghe Damsté. 2010. Symbiotic methane-oxidizing bacteria in peat moss: microbial diversity and environmental relevance. EGU General Assembly Conference Abstracts 12:12698.

Winkel, M., J. Mitzscherling, P. P. Overduin, F. Horn, M. Winterfeld, R. Rijkers, M. N. Grigoriev, C. Knoblauch, K. Mangelsdorf, D. Wagner, and S. Liebner. 2018. Anaerobic methanotrophic communities thrive in deep submarine permafrost. Scientific Reports 8:1–13.

Wojtuń, B., A. Sendyk, and D. Martyniak. 2013. Sphagnum species along environmental gradients in mires of the sudety mountains (SW Poland). Boreal Environment Research 18:74–88.

Woodin, S., M. C. Press, and J. A. Lee. 1985. Nitrate reductase activity in Sphagnum fuscum in relation to wet deposition of nitrate from the atmosphere. New Phytologist 99:381–388.

Wrede, C., A. Dreier, S. Kokoschka, and M. Hoppert. 2012. Archaea in symbioses. Archaea 2012.

Xiang, X., H. Wang, L. Gong, and Q. Liu. 2013. Vertical variations and associated ecological function of bacterial communities from Sphagnum to underlying sediments in Dajiuhu Peatland. Science China Earth Sciences 57:1–8.

Xiang, X., R. Wang, H. Wang, L. Gong, B. Man, and Y. Xu. 2017. Distribution of Bathyarchaeota Communities Across Different Terrestrial Settings and Their Potential Ecological Functions. Scientific Reports 7:1–11.

Yu, T., W. Wu, W. Liang, M. A. Lever, K. U. Hinrichs, and F. Wang. 2018. Growth of sedimentary Bathyarchaeota on lignin as an energy source. Proceedings of the National Academy of Sciences of the United States of America 115:6022–6027.

Yu, X., J. Yang, E. Wang, B. Li, and H. Yuan. 2015. Effects of growth stage and fulvic acid on the diversity and dynamics of endophytic bacterial community in stevia rebaudiana bertoni leaves. Frontiers in Microbiology 6:1–13.

Yurkov, V., and Elizabeth Hughes. 2017. Aerobic anoxygenic phototrophs: four decades of mystery. Modern Topics in the Phototrophic Prokaryotes: Environmental and Applied Aspects:193–214.

Yurkov, V., N. Gad´on, and G. Drews. 1993. The major part of polar carotenoids of the aerobic bacteria Roseococcus thiosulfatophilus RB3 and Erythromicrobium ramosum E5 is not bound to the bacteriochlorophyll a-complexes of the photosynthetic apparatus. Archives of Microbiology 160:372–376.

Yurkov, V. V., and J. T. Beatty. 1998. Aerobic Anoxygenic Phototrophic Bacteria. Microbiology and Molecular Biology Reviews 62:695–724.

Zaitseva, N. 2009. A polysaccharide extracted from Sphagnum moss as an antifungal agent in archaeological conservation:1–282.

Zhalnina, K., R. Dias, P. D. de Quadros, A. Davis-Richardson, F. A. O. Camargo, I. M. Clark, S. P. McGrath, P. R. Hirsch, and E. W. Triplett. 2014. Soil pH Determines Microbial Diversity and Composition in the Park Grass Experiment. Microbial Ecology 69:395–406.

Zhang, B., J. Chen, Y. Su, W. Sun, and A. Zhang. 2021. Utilization of Indole-3-acetic acid–Secreting Bacteria in Algal Environment to Increase Biomass Accumulation of Ochromonas and Chlorella. Bioenergy Research.

Zhang, J., K. Kobert, T. Flouri, and A. Stamatakis. 2014. PEAR: A fast and accurate Illumina Paired-End reAd mergeR. Bioinformatics 30:614–620.

Zhou, Z., J. Pan, F. Wang, J. D. Gu, and M. Li. 2018. Bathyarchaeota: Globally distributed metabolic generalists in anoxic environments. FEMS Microbiology Reviews 42:639–655.

Zibulski, R., U. Herzschuh, and L. A. Pestryakova. 2016. Vegetation patterns along transects in polygonal landscapes of the Siberian Arctic. Journal of vegetation science 27:377–386.

Zoltai, S. C., and C. Tarnocai. 1975. Perennially Frozen Peatlands in the Western Arctic and Subarctic of Canada. Canadian Journal of Earth Sciences 12:28–43.

Zoltai, S. C., and D. H. Vitt. 1995. Canadian wetlands: Environmental gradients and classification. Vegetatio 118:131–137.

Supplementary

i. OTU tables ii

ii. Data availability ii

iii. Table S1A: Environmental variables and meta-data of all samples. ii

iv. Supplementary Table S1B: Coordinates and primer sequences of individual samples i

v. Figure S2: Archaeal alpha-diversities. xvii

vi. Figure S3: Heatmap overview of OTUs within Acetobacteraceae. xviii

vii. Figure S4: Heatmap overview of OTUs within Acidobacteria. xix

viii. Figure S5: Heatmap overview of OTUs within Acidimicrobiales. xx

ix. Figure S6: Heatmap overview of OTUs within Cyanobacteria. xxi

x. Figure S7: Heat map overview of OTUs within methanotrophic bacteria. xxii

xi. Figure S8: Dendrogram showing the clustering of archaeal communities (OTU at 97% sequence similarity) in relation to the characteristics of their respective environments xxiii

xii. Figure S9: Heatmap overview of the OTUs within archaea at above 0.1% relative abundance (out of total sequences assigned to Archaea) in one or more samples xxiv

xiii. Supplementary Table S2: xxv

xiv. Supplementary Table S3: Diversity indeces for all MUE sites. xxvii

xv. Venn diagram showing the bacteriomes of Sphagnum and reference sedges from all subsites within the Mueritz sampling site. xxviii

XVI. Additional supplement (S_methanotrophs_fasta). xxix

xvii. Additional supplement (S_endophytes_taxonomy; S_endophytes_fasta) xxxiv

xviii. Supplementary Table S4: Methane oxidation and methane production rates. xxxvi

i. OTU tables

The complete OTU tables for bacteria and archaea are online available: https://www.nature.com/articles/s41598-020-79773-2#Sec24

ii. Data availability

Demultiplexed read sequence data has been deposited at NCBI/Genbank database under the BioProject PRJNA356121 with accession numbers SRR6442387- SRR6442509 for bacteria and SRR6442615-SRR6442637 for archaea.

iii. Table S1A: Environmental variables and meta-data of all samples.

KL=Klason lignin which is the fraction of lignin that is insoluble in acids (given in % of dry mass); sol-KL=acid-soluble Klason lignin (given in % of dry mass); HC=content of holocellulose (given in % of dry mass); CEC= cation exchange capacity (given in µeq/g); oxygen in mg L^{-1}; CH_4 concentration in µM; DOC in mg L^{-1}; C and N in % dry weight; water content in %.

Sample ID	**Name**	**StudySite**	**SubSite**	**Taxon**	**Taxon-2**	**Hydrol**	**Type**	**System**	**pH**	**CH4**	**DOC**	**Oxygen**	**Temp**	**CEC**	**KL**	**sol-KL**	**HC**	**N**	**C**	**C:N**	**Water cont**
1	GLU1 endo	SV	GLU 1	Amb	Amb	sub	endo	amb	7,00	7,04	4,40	8,57	8,93	668,20	35,10	2,00	32,90	1,09	30,75	27,92	51,10
2	GLU1 endo	SV	GLU 1	Amb	Amb	sub	endo	amb	7,00	7,04	4,40	8,57	8,93	668,20	35,10	2,00	32,90	1,09	30,75	27,92	51,10
3	TW2 endo	SV	TW 2	Amb	Amb	sub	endo	amb	5,90	0,84	1,08	6,62	11,00	430,50	48,00	1,40	56,40	1,27	28,22	22,20	51,70
4	TW2 endo	SV	TW 2	Amb	Amb	sub	endo	amb	5,90	0,84	1,08	6,62	11,00	430,50	48,00	1,40	56,40	1,27	28,22	22,20	51,70

78,80	78,80	93,80	93,80	51,10	51,10	79,10	79,10	93,60	93,60	93,70	93,70
60,11	60,11	34,38	34,38	27,92	27,92	95,26	95,26	18,16	18,16	24,61	24,61
45,88	45,88	44,46	44,46	30,75	30,75	45,03	45,03	41,80	41,80	43,28	43,28
0,76	0,76	1,29	1,29	1,09	1,09	0,47	0,47	2,30	2,30	1,76	1,76
46,00	46,00	48,30	48,30	32,90	32,90	49,10	49,10	51,30	51,30	NA	NA
5,10	5,10	4,20	4,20	2,00	2,00	7,60	7,60	3,60	3,60	NA	NA
4,80	4,80	10,30	10,30	35,10	35,10	7,60	7,60	14,70	14,70	NA	NA
461,90	461,90	468,90	468,90	668,20	668,20	729,40	729,40	386,30	386,30	359,10	359,10
12,16	12,16	9,59	9,59	8,93	8,93	13,82	13,82	12,58	12,58	13,73	13,73
3,85	3,85	7,23	7,23	8,57	8,57	NA	NA	2,24	2,24	NA	NA
59,98	59,98	31,45	31,45	4,40	4,40	NA	NA	18,10	18,10	NA	NA
151,60	151,60	95,06	95,06	7,04	7,04	198,32	198,32	136,30	136,30	454,62	454,62
3,75	3,75	4,03	4,03	7,00	7,00	3,92	3,92	4,95	4,95	4,35	4,35
sph	sph	sph	sph	amb	amb	sph	sph	sph	sph	sph	sph
endo	endo	endo	endo	endo	endo	endo	endo	endo	endo	endo	endo
sub	sub	sub	sub	sub	sub	emrs	emrs	sub	sub	sub	sub
S.rip	S.rip	S.rip	S.rip	Amb	Amb	S.lind	S.lind	S.rip	S.rip	S.rip	S.rip
Sph	Sph	Sph	Sph	Amb	Amb	Sph	Sph	Sph	Sph	Sph	Sph
1	1	6	6	GLU 2	GLU 2	2-2	2-2	4-2	4-2	4	4
NE	NE	NE	NE	SV	SV	NE	NE	NE	NE	NE	NE
NEI1 endo	NEI1 endo	NEI3 endo	NEI3 endo	GLU2 endo	GLU2 endo	NEI6 endo	NEI6 endo	NEI4 endo	NEI4 endo	NEI2 endo	NEI2 endo
5	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**

79,10	79,10	92,00	92,00	90,80	90,80	92,20	92,20	92,00	92,00	90,80	90,80
93,78	93,78	54,74	54,74	47,30	47,30	35,00	35,00	56,64	56,64	47,30	47,30
45,90	45,90	45,47	45,47	46,93	46,93	45,60	45,60	45,79	45,79	46,93	46,93
0,49	0,49	0,83	0,83	1,02	1,02	1,30	1,30	0,82	0,82	1,02	1,02
52,40	52,40	51,20	51,20	58,00	58,00	59,70	59,70	58,50	58,50	58,00	58,00
6,80	6,80	4,90	4,90	5,30	5,30	4,50	4,50	4,20	4,20	5,30	5,30
16,40	16,40	14,70	14,70	19,50	19,50	18,90	18,90	28,30	28,30	19,50	19,50
580,90	580,90	763,20	763,20	677,30	677,30	574,30	574,30	783,10	783,10	677,30	677,30
12,45	12,45	16,50	16,50	16,16	16,16	15,84	15,84	NA	NA	16,16	16,16
4,32	4,32	1,64	1,64	1,64	1,64	NA	NA	NA	NA	1,64	1,64
83,98	83,98	45,30	45,30	42,15	42,15	227,50	227,50	NA	NA	42,15	42,15
296,92	296,92	359,64	359,64	461,79	461,79	277,34	277,34	482,09	482,09	461,79	461,79
4,63	4,63	4,15	4,15	3,60	3,60	3,75	3,75	4,53	4,53	3,60	3,60
sph	sph	sph	sph	sph	sph	sph	sph	sph	sph	sph	sph
endo	endo	endo	endo	endo	endo	endo	endo	endo	endo	endo	endo
emrs	emrs	emrs	emrs	emrs	emrs	emrs	emrs	emrs	emrs	emrs	emrs
S.lind	S.lind	S.fall	S.fall	S.mag	S.mag	S.fall	S.fall	S.mag	S.mag	S.fall	S.fall
Sph	Sph	Sph	Sph	Sph	Sph	Sph	Sph	Sph	Sph	Sph	Sph
2	2	KLO-m 5	KLO-m 5	KLO-o 3	KLO-o 3	HEI 2	HEI 2	KIE 1	KIE 1	KLO-m 4	KLO-m 4
NE	NE	MUE	MUE	MUE	MUE	MUE	MUE	MUE	MUE	MUE	MUE
NEI5 endo	NEI5 endo	KLO2 endo	KLO2 endo	KLO1 endo	KLO1 endo	HEI2 endo	HEI2 endo	KIE1 endo	KIE1 endo	KLO2 endo	KLO2
17	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**

79,10	79,10	92,00	92,00	92,00	92,00	90,80	90,80	92,00	51,70	51,70	92,00
85,87	85,87	54,74	54,74	54,74	54,74	47,30	47,30	56,64	22,20	22,20	56,64
85,95	85,95	45,47	45,47	45,47	45,47	46,93	46,93	45,79	28,22	28,22	45,79
1,00	1,00	0,83	0,83	0,83	0,83	1,02	1,02	0,82	1,27	1,27	0,82
60,00	60,00	51,20	51,20	51,20	51,20	58,00	58,00	58,50	56,40	56,40	58,50
6,50	6,50	4,90	4,90	4,90	4,90	5,30	5,30	4,20	1,40	1,40	4,20
6,20	6,20	14,70	14,70	14,70	14,70	19,50	19,50	28,30	48,00	48,00	28,30
683,30	683,30	763,20	763,20	763,20	763,20	677,30	677,30	783,10	430,50	430,50	783,10
11,48	11,48	16,50	16,50	16,50	16,50	16,16	16,16	NA	11,00	11,00	NA
NA	NA	1,64	1,64	1,64	1,64	1,64	1,64	NA	6,62	6,62	NA
NA	NA	45,30	45,30	45,30	45,30	42,15	42,15	NA	1,08	1,08	NA
365,89	365,89	359,64	359,64	359,64	359,64	461,79	461,79	482,09	0,84	0,84	482,09
3,80	3,80	4,15	4,15	4,15	4,15	3,60	3,60	4,53	5,90	5,90	4,53
sph	sph	sph	sph	sph	sph	sph	sph	sph	amb	amb	sph
endo	endo	endo	endo	endo	endo	endo	endo	endo	endo	endo	endo
emrs	emrs	emrs	emrs	emrs	emrs	emrs	emrs	emrs	sub	sub	emrs
S.lind	S.lind	S.mag	S.mag	S.mag	S.mag	S.fall	S.fall	S.mag	Amb	Amb	S.mag
Sph	Sph	Sph	Sph	Sph	Sph	Sph	Sph	Sph	Amb	Amb	Sph
2-3	2-3	KLO-o 1	KLO-o 1	KLO-o 2	KLO-o 2	KLO-m 6	KLO-m 6	KIE 2	TW 1	TW 1	KIE 3
NE	NE	MUE	MUE	MUE	MUE	MUE	MUE	MUE	SV	SV	MUE
NEI7 endo	NEI7 endo	KLO1 endo	KLO1 endo	KLO1 endo	KLO1 endo	KLO2 endo	KLO2 endo	KIE2 endo	TW1 endo	TW1 endo	KIE3 endo
31	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**41**	**45**	**46**	**47**

92,00	57,10	57,10	57,10	57,10	57,10	57,10	92,20	92,20	92,20	92,20	97,20
56,64	39,93	39,93	39,93	39,93	52,76	52,76	35,00	35,00	35,00	35,00	32,00
45,79	33,99	33,99	33,99	33,99	64,12	64,12	45,60	45,60	45,60	45,60	48,90
0,82	0,85	0,85	0,85	0,85	1,22	1,22	1,30	1,30	1,30	1,30	1,50
58,50	42,20	42,20	42,20	42,20	37,30	37,30	59,70	59,70	59,70	59,70	NA
4,20	1,60	1,60	1,60	1,60	1,70	1,70	4,50	4,50	4,50	4,50	NA
28,30	14,00	14,00	14,00	14,00	27,50	27,50	18,90	18,90	18,90	18,90	NA
783,10	610,00	610,00	610,00	610,00	566,00	566,00	574,30	574,30	574,30	574,30	401,00
NA	12,65	12,65	12,65	12,65	NA	NA	15,84	15,84	15,84	15,84	14,93
NA	5,45	5,45	5,45	5,45	NA	NA	NA	NA	NA	NA	2,85
NA	4,00	4,00	4,00	4,00	NA	NA	227,50	227,50	227,50	227,50	72,90
482,09	27,47	27,47	27,47	27,47	7,03	7,03	277,34	277,34	277,34	277,34	354,18
4,53	6,58	6,58	6,58	6,58	6,45	6,45	3,75	3,75	3,75	3,75	4,26
sph	amb	amb	amb	amb	amb	amb	sph	sph	sph	sph	sph
endo	endo	endo	endo	endo	endo	endo	endo	endo	endo	endo	endo
emrs	sub	sub	sub	sub	sub	sub	emrs	emrs	emrs	emrs	sub
S.mag	Scor	Scor	Scor	Scor	Amb	Amb	S.fall	S.fall	S.fall	S.fall	S.fall
Sph	Amb	Amb	Amb	Amb	Amb	Amb	Sph	Sph	Sph	Sph	Sph
KIE 3	SuScor a	SuScor a	SuScor b	SuScor b	S9	S9	HEI 1	HEI 1	HEI 3	HEI 3	HEI 4
MUE	SA	SA	SA	SA	SA	SA	MUE	MUE	MUE	MUE	MUE
KIE3 endo	PP1 endo	PP1 endo	PP1 endo	PP1 endo	PC endo	PC endo	HEI2 endo	HEI2 endo	HEI2 endo	HEI2 endo	HEI1 endo
48	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**

97,20	NA	NA	NA	NA	NA	NA	NA	NA	57,10	57,10	NA
32,00	37,90	37,90	43,80	43,80	64,54	64,54	83,75	83,75	33,73	33,73	33,50
48,90	50,60	50,60	47,13	47,13	49,90	49,90	47,70	47,70	31,46	31,46	48,80
1,50	1,34	1,34	1,08	1,08	0,78	0,78	0,57	0,57	0,93	0,93	1,50
NA	58,90	58,90	46,90	46,90	58,70	58,70	61,10	61,10	40,50	40,50	53,10
NA	2,50	2,50	1,40	1,40	1,80	1,80	1,60	1,60	1,30	1,30	2,00
NA	39,30	39,30	26,40	26,40	45,10	45,10	37,60	37,60	48,20	48,20	43,10
401,00	NA	NA	NA	NA	NA	NA	NA	NA	569,00	569,00	NA
14,93	16,16	16,16	11,48	11,48	NA	NA	13,82	13,82	12,65	12,65	15,84
2,85	1,64	1,64	NA	NA	NA	NA	NA	NA	5,45	5,45	NA
72,90	42,15	42,15	NA	NA	NA	NA	NA	NA	4,00	4,00	227,50
354,18	461,79	461,79	365,89	365,89	482,09	482,09	198,32	198,32	27,47	27,47	277,34
4,26	3,60	3,60	3,80	3,80	4,53	4,53	3,92	3,92	6,58	6,58	3,75
sph	sph	sph	sph	sph	sph	sph	sph	sph	amb	amb	sph
endo	Ref	Ref	Ref	Ref	Ref	Ref	Ref	Ref	endo	endo	Ref
sub	emrs	emrs	emrs	emrs	emrs	emrs	emrs	emrs	sub	sub	emrs
S.fall	Cx	Cx	Vasc	Vasc	Cx	Cx	Cx	Cx	Scor	Scor	Erio
Sph	Vasc	Vasc	Vasc	Vasc	Vasc	Vasc	Vasc	Vasc	Amb	Amb	Vasc
HEI 4	KLO-m 6	KLO-m 6	2-3	2-3	KIE 1	KIE 1	2-2	2-2	SuCar	SuCar	HEI 1
MUE	MUE	MUE	NE	NE	MUE	MUE	NE	NE	SA	SA	MUE
HEI1 endo	KLO2 Vasc	KLO2 Vasc	NEI7 Vasc	NEI7 Vasc	KIE Vasc	KIE Vasc	NEI6 Vasc	NEI6 Vasc	PP2 endo	PP2 endo	HEI2 Vasc
60	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**

NA	57,10	92,00	92,00	90,80	90,80	92,00	78,80	79,10	79,10		93,70
33,50	33,73	54,74	54,74	47,30	47,30	54,74	60,11	93,78	95,26	85,87	24,61
48,80	31,46	45,47	45,47	46,93	46,93	45,47	45,88	45,90	45,03	85,95	43,28
1,50	0,93	0,83	0,83	1,02	1,02	0,83	0,76	0,49	0,47	1,00	1,76
53,10	40,50	51,20	51,20	58,00	58,00	51,20	46,00	52,40	49,10	60,00	NA
2,00	1,30	4,90	4,90	5,30	5,30	4,90	5,10	6,80	7,60	6,50	NA
43,10	48,20	14,70	14,70	19,50	19,50	14,70	4,80	16,40	7,60	6,20	NA
NA	569,00	763,20	763,20	677,30	677,30	763,20	461,90	580,90	729,40	683,30	359,10
15,84	12,65	16,50	16,50	16,16	16,16	16,50	12,16	12,45	13,82	11,48	13,73
NA	5,45	1,64	1,64	1,64	1,64	1,64	3,85	4,32	NA	NA	NA
227,50	4,00	45,30	45,30	42,15	42,15	45,30	59,98	83,98	NA	NA	NA
277,34	27,47	359,64	359,64	461,79	461,79	359,64	151,60	296,92	198,32	365,89	454,62
3,75	6,58	4,15	4,15	3,60	3,60	4,15	3,75	4,63	3,92	3,80	4,35
sph	amb	sph	sph	sph	sph	sph	sph	sph	sph	sph	sph
Ref	epi	epi	epi	epi	epi	epi	epi	epi	epi	epi	epi
emrs	sub	emrs	emrs	emrs	emrs	emrs	sub	emrs	emrs	emrs	sub
Erio	Scor	S.mag	S.mag	S.fall	S.fall	S.fall	S.rip	S.lind	S.lind	S.rip	S.rip
Vasc	Amb	Sph	Sph	Sph	Sph	Sph	Sph	Sph	Sph	Sph	Sph
HEI 1	SuCar	KLO-o 1	KLO-o 2	KLO-m 3	KLO-m 4	KLO-m 5	1	2	2-2	2-3	4
MUE	SA	MUE	MUE	MUE	MUE	MUE	NE	NE	NE	NE	NE
HEI2 Vasc	PP2 epi	KLO1 epi	KLO1 epi	KLO2 epi	KLO2 epi	KLO2 epi	NEI1 epi	NEI5 epi	NEI6 epi	NEI7 epi	NEI2 epi
78	**86**	**89**	**90**	**92**	**93**	**94**	**98**	**99**	**101**	**102**	**103**

93,60	93,80	51,10	51,10	92,20	92,20	92,20	97,20	92,00	92,00	92,00	51,70
18,16	34,38	27,92	27,92	35,00	35,00	35,00	32,00	56,64	56,64	56,64	22,20
41,80	44,46	30,75	30,75	45,60	45,60	45,60	48,90	45,79	45,79	45,79	28,22
2,30	1,29	1,09	1,09	1,30	1,30	1,30	1,50	0,82	0,82	0,82	1,27
51,30	48,30	32,90	32,90	59,70	59,70	59,70	NA	58,50	58,50	58,50	56,40
3,60	4,20	2,00	2,00	4,50	4,50	4,50	NA	4,20	4,20	4,20	1,40
14,70	10,30	35,10	35,10	18,90	18,90	18,90	NA	28,30	28,30	28,30	48,00
386,30	468,90	668,20	668,20	574,30	574,30	574,30	401,00	783,10	783,10	783,10	430,50
12,58	9,59	8,93	8,93	15,84	15,84	15,84	14,93	NA	NA	NA	11,00
2,24	7,23	8,57	8,57	NA	NA	NA	2,85	NA	NA	NA	6,62
18,10	31,45	4,40	4,40	227,50	227,50	227,50	72,90	NA	NA	NA	1,08
136,30	95,06	7,04	7,04	277,34	277,34	277,34	354,18	482,09	482,09	482,09	0,84
4,95	4,03	7,00	7,00	3,75	3,75	3,75	4,26	4,53	4,53	4,53	5,90
sph	sph	amb	amb	sph	sph	sph	sph	sph	sph	sph	amb
epi	epi	epi	epi	epi	epi	epi	epi	epi	epi	epi	epi
sub	sub	sub	sub	emrs	emrs	emrs	sub	emrs	emrs	emrs	sub
S.rip	S.rip	Amb	Amb	S.fall	S.fall	S.fall	S.fall	S.mag	S.mag	S.mag	Amb
Sph	Sph	Amb	Amb	Sph	Sph	Sph	Sph	Sph	Sph	Sph	Amb
4-2	6	GLU 1	GLU 2	HEI 1	HEI 2	HEI 3	HEI 4	KIE 1	KIE 2	KIE 3	TW 2
NE	NE	SV	SV	MUE	MUE	MUE	MUE	MUE	MUE	MUE	SV
NEI4 epi	NEI3 epi	GLU1 epi	GLU2 epi	HEI2 epi	HEI2 epi	HEI2 epi	HEI1 epi	KIE epi	KIE2 epi	KIE3 epi	TW2 epi
105	**106**	**107**	**109**	**111**	**112**	**114**	**116**	**118**	**119**	**121**	**123**

124	TW1 epi	SV	TW 1	Amb	Amb	sub	epi	amb	5,90	0,84	1,08	6,62	11,00	430,50	48,00	1,40	56,40	1,27	28,22	22,20	51,70
125	PC epi	SA	S9	Amb	Amb	sub	epi	amb	6,45	7,03	NA	NA	NA	566,00	27,50	1,70	37,30	1,22	64,12	52,76	57,10
126	PP1 epi	SA	SuScor a	Amb	Scor	sub	epi	amb	6,58	27,47	4,00	5,45	12,65	610,00	14,00	1,60	42,20	0,85	33,99	39,93	57,10
127	PP1 epi	SA	SuScor b	Amb	Scor	sub	epi	amb	6,58	27,47	4,00	5,45	12,65	610,00	14,00	1,60	42,20	0,85	33,99	39,93	57,10
128	GLU Sed	SV	GLU	Sed	Sed	sub	Ref	amb	7,00	91,53	NA	NA	7,20	NA	NA	NA	NA	NA	NA	NA	NA
129	GLU Sed	SV	GLU	Sed	Sed	sub	Ref	amb	7,00	91,53	NA	NA	7,20	NA	NA	NA	NA	NA	NA	NA	NA
130	TW Sed	SV	TW	Sed	Sed	sub	Ref	amb	5,90	NA	NA	NA	10,70	NA	NA	NA	NA	NA	NA	NA	NA
131	TW Sed	SV	TW	Sed	Sed	sub	Ref	amb	5,90	NA	NA	NA	10,70	NA	NA	NA	NA	NA	NA	NA	NA
132	KLO1 Vasc	MUE	KLO-o 2	Vasc	Erio	emrs	Ref	sph	4,15	359,64	45,30	1,64	16,50	NA	38,60	2,00	54,20	1,03	50,47	68,31	NA
133	KLO1 Vasc	MUE	KLO-o 2	Vasc	Erio	emrs	Ref	sph	4,15	359,64	45,30	1,64	16,50	NA	38,60	2,00	54,20	1,03	50,47	68,31	NA
134	KNU1	SV	KNU 1	Amb	Amb	sub	endo	amb	6,25	2,76	2,55	7,63	12,05	NA	NA	NA	NA	NA	NA	NA	52,30
135	KNU1	SV	KNU 1	Amb	Amb	sub	endo	amb	6,25	2,76	2,55	7,63	12,05	NA	NA	NA	NA	NA	NA	NA	52,30

136	KNU2	SV	KNU 2	Amb	Amb	sub	endo	amb	6,25	2,76	2,55	7,63	12,05	NA	NA	NA	NA	NA	NA	NA	52,30
137	KNU2	SV	KNU 2	Amb	Amb	sub	endo	amb	6,25	2,76	2,55	7,63	12,05	NA	NA	NA	NA	NA	NA	NA	52,30
138	PP1 Sed	SA	SuScor	Sed	Sed	sub	Ref	amb	6,58	9,42	NA	NA	7,05	NA	NA	NA	NA	NA	NA	NA	NA
139	PP2 Sed	SA	SuScor	Sed	Sed	sub	Ref	amb	6,58	9,42	NA	NA	7,05	NA	NA	NA	NA	NA	NA	NA	NA
140	PP2 Sed	SA	SuCar	Sed	Sed	sub	Ref	amb	6,58	9,42	NA	NA	7,05	NA	NA	NA	NA	NA	NA	NA	NA
141	PP2 Sed	SA	SuCar	Sed	Sed	sub	Ref	amb	6,58	9,42	NA	NA	7,05	NA	NA	NA	NA	NA	NA	NA	NA
142	NEI1 Vasc	NE	1	Vasc	Erio	emrs	Ref	sph	3,75	151,60	59,98	3,85	12,16	NA	NA	NA	NA	NA	NA	NA	NA
143	NEI1 Vasc	NE	1	Vasc	Erio	emrs	Ref	sph	3,75	151,60	59,98	3,85	12,16	NA	NA	NA	NA	NA	NA	NA	NA
144	NEI5 Cx	NE	2	Vasc	Cx	emrs	Ref	sph	4,63	296,92	83,98	4,32	12,45	NA	NA	NA	NA	NA	NA	NA	NA
145	NEI5 Cx	NE	2	Vasc	Cx	emrs	Ref	sph	4,63	296,92	83,98	4,32	12,45	NA	NA	NA	NA	NA	NA	NA	NA
146	PC Sed	SA	S9	Sed	Sed	sub	Ref	amb	6,45	522,87	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
147	PC Sed	SA	S9	Sed	Sed	sub	Ref	amb	6,45	522,87	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

NA	NA	NA	NA	NA	NA	NA	NA	52,30	52,30
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
10,99	10,99	NA	NA	NA	NA	4,56	4,56	12,05	12,05
NA	NA	NA	NA	NA	NA	NA	NA	7,63	7,63
NA	NA	NA	NA	NA	NA	0,00	0,00	2,55	2,55
282,62	282,62	979,62	979,62	618,29	618,29	262,27	262,27	2,76	2,76
3,75	3,75	4,35	4,35	4,35	4,95	4,03	4,03	6,25	6,25
sph	sph	sph	sph	sph	sph	sph	sph	amb	amb
Ref	Ref	Ref	Ref	Ref	Ref	Ref	Ref	epi	epi
sub	sub	sub	sub	sub	sub	sub	sub	sub	sub
Sed	Sed	Sed	Sed	Sed	Sed	Sed	Sed	Amb	Amb
Sed	Sed	Sed	Sed	Sed	Sed	Sed	Sed	Amb	Amb
1	1	4	4	4-2	4-2	6	6	KNU 1	KNU 2
NE	NE	NE	NE	NE	NE	NE	NE	SV	SV
NEI1 Sed	NEI1 Sed	NEI2 Sed	NEI2 Sed	NEI4 Sed	NEI4 Sed	NEI3 Sed	NEI3 Sed	KNU1 epi	KNU2 epi
148	**149**	**150**	**151**	**152**	**153**	**154**	**155**	**156**	**157**

iv. Supplementary Table S1B: Coordinates and primer sequences of individual samples

Sample ID	Name	StudySite	SubSite	Taxon	Taxon-2	Hydrol	Type	System	Coordinates	Sequence primer F BACTERIA	Sequence primerR BACTERIA	Sequence primer F ARCHAEA	Sequence primerR ARCHAEA
1	GLU1 endo	SV	GLU 1	Amb	Amb	sub	endo	amb	N78° 32' 48.948" E12° 2' 51.576"	ACACGT CCTACGGGN GGCWGCAG	CAGTCA GACTACHVGG GTATCTAATCC	ACACGT gYg CAS CAg KCg MgA AW	CGATAT GGACTACVSGG GTATCTAAT
2	GLU1 endo	SV	GLU 1	Amb	Amb	sub	endo	amb	N78° 32' 48.948" E12° 2' 51.576"	ACACGT CCTACGGGN GGCWGCAG	CATGAC GACTACHVGG GTATCTAATCC	ACACGT gYg CAS CAg KCg MgA AW	CGCGCG GGACTACVSGG GTATCTAAT
3	TW2 endo	SV	TW 2	Amb	Amb	sub	endo	amb	N78° 33' 0.18" E11° 31' 39.144"	ACGTAC CCTACGGGN GGCWGCAG	CATGAC GACTACHVGG GTATCTAATCC	ACGTAC gYg CAS CAg KCg MgA AW	CGCGCG GGACTACVSGG GTATCTAAT
4	TW2 endo	SV	TW 2	Amb	Amb	sub	endo	amb	N78° 33' 0.18" E11° 31' 39.144"	ACGTAC CCTACGGGN GGCWGCAG	GACTAG GACTACHVGG GTATCTAATCC	ACGTAC gYg CAS CAg KCg MgA AW	CGTATA GGACTACVSGG GTATCTAAT
5	NEI1 endo	NE	1	Sph	S.rip	sub	endo	sph	N69° 24' 36" E29° 6' 36"	ACTGCA CCTACGGGN GGCWGCAG	GACTAG GACTACHVGG GTATCTAATCC	ACTGCA gYg CAS CAg KCg MgA AW	CGTATA GGACTACVSGG GTATCTAAT
6	NEI1 endo	NE	1	Sph	S.rip	sub	endo	sph	N69° 24' 36" E29° 6' 36"	ACTGCA CCTACGGGN GGCWGCAG	GAGATC GACTACHVGG GTATCTAATCC	ATATCG gYg CAS CAg KCg MgA AW	TATACG GGACTACVSGG GTATCTAAT

7	NEI3 endo	NE	6	Sph	S.rip	sub	endo	sph	N69° 24' 38.988" E2° 54' 43.106"	AGCTGA CCTACGGGN GGCWGCAG	GATCGA GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	TAGCAT GGACTACVSGG GTATCTAAT
8	NEI3 endo	NE	6	Sph	S.rip	sub	endo	sph	N69° 24' 38.988" E2° 54' 43.106"	AGCTGA CCTACGGGN GGCWGCAG	GTACAC GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	TATACG GGACTACVSGG GTATCTAAT
9	GLU2 endo	SV	GLU 2	Amb	Amb	sub	endo	amb	N78° 32' 48.948" E12° 2' 51.576"	ACACGT CCTACGGGN GGCWGCAG	GAGATC GACTACHVGG GTATCTAATCC	ACACGT gYg CAS CAg KCg MgA AW	TACGTA GGACTACVSGG GTATCTAAT
10	GLU2 endo	SV	GLU 2	Amb	Amb	sub	endo	amb	N78° 32' 48.948" E12° 2' 51.576"	ACACGT CCTACGGGN GGCWGCAG	GATCGA GACTACHVGG GTATCTAATCC	ACACGT gYg CAS CAg KCg MgA AW	TAGCAT GGACTACVSGG GTATCTAAT
11	NEI6 endo	NE	2-2	Sph	S.lind	emrs	endo	sph	N69° 24' 40.752" E2° 17' 28.239"	AGAGTC CCTACGGGN GGCWGCAG	GATCGA GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	TAGCAT GGACTACVSGG GTATCTAAT
12	NEI6 endo	NE	2-2	Sph	S.lind	emrs	endo	sph	N69° 24' 40.752" E2° 17' 28.239"	AGAGTC CCTACGGGN GGCWGCAG	GTACAC GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	TATACG GGACTACVSGG GTATCTAAT
13	NEI4 endo	NE	4-2	Sph	S.rip	sub	endo	sph	N69° 24' 38.34" E29° 7' 15.6"	ACACGT CCTACGGGN GGCWGCAG	GTGTGT GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	CGTATA GGACTACVSGG GTATCTAAT
14	NEI4 endo	NE	4-2	Sph	S.rip	sub	endo	sph	N69° 24' 38.34" E29° 7' 15.6"	ACACGT CCTACGGGN GGCWGCAG	TCAGAG GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	TACGTA GGACTACVSGG GTATCTAAT

15	NEI2 endo	NE	4	Sph	S.rip	sub	endo	sph	N69° 24' 36" E29° 7' 12"	ACACGT CCTACGGGN GGCWGCAG	CAGTCA GACTACHVGG GTATCTAATCC	ACTGCA gYg CAS CAg KCg MgA AW	TGCATG GGACTACVSGG GTATCTAAT
16	NEI2 endo	NE	4	Sph	S.rip	sub	endo	sph	N69° 24' 36" E29° 7' 12"	ACACGT CCTACGGGN GGCWGCAG	CATGAC GACTACHVGG GTATCTAATCC	ACTGCA gYg CAS CAg KCg MgA AW	TGACGT GGACTACVSGG GTATCTAAT
17	NEI5 endo	NE	2	Sph	S.lind	emrs	endo	sph	N69° 24' 36" E29° 6' 36"	ACTGCA CCTACGGGN GGCWGCAG	TCGAGA GACTACHVGG GTATCTAATCC	ACTGCA gYg CAS CAg KCg MgA AW	TGTGAC GGACTACVSGG GTATCTAAT
18	NEI5 endo	NE	2	Sph	S.lind	emrs	endo	sph	N69° 24' 36" E29° 6' 36"	AGAGTC CCTACGGGN GGCWGCAG	CAGTCA GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	CGATAT GGACTACVSGG GTATCTAAT
19	KLO2 endo	MUE	KLO-m 5	Sph	S.fall	emrs	endo	sph	N53° 12' 21.816" E13° 7' 8.904"	CACAGT CCTACGGGN GGCWGCAG	GAGATC GACTACHVGG GTATCTAATCC	CACAGT gYg CAS CAg KCg MgA AW	TACGTA GGACTACVSGG GTATCTAAT
20	KLO2 endo	MUE	KLO-m 5	Sph	S.fall	emrs	endo	sph	N53° 12' 21.816" E13° 7' 8.904"	CACAGT CCTACGGGN GGCWGCAG	GATCGA GACTACHVGG GTATCTAATCC	CACAGT gYg CAS CAg KCg MgA AW	TAGCAT GGACTACVSGG GTATCTAAT
21	KLO1 endo	MUE	KLO-o 3	Sph	S.mag	emrs	endo	sph	N53° 12' 21.888" E13° 7' 10.524"	ATGCTA CCTACGGGN GGCWGCAG	GTGTGT GACTACHVGG GTATCTAATCC	ATGCTA gYg CAS CAg KCg MgA AW	TGCATG GGACTACVSGG GTATCTAAT
22	KLO1 endo	MUE	KLO-o 3	Sph	S.mag	emrs	endo	sph	N53° 12' 21.888" E13° 7' 10.524"	ATGCTA CCTACGGGN GGCWGCAG	TCAGAG GACTACHVGG GTATCTAATCC	ATGCTA gYg CAS CAg KCg MgA AW	TGACGT GGACTACVSGG GTATCTAAT

23	HEI2 endo	MUE	HEI 2	Sph	S.fall	emrs	endo	sph	N53° 12' 8.46" E13° 8' 45.924"	ACGTAC CCTACGGGN GGCWGCAG	TCAGAG GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	TACGTA GGACTACVSGG GTATCTAAT
24	HEI2 endo	MUE	HEI 2	Sph	S.fall	emrs	endo	sph	N53° 12' 8.46" E13° 8' 45.924"	ACGTAC CCTACGGGN GGCWGCAG	TCGAGA GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	TAGCAT GGACTACVSGG GTATCTAAT
25	KIE1 endo	MUE	KIE 1	Sph	S.mag	emrs	endo	sph	N53° 13' 11.316" E13° 7' 1.992"	ATATCG CCTACGGGN GGCWGCAG	TCAGAG GACTACHVGG GTATCTAATCC	ATATCG gYg CAS CAg KCg MgA AW	TGACGT GGACTACVSGG GTATCTAAT
26	KIE1 endo	MUE	KIE 1	Sph	S.mag	emrs	endo	sph	N53° 13' 11.316" E13° 7' 1.992"	ATATCG CCTACGGGN GGCWGCAG	TCGAGA GACTACHVGG GTATCTAATCC	ATATCG gYg CAS CAg KCg MgA AW	TGTGAC GGACTACVSGG GTATCTAAT
27	KLO2 endo	MUE	KLO-m 4	Sph	S.fall	emrs	endo	sph	N53° 12' 21.888" E13° 7' 10.524"	CACAGT CCTACGGGN GGCWGCAG	CAGTCA GACTACHVGG GTATCTAATCC	CACAGT gYg CAS CAg KCg MgA AW	CGATAT GGACTACVSGG GTATCTAAT
28	KLO2 endo	MUE	KLO-m 4	Sph	S.fall	emrs	endo	sph	N53° 12' 21.888" E13° 7' 10.524"	CACAGT CCTACGGGN GGCWGCAG	CATGAC GACTACHVGG GTATCTAATCC	CACAGT gYg CAS CAg KCg MgA AW	CGCGCG GGACTACVSGG GTATCTAAT
31	NEI7 endo	NE	2-3	Sph	S.lind	emrs	endo	sph	N69° 24' 40.968" E29° 7' 1.812"	AGAGTC CCTACGGGN GGCWGCAG	TCGAGA GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	TGTGAC GGACTACVSGG GTATCTAAT
32	NEI7 endo	NE	2-3	Sph	S.lind	emrs	endo	sph	N69° 24' 40.968" E29° 7' 1.812"	AGCTGA CCTACGGGN GGCWGCAG	CAGTCA GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	CGATAT GGACTACVSGG GTATCTAAT

33	KLO1 endo	MUE	KLO-o 1	Sph	S.mag	emrs	endo	sph	N53° 12' 22.896" E13° 7' 10.92"	ATCGAT CCTACGGGN GGCWGCAG	TCGAGA GACTACHVGG GTATCTAATCC	ATCGAT gYg CAS CAg KCg MgA AW	TGTGAC GGACTACVSGG GTATCTAAT
34	KLO1 endo	MUE	KLO-o 1	Sph	S.mag	emrs	endo	sph	N53° 12' 22.896" E13° 7' 10.92"	ATGCTA CCTACGGGN GGCWGCAG	CAGTCA GACTACHVGG GTATCTAATCC	ATGCTA gYg CAS CAg KCg MgA AW	CGATAT GGACTACVSGG GTATCTAAT
35	KLO1 endo	MUE	KLO-o 2	Sph	S.mag	emrs	endo	sph	N53° 12' 22.392" E13° 7' 10.2"	ATGCTA CCTACGGGN GGCWGCAG	GACTAG GACTACHVGG GTATCTAATCC	ATGCTA gYg CAS CAg KCg MgA AW	CGTATA GGACTACVSGG GTATCTAAT
36	KLO1 endo	MUE	KLO-o 2	Sph	S.mag	emrs	endo	sph	N53° 12' 22.392" E13° 7' 10.2"	ATGCTA CCTACGGGN GGCWGCAG	GAGATC GACTACHVGG GTATCTAATCC	ATGCTA gYg CAS CAg KCg MgA AW	TACGTA GGACTACVSGG GTATCTAAT
37	KLO2 endo	MUE	KLO-m 6	Sph	S.fall	emrs	endo	sph	N53° 12' 22.716" E13° 7' 9.516"	CACAGT CCTACGGGN GGCWGCAG	GTCACA GACTACHVGG GTATCTAATCC	CACAGT gYg CAS CAg KCg MgA AW	TCTCTC GGACTACVSGG GTATCTAAT
38	KLO2 endo	MUE	KLO-m 6	Sph	S.fall	emrs	endo	sph	N53° 12' 22.716" E13° 7' 9.516"	CACAGT CCTACGGGN GGCWGCAG	GTGTGT GACTACHVGG GTATCTAATCC	CACAGT gYg CAS CAg KCg MgA AW	TGCATG GGACTACVSGG GTATCTAAT
41	KIE2 endo	MUE	KIE 2	Sph	S.mag	emrs	endo	sph	N53° 13' 11.82" E13° 7' 1.956"	ATCGAT CCTACGGGN GGCWGCAG	GAGATC GACTACHVGG GTATCTAATCC	ATCGAT gYg CAS CAg KCg MgA AW	TACGTA GGACTACVSGG GTATCTAAT
45	TW1 endo	SV	TW 1	Amb	Amb	sub	endo	amb	N78° 33' 0.18" E11° 31' 39.144"	ACACGT CCTACGGGN GGCWGCAG	TCAGAG GACTACHVGG GTATCTAATCC	ACACGT gYg CAS CAg KCg MgA AW	TGACGT GGACTACVSGG GTATCTAAT

46	TW1 endo	SV	TW 1	Amb	Amb	sub	endo	amb	N78° 33' 0.18" E11° 31' 39.144"	ACACGT CCTACGGGN GGCWGCAG	TCGAGA GACTACHVGG GTATCTAATCC	ACACGT gYg CAS CAg KCg MgA AW	TGTGAC GGACTACVSGG GTATCTAAT
47	KIE3 endo	MUE	KIE 3	Sph	S.mag	emrs	endo	sph	N53° 13' 11.604" E13° 7' 1.884"	ATCGAT CCTACGGGN GGCWGCAG	GTCACA GACTACHVGG GTATCTAATCC	ATCGAT gYg CAS CAg KCg MgA AW	TCTCTC GGACTACVSGG GTATCTAAT
48	KIE3 endo	MUE	KIE 3	Sph	S.mag	emrs	endo	sph	N53° 13' 11.604" E13° 7' 1.884"	ATCGAT CCTACGGGN GGCWGCAG	GTGTGT GACTACHVGG GTATCTAATCC	ATCGAT gYg CAS CAg KCg MgA AW	TGCATG GGACTACVSGG GTATCTAAT
49	PP1 endo	SA	SuScor a	Amb	Scor	sub	endo	amb	N72° 22' 11.82" E12° 38' 53.722"	AGTCAG CCTACGGGN GGCWGCAG	CAGTCA GACTACHVGG GTATCTAATCC	AGTCAG gYg CAS CAg KCg MgA AW	CGATAT GGACTACVSGG GTATCTAAT
50	PP1 endo	SA	SuScor a	Amb	Scor	sub	endo	amb	N72° 22' 11.82" E12° 38' 53.722"	AGTCAG CCTACGGGN GGCWGCAG	CATGAC GACTACHVGG GTATCTAATCC	AGTCAG gYg CAS CAg KCg MgA AW	CGCGCG GGACTACVSGG GTATCTAAT
51	PP1 endo	SA	SuScor b	Amb	Scor	sub	endo	amb	N72° 22' 11.82" E12° 38' 53.722"	AGTCAG CCTACGGGN GGCWGCAG	GAGATC GACTACHVGG GTATCTAATCC	AGTCAG gYg CAS CAg KCg MgA AW	TACGTA GGACTACVSGG GTATCTAAT
52	PP1 endo	SA	SuScor b	Amb	Scor	sub	endo	amb	N72° 22' 11.82" E12° 38' 53.722"	AGTCAG CCTACGGGN GGCWGCAG	GATCGA GACTACHVGG GTATCTAATCC	AGTCAG gYg CAS CAg KCg MgA AW	TAGCAT GGACTACVSGG GTATCTAAT
53	PC endo	SA	S9	Amb	Amb	sub	endo	amb	N72° 22' 16.104" E12° 38' 56.4"	ATATCG CCTACGGGN GGCWGCAG	GAGATC GACTACHVGG GTATCTAATCC	ATATCG gYg CAS CAg KCg MgA AW	TACGTA GGACTACVSGG GTATCTAAT

54	PC endo	SA	S9	Amb	Amb	sub	endo	amb	N72° 22' 16.104" E12° 38' 56.4"	ATATCG CCTACGGGN GGCWGCAG	GATCGA GACTACHVGG GTATCTAATCC	ATATCG gYg CAS CAg KCg MgA AW	TAGCAT GGACTACVSGG GTATCTAAT
55	HEI2 endo	MUE	HEI 1	Sph	S.fall	emrs	endo	sph	N53° 12' 8.568" E13° 8' 45.996"	ACGTAC CCTACGGGN GGCWGCAG	GACTAG GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	TGACGT GGACTACVSGG GTATCTAAT
56	HEI2 endo	MUE	HEI 1	Sph	S.fall	emrs	endo	sph	N53° 12' 8.568" E13° 8' 45.996"	ACGTAC CCTACGGGN GGCWGCAG	GATCGA GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	TGTGAC GGACTACVSGG GTATCTAAT
57	HEI2 endo	MUE	HEI 3	Sph	S.fall	emrs	endo	sph	N53° 12' 8.136" E13° 8' 47.004"	ACTGCA CCTACGGGN GGCWGCAG	CATGAC GACTACHVGG GTATCTAATCC	AGTCAG gYg CAS CAg KCg MgA AW	CGTATA GGACTACVSGG GTATCTAAT
58	HEI2 endo	MUE	HEI 3	Sph	S.fall	emrs	endo	sph	N53° 12' 8.136" E13° 8' 47.004"	ACTGCA CCTACGGGN GGCWGCAG	GACTAG GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	TGCATG GGACTACVSGG GTATCTAAT
59	HEI1 endo	MUE	HEI 4	Sph	S.fall	sub	endo	sph	N53° 12' 7.128" E13° 8' 46.32"	ACTGCA CCTACGGGN GGCWGCAG	GATCGA GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	TGTGAC GGACTACVSGG GTATCTAAT
60	HEI1 endo	MUE	HEI 4	Sph	S.fall	sub	endo	sph	N53° 12' 7.128" E13° 8' 46.32"	ACTGCA CCTACGGGN GGCWGCAG	GTACAC GACTACHVGG GTATCTAATCC	AGTCAG gYg CAS CAg KCg MgA AW	CGATAT GGACTACVSGG GTATCTAAT
67	KLO2 Vasc	MUE	KLO-m 6	Vasc	Cx	emrs	Ref	sph	N53° 12' 22.716" E13° 7' 9.516"	CACAGT CCTACGGGN GGCWGCAG	TCAGAG GACTACHVGG GTATCTAATCC	CACAGT gYg CAS CAg KCg MgA AW	TGACGT GGACTACVSGG GTATCTAAT

68	KLO2 Vasc	MUE	KLO-m 6	Vasc	Cx	emrs	Ref	sph	N53° 12' 22.716" E13° 7' 9.516"	CACAGT CCTACGGGN GGCWGCAG	TCGAGA GACTACHVGG GTATCTAATCC	CACAGT gYg CAS CAg KCg MgA AW	TGTGAC GGACTACVSGG GTATCTAAT
69	NEI7 Vasc	NE	2-3	Vasc	Vasc	emrs	Ref	sph	N69° 24' 40.968" E29° 7' 1.812"	AGCTGA CCTACGGGN GGCWGCAG	GACTAG GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	TGTGAC GGACTACVSGG GTATCTAAT
70	NEI7 Vasc	NE	2-3	Vasc	Vasc	emrs	Ref	sph	N69° 24' 40.968" E29° 7' 1.812"	AGCTGA CCTACGGGN GGCWGCAG	GAGATC GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	TACGTA GGACTACVSGG GTATCTAAT
71	KIE Vasc	MUE	KIE 1	Vasc	Cx	emrs	Ref	sph	N53° 13' 11.316" E13° 7' 1.992"	ATCGAT CCTACGGGN GGCWGCAG	CAGTCA GACTACHVGG GTATCTAATCC	ATCGAT gYg CAS CAg KCg MgA AW	CGATAT GGACTACVSGG GTATCTAAT
72	KIE Vasc	MUE	KIE 1	Vasc	Cx	emrs	Ref	sph	N53° 13' 11.316" E13° 7' 1.992"	ATCGAT CCTACGGGN GGCWGCAG	CATGAC GACTACHVGG GTATCTAATCC	ATCGAT gYg CAS CAg KCg MgA AW	CGCGCG GGACTACVSGG GTATCTAAT
73	NEI6 Vasc	NE	2-2	Vasc	Cx	emrs	Ref	sph	N69° 24' 40.752" E2° 17' 28.239"	AGAGTC CCTACGGGN GGCWGCAG	GTGTGT GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	TGCATG GGACTACVSGG GTATCTAAT
74	NEI6 Vasc	NE	2-2	Vasc	Cx	emrs	Ref	sph	N69° 24' 40.752" E2° 17' 28.239"	AGAGTC CCTACGGGN GGCWGCAG	TCAGAG GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	TGACGT GGACTACVSGG GTATCTAAT
75	PP2 endo	SA	SuCar	Amb	Scor	sub	endo	amb	N72° 22' 11.82" E12° 38' 53.722"	AGTCAG CCTACGGGN GGCWGCAG	TCAGAG GACTACHVGG GTATCTAATCC	AGTCAG gYg CAS CAg KCg MgA AW	TGACGT GGACTACVSGG GTATCTAAT

76	PP2 endo	SA	SuCar	Amb	Scor	sub	endo	amb	N72° 22' 11.82" E12° 38' 53.722"	AGTCAG CCTACGGGN GGCWGCAG	TCGAGA GACTACHVGG GTATCTAATCC	AGTCAG gYg CAS CAg KCg MgA AW	TGTGAC GGACTACVSGG GTATCTAAT
77	HEI2 Vasc	MUE	HEI 1	Vasc	Erio	emrs	Ref	sph	N53° 12' 8.568" E13° 8' 45.996"	ACGTAC CCTACGGGN GGCWGCAG	GTCACA GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	CGCGCG GGACTACVSGG GTATCTAAT
78	HEI2 Vasc	MUE	HEI 1	Vasc	Erio	emrs	Ref	sph	N53° 12' 8.568" E13° 8' 45.996"	ACGTAC CCTACGGGN GGCWGCAG	GTGTGT GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	CGTATA GGACTACVSGG GTATCTAAT
86	PP2 epi	SA	SuCar	Amb	Scor	sub	epi	amb	N72° 22' 11.82" E12° 38' 53.722"	ATATCG CCTACGGGN GGCWGCAG	CAGTCA GACTACHVGG GTATCTAATCC	ATATCG gYg CAS CAg KCg MgA AW	CGATAT GGACTACVSGG GTATCTAAT
89	KLO1 epi	MUE	KLO-o 1	Sph	S.mag	emrs	epi	sph	N53° 12' 22.896" E13° 7' 10.92"	ATGCTA CCTACGGGN GGCWGCAG	CATGAC GACTACHVGG GTATCTAATCC	ATGCTA gYg CAS CAg KCg MgA AW	CGCGCG GGACTACVSGG GTATCTAAT
90	KLO1 epi	MUE	KLO-o 2	Sph	S.mag	emrs	epi	sph	N53° 12' 22.392" E13° 7' 10.2"	ATGCTA CCTACGGGN GGCWGCAG	GATCGA GACTACHVGG GTATCTAATCC	ATGCTA gYg CAS CAg KCg MgA AW	TAGCAT GGACTACVSGG GTATCTAAT
92	KLO2 epi	MUE	KLO-m 3	Sph	S.fall	emrs	epi	sph	N53° 12' 21.888" E13° 7' 10.524"	ATGCTA CCTACGGGN GGCWGCAG	TCGAGA GACTACHVGG GTATCTAATCC	ATGCTA gYg CAS CAg KCg MgA AW	TGTGAC GGACTACVSGG GTATCTAAT
93	KLO2 epi	MUE	KLO-m 4	Sph	S.fall	emrs	epi	sph	N53° 12' 21.888" E13° 7' 10.524"	CACAGT CCTACGGGN GGCWGCAG	GACTAG GACTACHVGG GTATCTAATCC	CACAGT gYg CAS CAg KCg MgA AW	CGTATA GGACTACVSGG GTATCTAAT

94	KLO2 epi	MUE	KLO-m 5	Sph	S.fall	emrs	epi	sph	N53° 12' 21.816" E13° 7' 8.904"	CACAGT CCTACGGGN GGCWGCAG	GTACAC GACTACHVGG GTATCTAATCC	CACAGT gYg CAS CAg KCg MgA AW	TATACG GGACTACVSGG GTATCTAAT
98	NEI1 epi	NE	1	Sph	S.rip	sub	epi	sph	N69° 24' 36" E29° 6' 36"	ACTGCA CCTACGGGN GGCWGCAG	GATCGA GACTACHVGG GTATCTAATCC	ACTGCA gYg CAS CAg KCg MgA AW	TAGCAT GGACTACVSGG GTATCTAAT
99	NEI5 epi	NE	2	Sph	S.lind	emrs	epi	sph	N69° 24' 36" E29° 6' 36"	AGAGTC CCTACGGGN GGCWGCAG	CATGAC GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	CGCGCG GGACTACVSGG GTATCTAAT
101	NEI6 epi	NE	2-2	Sph	S.lind	emrs	epi	sph	N69° 24' 40.752" E2° 17' 28.239"	ATATCG CCTACGGGN GGCWGCAG	GTCACA GACTACHVGG GTATCTAATCC	ATATCG gYg CAS CAg KCg MgA AW	TGCATG GGACTACVSGG GTATCTAAT
102	NEI7 epi	NE	2-3	Sph	S.rip	emrs	epi	sph	N69° 24' 40.968" E29° 7' 1.812"	AGCTGA CCTACGGGN GGCWGCAG	CATGAC GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	CGCGCG GGACTACVSGG GTATCTAAT
103	NEI2 epi	NE	4	Sph	S.rip	sub	epi	sph	N69° 24' 36" E29° 7' 12"	ACACGT CCTACGGGN GGCWGCAG	GAGATC GACTACHVGG GTATCTAATCC	ACTGCA gYg CAS CAg KCg MgA AW	TGTGAC GGACTACVSGG GTATCTAAT
105	NEI4 epi	NE	4-2	Sph	S.rip	sub	epi	sph	N69° 24' 38.34" E29° 7' 15.6"	ACACGT CCTACGGGN GGCWGCAG	TCGAGA GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	TAGCAT GGACTACVSGG GTATCTAAT
106	NEI3 epi	NE	6	Sph	S.rip	sub	epi	sph	N69° 24' 38.988" E2° 54' 43.106"	AGCTGA CCTACGGGN GGCWGCAG	GTCACA GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	TCTCTC GGACTACVSGG GTATCTAAT

107	GLU1 epi	SV	GLU 1	Amb	Amb	sub	epi	amb	N78° 32' 48.948" E12° 2' 51.576"	ATATCG CCTACGGGN GGCWGCAG	CAGTCA GACTACHVGG GTATCTAATCC	ATATCG gYg CAS CAg KCg MgA AW	CGCGCG GGACTACVSGG GTATCTAAT
109	GLU2 epi	SV	GLU 2	Amb	Amb	sub	epi	amb	N78° 32' 48.948" E12° 2' 51.576"	ACACGT CCTACGGGN GGCWGCAG	GTACAC GACTACHVGG GTATCTAATCC	ACACGT gYg CAS CAg KCg MgA AW	TATACG GGACTACVSGG GTATCTAAT
111	HEI2 epi	MUE	HEI 1	Sph	S.fall	emrs	epi	sph	N53° 12' 8.568" E13° 8' 45.996"	ACGTAC CCTACGGGN GGCWGCAG	GTACAC GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	CGATAT GGACTACVSGG GTATCTAAT
112	HEI2 epi	MUE	HEI 2	Sph	S.fall	emrs	epi	sph	N53° 12' 8.46" E13° 8' 45.924"	ACTGCA CCTACGGGN GGCWGCAG	CAGTCA GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	TATACG GGACTACVSGG GTATCTAAT
114	HEI2 epi	MUE	HEI 3	Sph	S.fall	emrs	epi	sph	N53° 12' 8.136" E13° 8' 47.004"	ACTGCA CCTACGGGN GGCWGCAG	GAGATC GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	TGACGT GGACTACVSGG GTATCTAAT
116	HEI1 epi	MUE	HEI 4	Sph	S.fall	sub	epi	sph	N53° 12' 7.128" E13° 8' 46.32"	ACTGCA CCTACGGGN GGCWGCAG	GTCACA GACTACHVGG GTATCTAATCC	AGTCAG gYg CAS CAg KCg MgA AW	CGCGCG GGACTACVSGG GTATCTAAT
118	KIE epi	MUE	KIE 1	Sph	S.mag	emrs	epi	sph	N53° 13' 11.316" E13° 7' 1.992"	ATCGAT CCTACGGGN GGCWGCAG	GACTAG GACTACHVGG GTATCTAATCC	ATCGAT gYg CAS CAg KCg MgA AW	CGTATA GGACTACVSGG GTATCTAAT
119	KIE2 epi	MUE	KIE 2	Sph	S.mag	emrs	epi	sph	N53° 13' 11.82" E13° 7' 1.956"	ATCGAT CCTACGGGN GGCWGCAG	GTACAC GACTACHVGG GTATCTAATCC	ATCGAT gYg CAS CAg KCg MgA AW	TATACG GGACTACVSGG GTATCTAAT

121	KIE3 endo	MUE	KIE 3	Sph	S.mag	emrs	epi	sph	N53° 13' 11.604" E13° 7' 1.884"	ATCGAT CCTACGGGN GGCWGCAG	TCAGAG GACTACHVGG GTATCTAATCC	ATCGAT gYg CAS CAg KCg MgA AW	TGACGT GGACTACVSGG GTATCTAAT
123	TW2 epi	SV	TW 2	Amb	Amb	sub	epi	amb	N78° 33' 0.18" E11° 31' 39.144"	ACGTAC CCTACGGGN GGCWGCAG	GAGATC GACTACHVGG GTATCTAATCC	ACGTAC gYg CAS CAg KCg MgA AW	TACGTA GGACTACVSGG GTATCTAAT
124	TW1 epi	SV	TW 1	Amb	Amb	sub	epi	amb	N78° 33' 0.18" E11° 31' 39.144"	ACGTAC CCTACGGGN GGCWGCAG	CAGTCA GACTACHVGG GTATCTAATCC	ACGTAC gYg CAS CAg KCg MgA AW	CGATAT GGACTACVSGG GTATCTAAT
125	PC epi	SA	S9	Amb	Amb	sub	epi	amb	N72° 22' 16.104" E12° 38' 56.4"	ATATCG CCTACGGGN GGCWGCAG	GTACAC GACTACHVGG GTATCTAATCC	ATATCG gYg CAS CAg KCg MgA AW	TATACG GGACTACVSGG GTATCTAAT
126	PP1 epi	SA	SuScor a	Amb	Scor	sub	epi	amb	N72° 22' 11.82" E12° 38' 53.722"	AGTCAG CCTACGGGN GGCWGCAG	GACTAG GACTACHVGG GTATCTAATCC	AGTCAG gYg CAS CAg KCg MgA AW	CGTATA GGACTACVSGG GTATCTAAT
127	PP1 epi	SA	SuScor b	Amb	Scor	sub	epi	amb	N72° 22' 11.82" E12° 38' 53.722"	AGTCAG CCTACGGGN GGCWGCAG	GTACAC GACTACHVGG GTATCTAATCC	AGTCAG gYg CAS CAg KCg MgA AW	TATACG GGACTACVSGG GTATCTAAT
128	GLU Sed	SV	GLU	Sed	Sed	sub	Ref	amb	N78° 32' 48.948" E12° 2' 51.576"	ACACGT CCTACGGGN GGCWGCAG	GTCACA GACTACHVGG GTATCTAATCC	ACACGT gYg CAS CAg KCg MgA AW	TCTCTC GGACTACVSGG GTATCTAAT
129	GLU Sed	SV	GLU	Sed	Sed	sub	Ref	amb	N78° 32' 48.948" E12° 2' 51.576"	ACACGT CCTACGGGN GGCWGCAG	GTGTGT GACTACHVGG GTATCTAATCC	ACACGT gYg CAS CAg KCg MgA AW	TGCATG GGACTACVSGG GTATCTAAT

130	TW Sed	SV	TW	Sed	Sed	sub	Ref	amb	N78° 33' 0.18" E11° 31' 39.144"	ACGTAC CCTACGGGN GGCWGCAG	GATCGA GACTACHVGG GTATCTAATCC	ATATCG gYg CAS CAg KCg MgA AW	CGTATA GGACTACVSGG GTATCTAAT
131	TW Sed	SV	TW	Sed	Sed	sub	Ref	amb	N78° 33' 0.18" E11° 31' 39.144"	ACGTAC CCTACGGGN GGCWGCAG	GTACAC GACTACHVGG GTATCTAATCC	ATATCG gYg CAS CAg KCg MgA AW	TACGTA GGACTACVSGG GTATCTAAT
132	KLO1 Vasc	MUE	KLO-o 2	Vasc	Erio	emrs	Ref	sph	N53° 12' 22.392" E13° 7' 10.2"	ATATCG CCTACGGGN GGCWGCAG	TCAGAG GACTACHVGG GTATCTAATCC	ATATCG gYg CAS CAg KCg MgA AW	TGTGAC GGACTACVSGG GTATCTAAT
133	KLO1 Vasc	MUE	KLO-o 2	Vasc	Erio	emrs	Ref	sph	N53° 12' 22.392" E13° 7' 10.2"	ATGCTA CCTACGGGN GGCWGCAG	GTCACA GACTACHVGG GTATCTAATCC	ATGCTA gYg CAS CAg KCg MgA AW	TCTCTC GGACTACVSGG GTATCTAAT
134	KNU1 endo	SV	KNU 1	Amb	Amb	sub	endo	amb	N78° 33' 55.584" E11° 29' 25.98"	ACGTAC CCTACGGGN GGCWGCAG	GTCACA GACTACHVGG GTATCTAATCC	ATATCG gYg CAS CAg KCg MgA AW	TAGCAT GGACTACVSGG GTATCTAAT
135	KNU1 endo	SV	KNU 1	Amb	Amb	sub	endo	amb	N78° 33' 55.584" E11° 29' 25.98"	ACGTAC CCTACGGGN GGCWGCAG	GTGTGT GACTACHVGG GTATCTAATCC	ACGTAC gYg CAS CAg KCg MgA AW	TGCATG GGACTACVSGG GTATCTAAT
136	KNU2 endo	SV	KNU 2	Amb	Amb	sub	endo	amb	N78° 33' 55.584" E11° 29' 25.98"	ACGTAC CCTACGGGN GGCWGCAG	TCGAGA GACTACHVGG GTATCTAATCC	ACGTAC gYg CAS CAg KCg MgA AW	TGTGAC GGACTACVSGG GTATCTAAT
137	KNU2 endo	SV	KNU 2	Amb	Amb	sub	endo	amb	N78° 33' 55.584" E11° 29' 25.98"	ACTGCA CCTACGGGN GGCWGCAG	CAGTCA GACTACHVGG GTATCTAATCC	ACTGCA gYg CAS CAg KCg MgA AW	CGATAT GGACTACVSGG GTATCTAAT

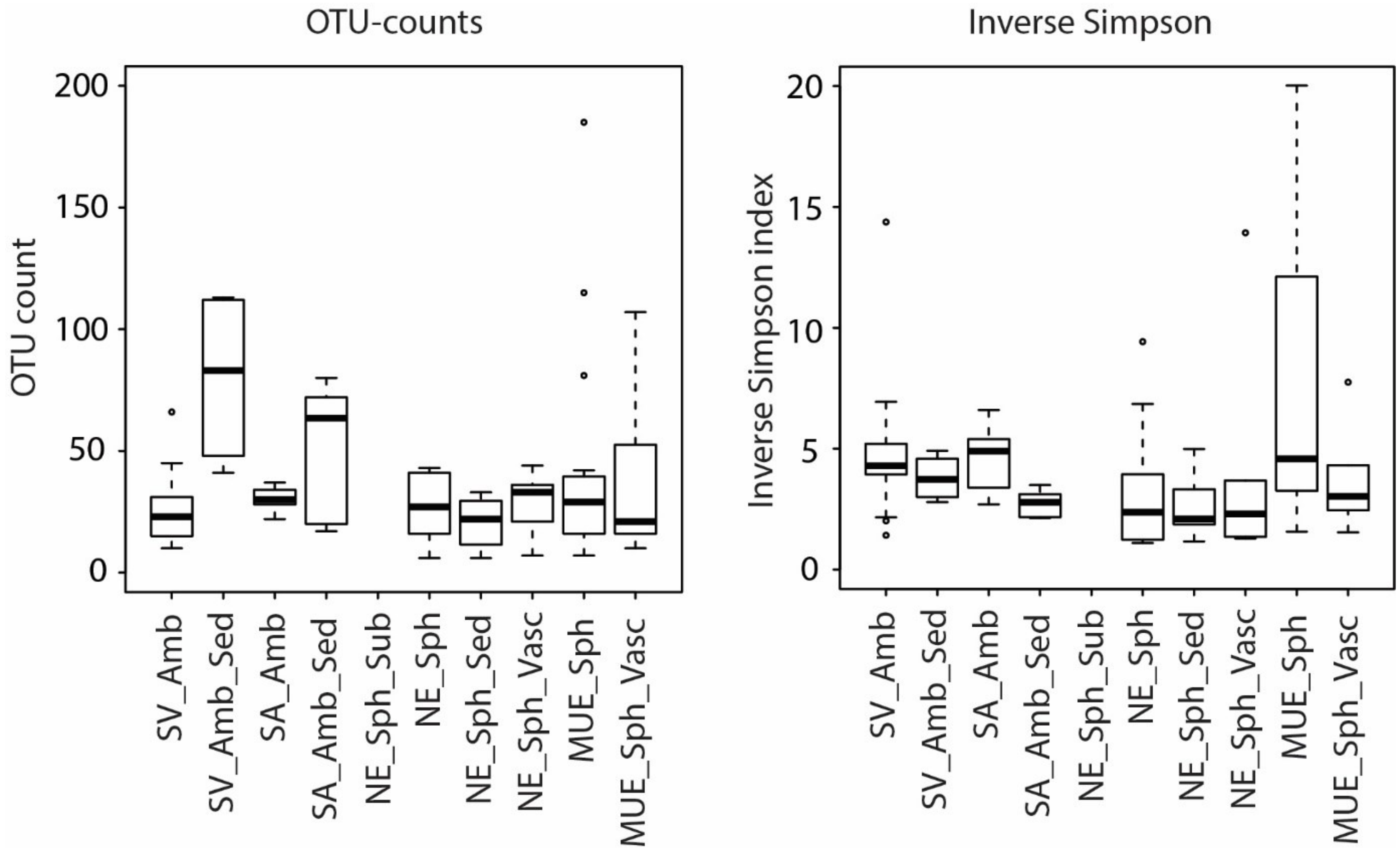
138	PP1 Sed	SA	SuScor	Sed	Sed	sub	Ref	amb	N72° 22' 11.82" E12° 38' 53.722"	AGTCAG CCTACGGGN GGCWGCAG	GTCACA GACTACHVGG GTATCTAATCC	AGTCAG gYg CAS CAg KCg MgA AW	TCTCTC GGACTACVSGG GTATCTAAT
139	PP2 Sed	SA	SuScor	Sed	Sed	sub	Ref	amb	N72° 22' 11.82" E12° 38' 53.722"	AGTCAG CCTACGGGN GGCWGCAG	GTGTGT GACTACHVGG GTATCTAATCC	AGTCAG gYg CAS CAg KCg MgA AW	TGCATG GGACTACVSGG GTATCTAAT
140	PP2 Sed	SA	SuCar	Sed	Sed	sub	Ref	amb	N72° 22' 11.82" E12° 38' 53.722"	ATATCG CCTACGGGN GGCWGCAG	CATGAC GACTACHVGG GTATCTAATCC	ATATCG gYg CAS CAg KCg MgA AW	CGCGCG GGACTACVSGG GTATCTAAT
141	PP2 Sed	SA	SuCar	Sed	Sed	sub	Ref	amb	N72° 22' 11.82" E12° 38' 53.722"	ATATCG CCTACGGGN GGCWGCAG	GACTAG GACTACHVGG GTATCTAATCC	ATATCG gYg CAS CAg KCg MgA AW	CGTATA GGACTACVSGG GTATCTAAT
142	NEI1 Vasc	NE	1	Vasc	Erio	emrs	Ref	sph	N69° 24' 36" E29° 6' 36"	ACTGCA CCTACGGGN GGCWGCAG	GTACAC GACTACHVGG GTATCTAATCC	ACTGCA gYg CAS CAg KCg MgA AW	TATACG GGACTACVSGG GTATCTAAT
143	NEI1 Vasc	NE	1	Vasc	Erio	emrs	Ref	sph	N69° 24' 36" E29° 6' 36"	ACTGCA CCTACGGGN GGCWGCAG	GTCACA GACTACHVGG GTATCTAATCC	ACTGCA gYg CAS CAg KCg MgA AW	TCTCTC GGACTACVSGG GTATCTAAT
144	NEI5 Cx	NE	2	Vasc	Cx	emrs	Ref	sph	N69° 24' 36" E29° 6' 36"	AGAGTC CCTACGGGN GGCWGCAG	GACTAG GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	CGTATA GGACTACVSGG GTATCTAAT
145	NEI5 Cx	NE	2	Vasc	Cx	emrs	Ref	sph	N69° 24' 36" E29° 6' 36"	AGAGTC CCTACGGGN GGCWGCAG	GAGATC GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	TACGTA GGACTACVSGG GTATCTAAT

146	PC Sed	SA	S9	Sed	Sed	sub	Ref	amb	N72° 22' 16.104" E12° 38' 56.4"	ATATCG CCTACGGGN GGCWGCAG	GTCACA GACTACHVGG GTATCTAATCC	ATATCG gYg CAS CAg KCg MgA AW	TCTCTC GGACTACVSGG GTATCTAAT
147	PC Sed	SA	S9	Sed	Sed	sub	Ref	amb	N72° 22' 16.104" E12° 38' 56.4"	ATATCG CCTACGGGN GGCWGCAG	GTGTGT GACTACHVGG GTATCTAATCC	ATATCG gYg CAS CAg KCg MgA AW	TGCATG GGACTACVSGG GTATCTAAT
148	NEI1 Sed	NE	1	Sed	Sed	sub	Ref	sph	N69° 24' 36" E29° 6' 36"	ACTGCA CCTACGGGN GGCWGCAG	GTGTGT GACTACHVGG GTATCTAATCC	ACTGCA gYg CAS CAg KCg MgA AW	TGCATG GGACTACVSGG GTATCTAAT
149	NEI1 Sed	NE	1	Sed	Sed	sub	Ref	sph	N69° 24' 36" E29° 6' 36"	ACTGCA CCTACGGGN GGCWGCAG	TCAGAG GACTACHVGG GTATCTAATCC	ACTGCA gYg CAS CAg KCg MgA AW	TGACGT GGACTACVSGG GTATCTAAT
150	NEI2 Sed	NE	4	Sed	Sed	sub	Ref	sph	N69° 24' 36" E29° 7' 12"	ACACGT CCTACGGGN GGCWGCAG	GATCGA GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	CGATAT GGACTACVSGG GTATCTAAT
151	NEI2 Sed	NE	4	Sed	Sed	sub	Ref	sph	N69° 24' 36" E29° 7' 12"	ACACGT CCTACGGGN GGCWGCAG	GTCACA GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	CGCGCG GGACTACVSGG GTATCTAAT
152	NEI4 Sed	NE	4-2	Sed	Sed	sub	Ref	sph	N69° 24' 38.34" E29° 7' 15.6"	ACGTAC CCTACGGGN GGCWGCAG	CAGTCA GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	TATACG GGACTACVSGG GTATCTAAT
153	NEI4 Sed	NE	4-2	Sed	Sed	sub	Ref	sph	N69° 24' 38.34" E29° 7' 15.6"	ACGTAC CCTACGGGN GGCWGCAG	CATGAC GACTACHVGG GTATCTAATCC	AGAGTC gYg CAS CAg KCg MgA AW	TGCATG GGACTACVSGG GTATCTAAT

154	NEI3 Sed	NE	6	Sed	Sed	sub	Ref	sph	N69° 24' 38.988" E2° 54' 43.106"	AGCTGA CCTACGGGN GGCWGCAG	GTGTGT GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	TGCATG GGACTACVSGG GTATCTAAT
155	NEI3 Sed	NE	6	Sed	Sed	sub	Ref	sph	N69° 24' 38.988" E2° 54' 43.106"	AGCTGA CCTACGGGN GGCWGCAG	TCAGAG GACTACHVGG GTATCTAATCC	AGCTGA gYg CAS CAg KCg MgA AW	TGACGT GGACTACVSGG GTATCTAAT
156	KNU1 epi	SV	KNU 1	Amb	Amb	sub	epi	amb	N78° 32' 48.948" E12° 2' 51.576"	ACGTAC CCTACGGGN GGCWGCAG	TCAGAG GACTACHVGG GTATCTAATCC	ACGTAC gYg CAS CAg KCg MgA AW	TGACGT GGACTACVSGG GTATCTAAT
157	KNU2 epi	SV	KNU 2	Amb	Amb	sub	epi	amb	N78° 32' 48.948" E12° 2' 51.576"	ACTGCA CCTACGGGN GGCWGCAG	CATGAC GACTACHVGG GTATCTAATCC	ACTGCA gYg CAS CAg KCg MgA AW	CGCGCG GGACTACVSGG GTATCTAAT

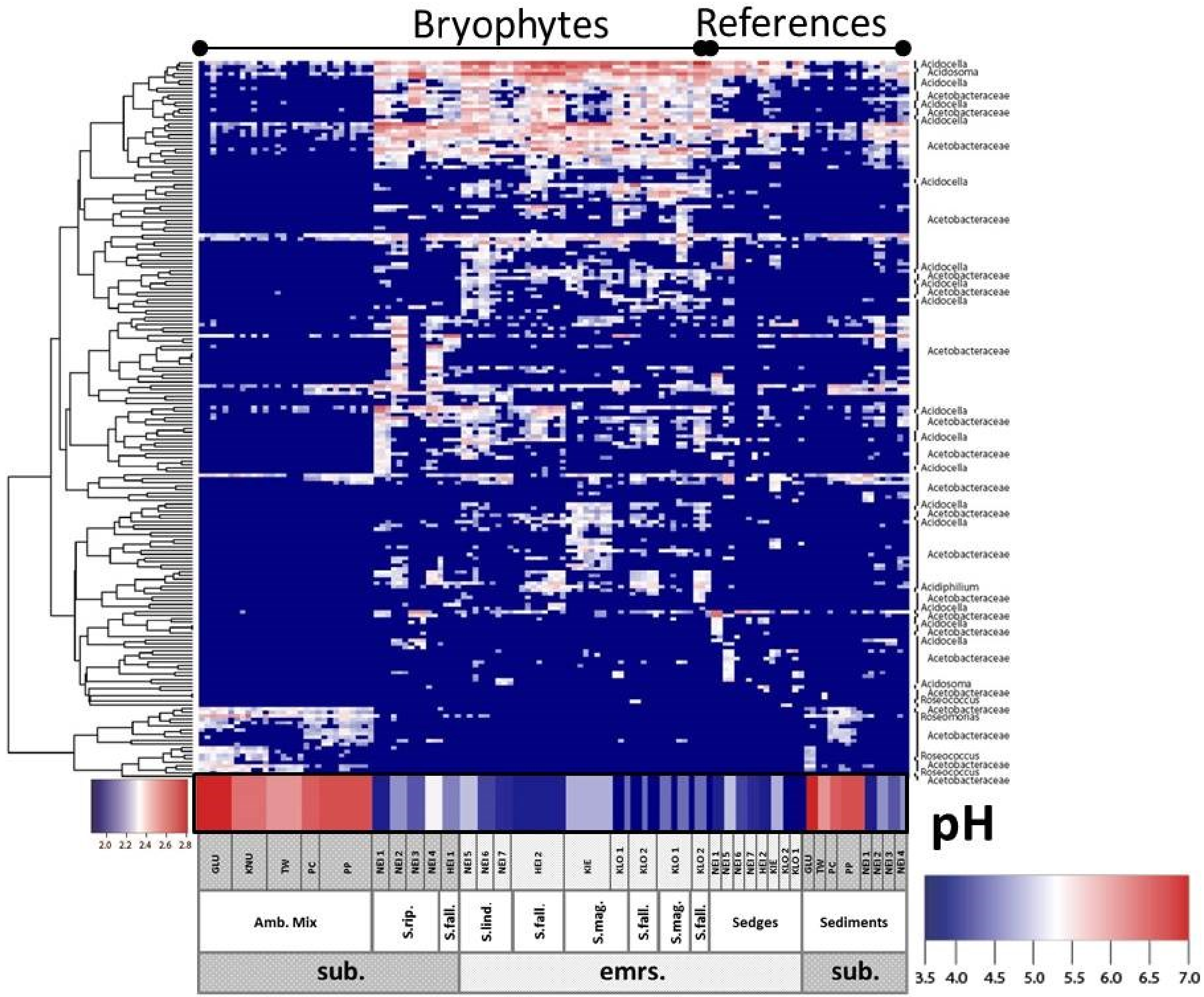
v. Figure S2: Archaeal alpha-diversities.

Box plots illustrating archaeal alpha-diversities for Amblystegiaceae (Amb), sediment references to Amblystegiaceae (Amb_Sed), *Sphagnum* (Sph), sediment references to *Sphagnum* (Sph_Sed) and vascular plant references to *Sphagnum* (Sph_Vasc). A: Observed OTU; B: Calculated Inverse Simpson Index. Graph: Alexander T. Tveit



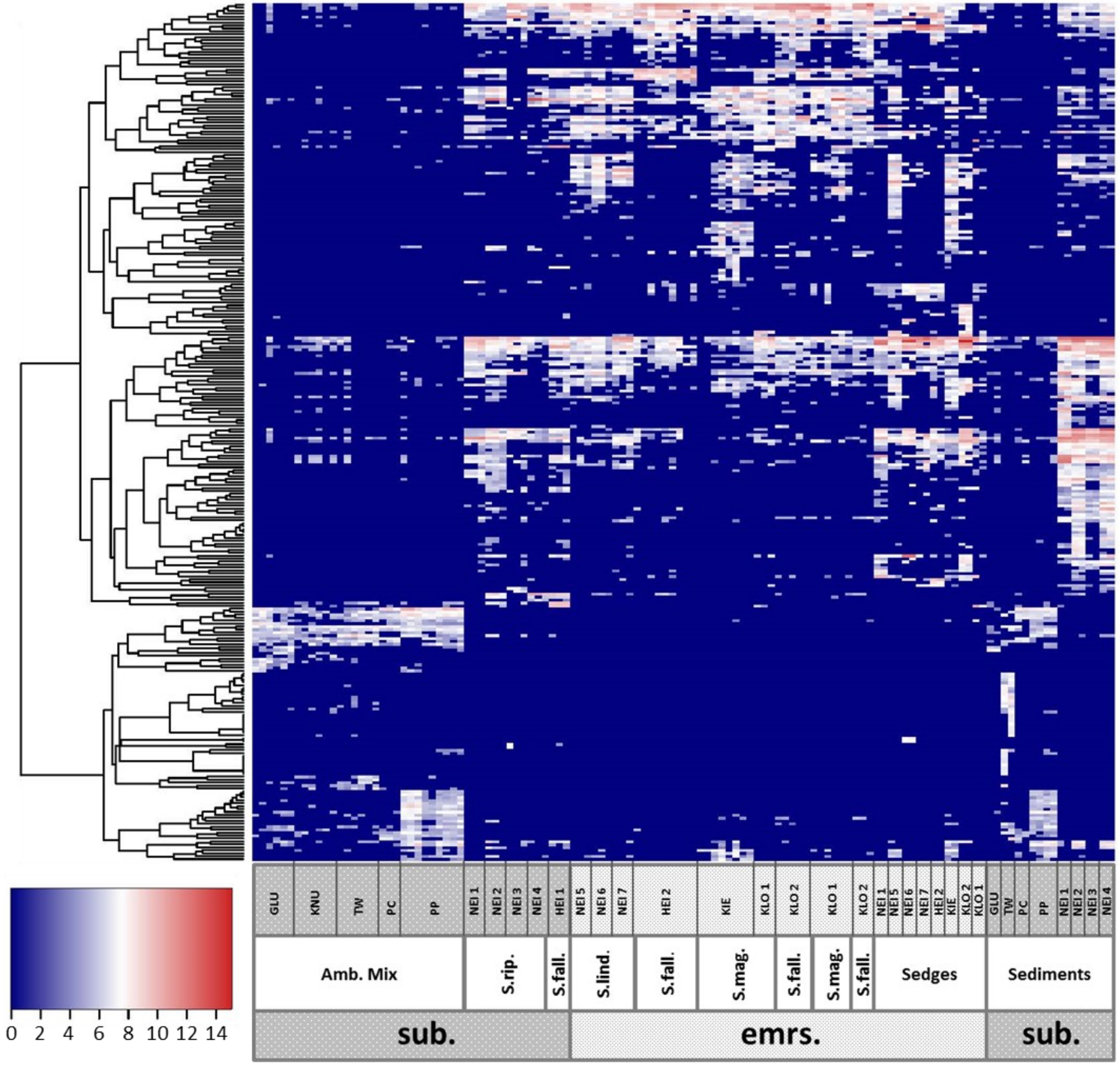
vi. Figure S3: Heatmap overview of OTUs within Acetobacteraceae.

For each heatmap: The color intensity of the main heatmap (at the top left of both heatmaps) corresponds to the binary logarithm of the relative abundance of the OTU multiplied by 100,000. Pearson correlation was used as the basis for the hierarchical clustering of OTUs in the heatmap. The color intensity of the pH heatmap corresponds to the pH. The samples are sorted by ecosystem types and latitude from left to right. sub. = submerged. emrs. = emerged/above the water table. Amb. Mix. = a mix of *Amblystegiaceae*. S. rip. = *Sphagnum riparium*. S. fall. = *Sphagnum fallax.* S. mag = *Sphagnum magellanicum*. S. lind. = *Sphagnum lindbergii.*



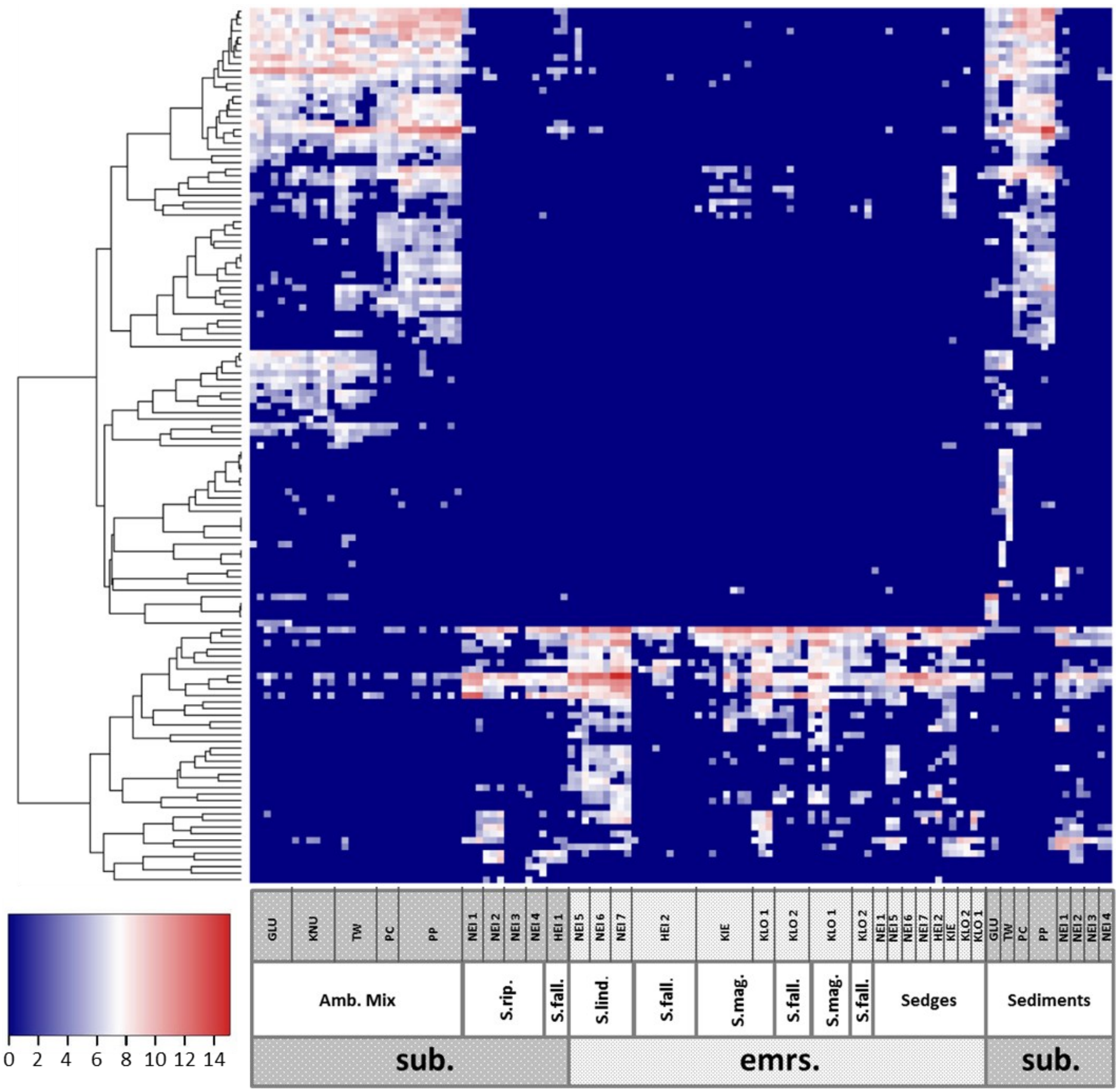
vii. Figure S4: Heatmap overview of OTUs within Acidobacteria.

The color intensity of the main heatmap corresponds to the binary logarithm of the average relative abundance of the OTU multiplied by 100,000. Pearson correlation was used as the basis for the hierarchical clustering of OTUs in the heatmap. The samples are sorted by ecosystem types and latitude from left to right. sub. = submerged. emrs. = emerged/above the water table. Amb. Mix. = a mix of *Amblystegiaceae*. S. rip. = *Sphagnum riparium*. S. fall. = *Sphagnum fallax*. S. mag = *Sphagnum magellanicum*. S. lind. = *Sphagnum lindbergii*.



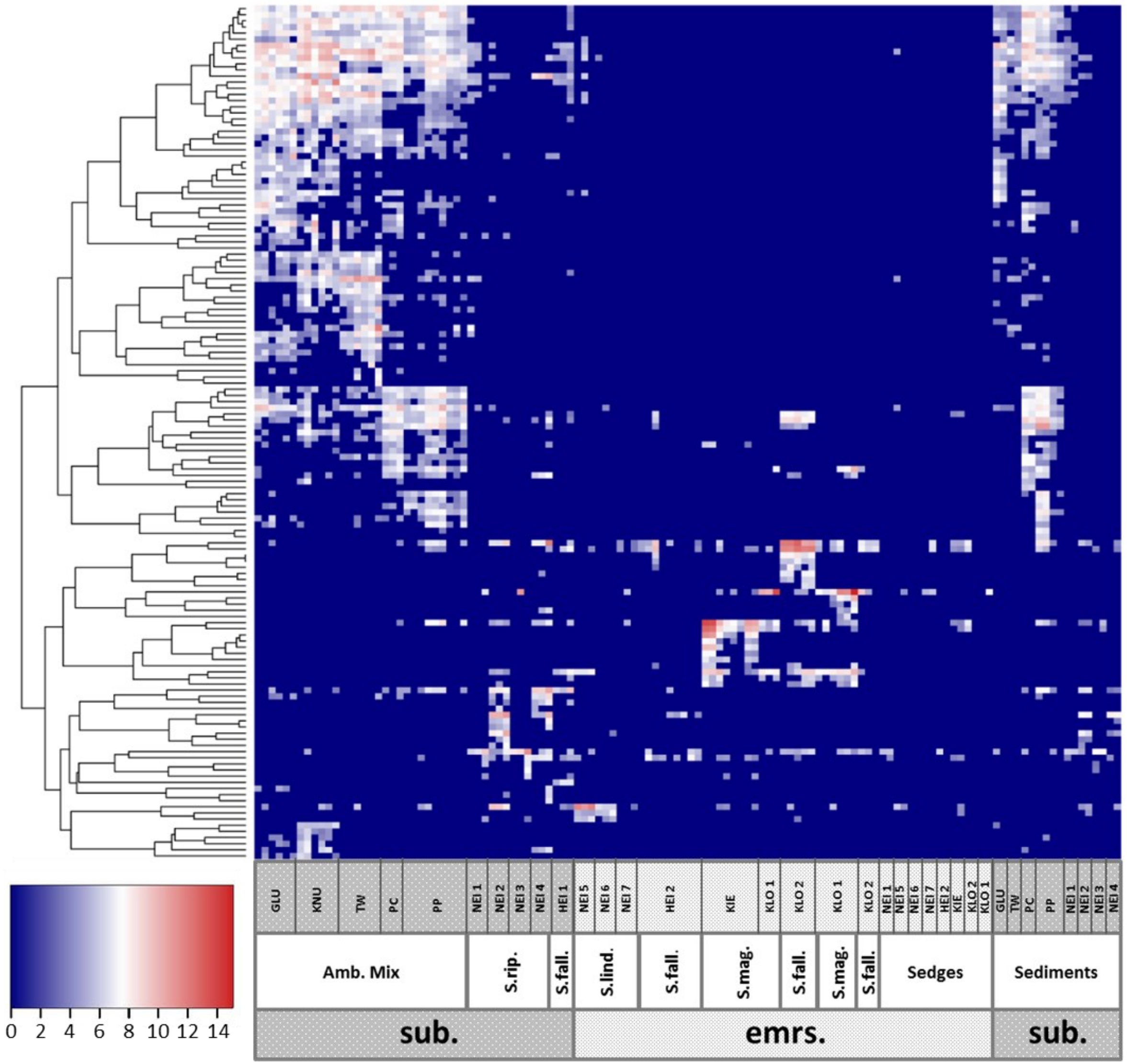
viii. Figure S5: Heatmap overview of OTUs within Acidimicrobiales.

The color intensity of the main heatmap corresponds to the binary logarithm of the average relative abundance of the OTU multiplied by 100,000. Pearson correlation was used as the basis for the hierarchical clustering of OTUs in the heat map. The samples are sorted by ecosystem types and latitude from left to right. sub. = submerged. emrs. = emerged/above the water table. Amb. Mix. = a mix of *Amblystegiaceae*. S. rip. = *Sphagnum riparium*. S. fall. = *Sphagnum fallax*. S. mag = *Sphagnum magellanicum*. S. lind. = *Sphagnum lindbergii*.



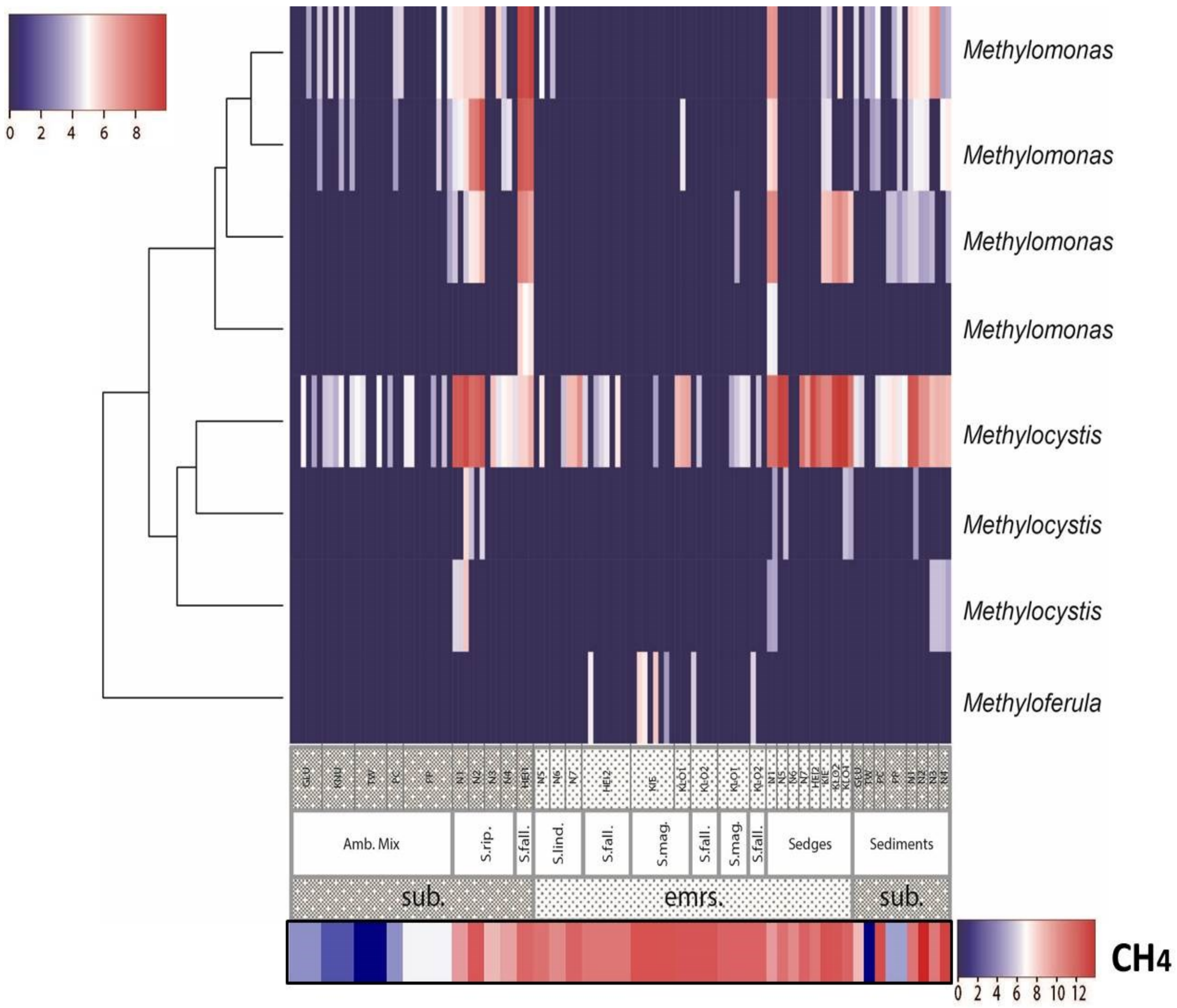
ix. Figure S6: Heatmap overview of OTUs within Cyanobacteria.

The color intensity of the main heatmap corresponds to the binary logarithm of the average relative abundance of the OTU multiplied by 100,000. Pearson correlation was used as the basis for the hierarchical clustering of OTUs in the heatmap. The samples are sorted by ecosystem types and latitude from left to right. sub. = submerged. emrs. = emerged/above the water table. Amb. Mix. = a mix of *Amblystegiaceae*. S. rip. = *Sphagnum riparium*. S. fall. = *Sphagnum fallax*. S. mag = *Sphagnum magellanicum*. S. lind. = *Sphagnum lindbergii*.



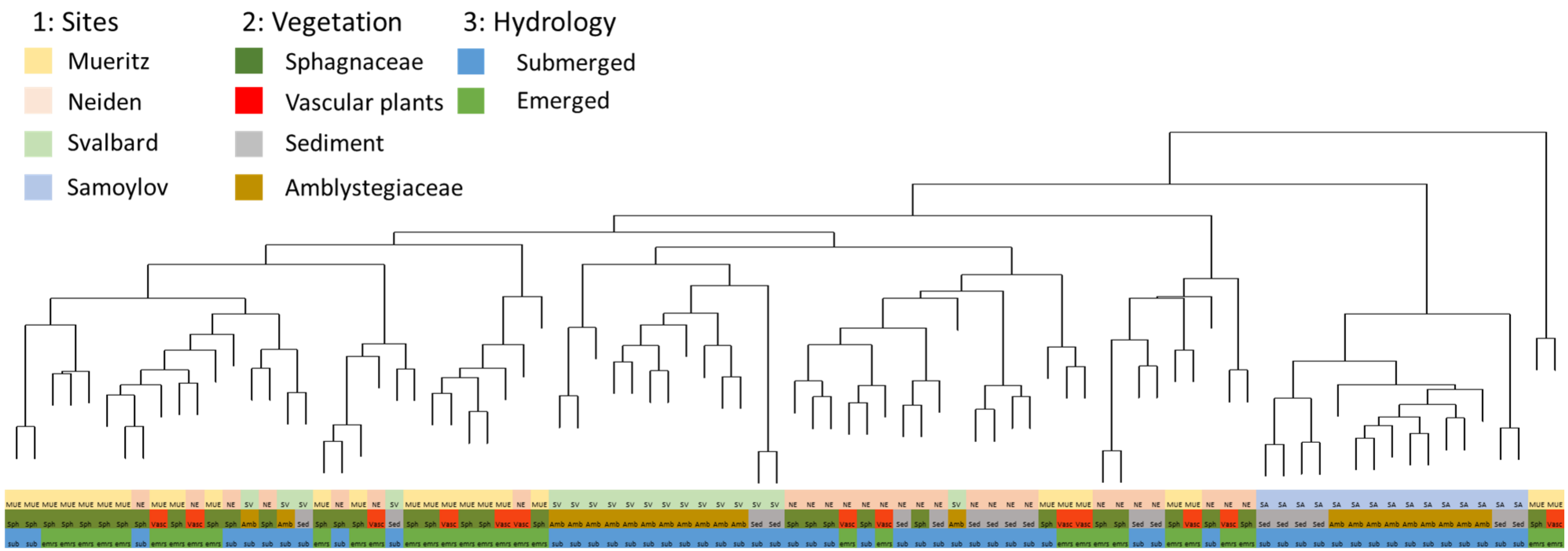
x. Figure S7: Heat map overview of OTUs within methanotrophic bacteria.

The color intensity of the main heatmap (at the top left of both heatmaps) corresponds to the binary logarithm of the relative abundance of the OTU multiplied by 100,000. Pearson correlation was used as the basis for the hierarchical clustering of OTUs in the heatmap. The color intensity of the CH_4 heatmap corresponds to the binary logarithm of the pore water CH_4 concentration. The samples are sorted by ecosystem types and latitude from left to right. sub. = submerged. emrs. = emerged/above the water table. Amb. Mix. = a mix of *Amblystegiaceae*. S. rip. = *Sphagnum riparium*. S. fall. = *Sphagnum fallax*. S. mag = *Sphagnum magellanicum*. S. Lind. = *Sphagnum lindbergii.* All OTUs taxonomically assigned as potential MOB (it means all Methylocystaceae and all Methylococcales) were manually blasted in NCBI for their closest relative. Only OTUs that were confirmed to be MOB were used for constructing this heatmap.



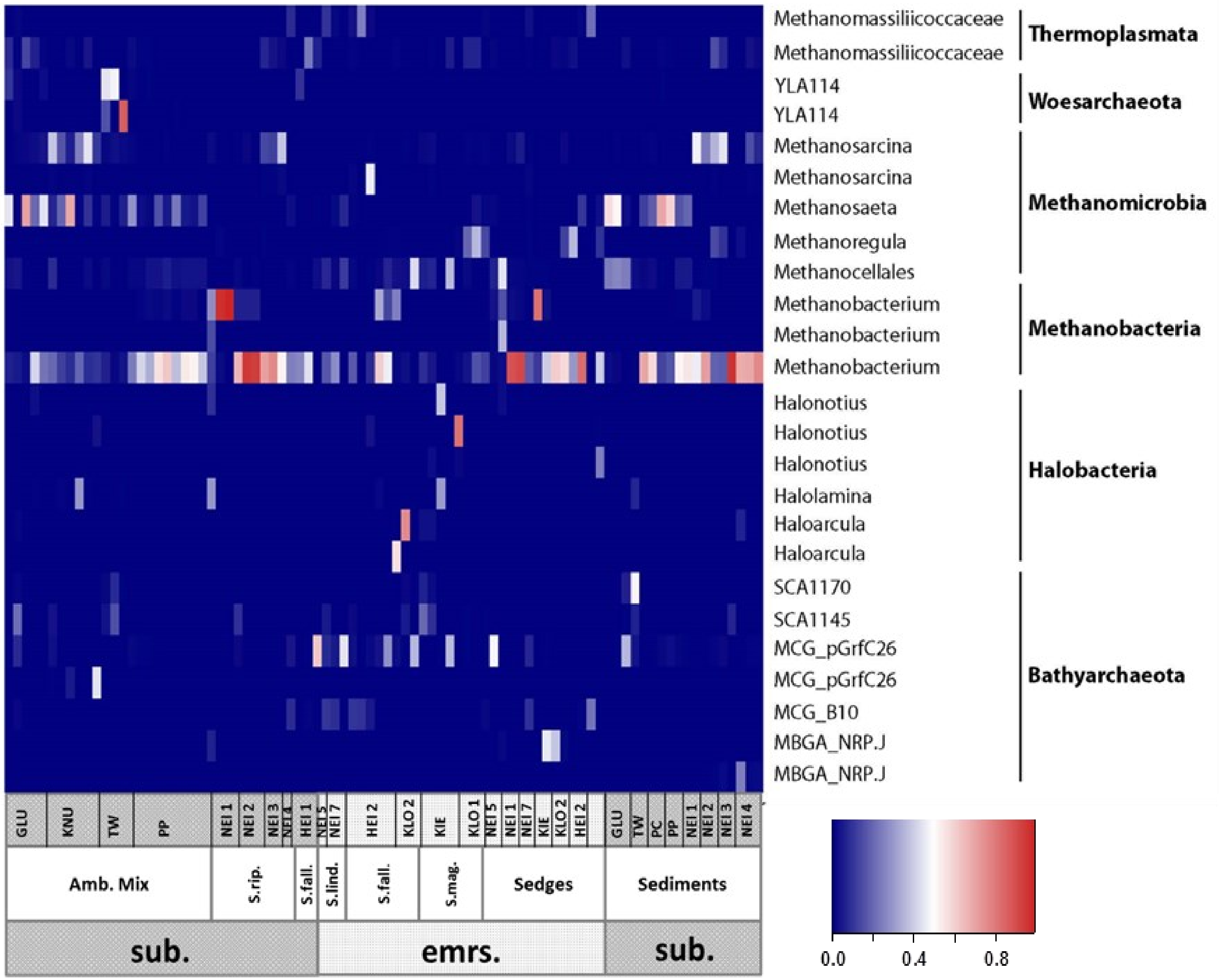
xi. **Figure S8: Dendrogram showing the clustering of archaeal communities (OTU at 97% sequence similarity) in relation to the characteristics of their respective environments.**

Each node of the dendrogram corresponds to the community profile of a moss, vascular plant or sediment sample. All possible pairwise pearson correlation factors were calculated from the community profiles and the resulting distance matrix used to cluster the samples applying the agnes hierarchical clustering algorithm.



xii. **Figure S9: Heatmap overview of the OTUs within archaea at above 0.1% relative abundance (out of total sequences assigned to Archaea) in one or more samples.**

The color intensity corresponds to the binary logarithm of the average relative abundance of the OTU multiplied by 100,000. Pearson correlation was used as the basis for the hierarchical clustering of OTUs in the heatmap. The samples are sorted by ecosystem types and latitude from left to right. sub. = submerged. emrs. = emerged/above the water table. Amb. Mix. = a mix of *Amblystegiaceae*. S. rip. = *Sphagnum riparium*. S. fall. = *Sphagnum fallax*. S. mag = *Sphagnum magellanicum*. S. lind. = *Sphagnum lindbergii*.



xiii. Supplementary Table S2:

Core microbiomes of Amblystegiaceae and Sphagnum ecosystems (A), different moss types within these (B) and intersects between the moss core microbiomes (C). Letters A-F in (C) refers to letters A-F in (B) column one.

S2 A	OTU total	OTU core	Number of Amplicon libraries	Threshold for core microbiome calculation	Contribution to relative abundance
Total ecosystem	13799	49	122	66 %	1 - 65%
Total moss	10930	52	88	66 %	2 - 60%
Sphagnum ecosystem	7197	119	82	66 %	16 - 83%
Sphagnum moss	5669	142	58	66 %	22 - 84%
Amblystegiaceae ecosystem	7612	322	40	66 %	20 - 77%
Amblystegiaceae moss	6057	348	30	66 %	44 - 78%

S2 B	Site	OTU total	OTU core	Number of Amplicon libraries	Threshold for core microbiome calculation	Contribution to relative abundance
A - Mosses svalbard	SV	4681	295	18	75 %	44 - 76%
B - Scorpidium	SA	3022	548	12	75 %	66 - 83%
C - Sphagnum riparium	NE	1905	126	12	75 %	36 - 88%
D - Sphagum fallax	MUE	2689	132	20	75 %	34 - 84%
E - Sphagnum lindbergii	NE	1560	252	9	75 %	60 - 90%
F - Sphagnum magellanicum	MUE	2888	154	17	75 %	25 - 75%

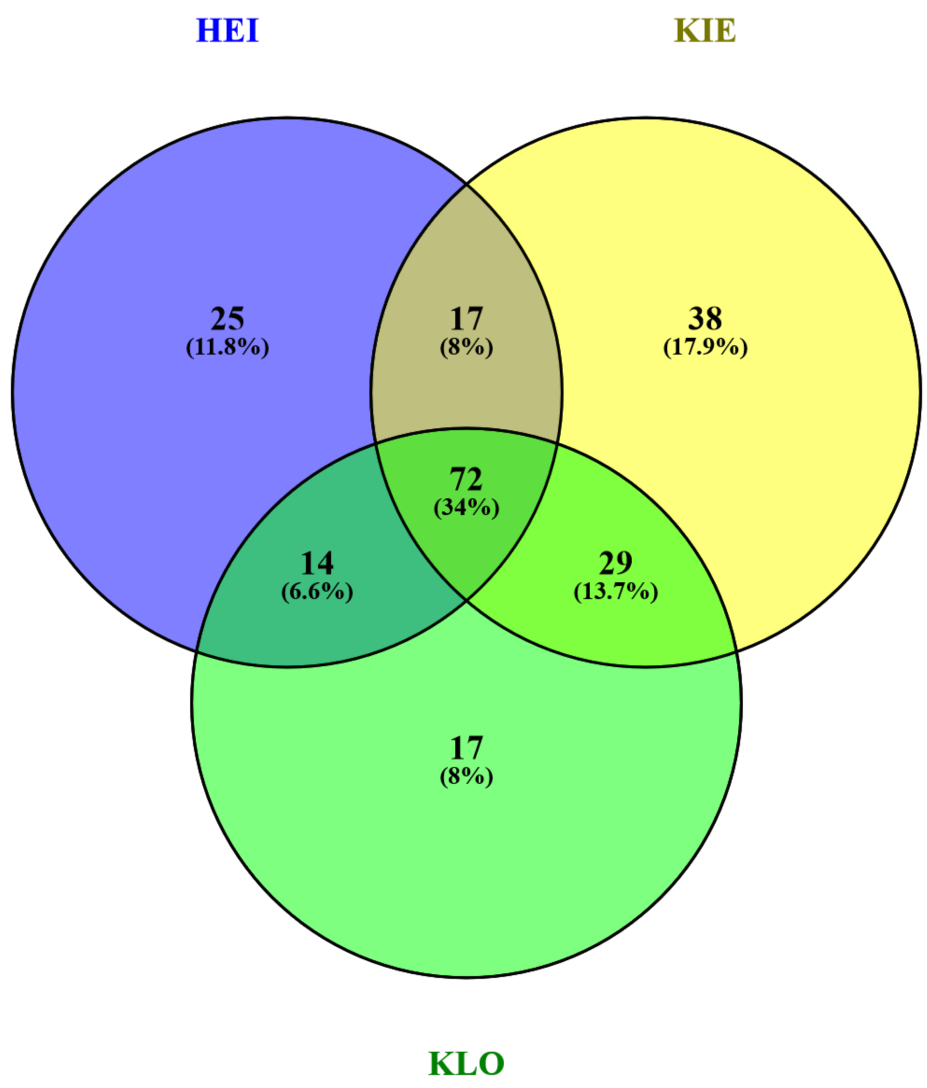
S2 C	A	B	C	D	E	F
A						
B	195					
C	11	20				
D	10	19	84			
E	12	25	89	100		
F	12	20	81	94	113	

xiv. Supplementary Table S3: Diversity indeces for all MUE sites.

	HEI	KLO	KIE	HEI moss+Ref	KLO moss+Ref	KIE moss+Ref
Taxa_S	109	106	137	128	132	156
Individuals	677364	799931	636767	736556	900740	746448
Dominance_D	0.0521	0.08653	0.05203	0.05018	0.0763	0.04519
Simpson_1-D	0.9479	0.9135	0.948	0.9498	0.9237	0.9548
Shannon_H	3.513	3.072	3.616	3.571	3.238	3.74
Eveness_e^H/S	0.3076	0.2037	0.2718	0.278	0.1391	0.1806
Brillouin	3.512	3.072	3.616	3.571	3.238	3.739
Menhinick	0.1324	0.1185	0.1717	0.1491	0.1391	0.1806
Margalef	8.044	7.725	10.18	9.401	9.554	11.46
Equitability_J	0.7487	0.6588	0.7352	0.7362	0.6633	0.7406
Fisher_alpha	9.78	9.332	12.65	11.57	11.73	14.37
Berger-Parker	0.1312	0.2032	0.1498	0.122	0.1807	0.1332
Chao-1	109	106	137	128	132	156

xv. **Venn diagram showing the bacteriomes of Sphagnum and reference sedges from all subsites within the Mueritz sampling site.**

Heidbergmoor (HEI), Kiebitzmoor (KIE) and Klockenbruch (KLO) Created at: https://bioinfogp.cnb.csic.es/tools/venny/index.html (Oliveros, J.C. (2007-2015) Venny. An interactive tool for comparing lists with Venn's diagrams).



xvi. Additional supplement (S_methanotrophs_fasta).

```
>1015820 106B_38282
TGGGGAATCTTGCGCAATGGGCGAAAGCCTGACGCAGCAACGCCGCGTGCGGGAAGAAGG
CCTTAGGGTTGTAAACCGCTTTCAGTAGGAACGAAAATGACGGTACCTGCAGAAGAAGGT
GCGGCCAACTACGTGCCAGCAGCCGCGGTGACACGTAGGCACCAAGCGTTGTCCGGATTT
ATTGGGCGTAAAGAGCTCGTAGGCGGTTGAGTAAGTCGGGTGTGAAAACTCTGGGCTTAA
CCCAGAGCCGCCACTCGATACTGCTCTGACTTGAGTTCGGTAGGGGAGCAGGGAATTCCT
AGTGTAGCGGTGAAATGCGCAGATATTAGGAGGAACACCGGTGGCGAAGGCGCTGCTCTG
GGCCGAAACTGACGCTGAGGAGCGAAAGCGTGGGTAGCAAACA
>1105814 101B_1589
TGGGGAATATTGGACAATGGGCGCAAGCCTGATCCAGCCATGCCGCGTGAGTGATGAAGG
CCCTAGGGTTGTAAAGCTCTTTTGTGCGGGAAGATAATGACGGTACCGCAAGAATAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGCTCGGAATC
ACTGGGCGTAAAGGGTGCGTAGGCGGGTCTTTAAGTCAGGGGTGAAATCCTGGAGCTCAA
CTCCAGAACTGCCTTTGATACTGAGGATCTTGAGTTCGGGAGAGGTGAGTGGAACTGCGA
GTGTAGAGGTGAAATTCGTAGATATTCGCAAGAACACCAGTGGCGAAGGCGGCTCACTGG
CCCGATACTGACGCTGAGGCACGAAAGCGTGGGGAGCAAACA
>1114358 101B_71229
TGGGGAATATTGCGCAATGGGCGAAAGCCTGACGCAGCAACGCCGCGTGGGGGATGAAGG
CCTTCGGGTTGTAAACCTCTTTCAGCAGGGAAGAAGCGAAAGTGACGGTACCTGCAGAAG
AAGCACCGGCTAACTACGTGCCAGCAGCCGCGGTAATACGTAGGGTGCAAGCGTTGTCCG
GAATTATTGGGCGTAAAGAGCTCGTAGGCGGTTTGTCGCGTCTGCTGTGAAAATTCGGGG
CTCAACCCCGGACTTGCAGTGGGTACGGGCAGACTAGAGTGTGGTAGAGGAGACTGGAAT
TCCTGGTGTAGCGGTGGAATGCGCAGATATCAGGAGGAACACCAGTGGCGAAGGCGGGTC
TCTGGGCCACAACTGACGCTGAGGAGCGAAAGCGTGGGGAGCGAACA
>1119629 10B_268632
CAAGGAATTTTCGTCAATGGGCGCAAGCCTGAACGAGCAACGCCGCGTGCGGGATGACGG
CCTTCGGGTTGTAAACCGCTTTTTGGGGGGACGATGATGACGGTACCCTCGGAATAAGCC
CCGGCTAACTCTGTGCCAGCAGCCGCGGTAATACAGAGGGGGCAAGCGTTGTCCGGAATT
ACTGGGCGTAAAGCGTCCGCAGGTGGCCCAGCACGTGTTCTGTGAAAGCCCCGCGCTTAA
CGCGGGGAGGCCAGGACAGACTGCTGAGCTGGAGGGGTGCAGAGGGTCGTGGAATTGCCG
GTGTAGTGGTGAAATGCGTAGAGATCGGCAGGAACACCAAGGACGAAGGTAGCGACCTGG
GCACTACCTGACACTCAGGGACGACAGCGTGGGGAGCAAACC
>13505 101B_442
TAGGGAATCTTGCGCAATGGACGAAAGTCTGACGCAGCAACGCCGCGTGAGGGACGAAGG
CTTTCTGAGTTGTAAACCTCTTTCGACAGGAACGATTGTGACGGTACCTGTAGAAGAAGC
ACCGGCCAACTATGTGCCAGCAGCCGCGGTGATACATAGGGTGCAAGCGTTATTCGGATT
TATTGGGCGTAAAGAGCTCGTAGGCGGTTCGACAAGTCGGGTGTTAAACCCCCAGGCTTA
ACCTGGGGCCGCCACCCGAAACTGTTGTGACTAGAGTTTGGTAGGGGATCACGGAATTCC
TGGTGTAGCGGTGGAATGCGCAGATATCAGGAGGAACACCAGTAGCGAAGGCGGTGATCT
GGGCCAATACTGACGCTGAGGAGCGAAAGCGTGGGGAGCGAACA
>155989 101B_4385
TGGGGAATATTGGACAATGGGGGAAACCCTGATCCAGCGACGCCGCGTGTGTGAAGAAGG
CCTGCGGGTTGTAAAGCACTTTTAGTGGGGACAAAAAGCCATGGATTAATACTCTGTGGT
CTTGATTTAACCCAAAGAAAAAGCACCGGCTAACTCTGTGCCAGCAGCCGCGGTAATACA
GAGGGTGCGAGCGTTAATCGGAATTACTGGGCGTAAAGCGCGCGTAGACGGTTTTGTAAG
TCAGATGTGAAATCCCTGGGCTCAACCTGGGAACTGCATTTGAAACTGCATGGCTAGAGT
ATGGTAGAGGGAAGTGGAATTTCCGGTGTAGCGGTGAAATGCGTAGATATCGGAAGGAAC
ACCAGTGGCGAAAGCGACTTCCTGGACCAATACTGACGTTCATGTGCGAAAGCGTGGGGA
GCAAACA
>205348 106B_99453
TGGGGAATCTTGGACAATGGGCGCAAGCCTGATCCAGCCATGCCGCGTGGATGATGAAGG
CCCTAGGGTTGTAAAATCCTTTCGTCAGGGACGATAATGACGGTACCTGAAGAAGAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGTTCGGAATT
ACTGGGCGTAAAGCGCATGTAGGCGGGTCGTTAAGTCGGGGGTGAAAGCCCAGAGCTCAA
CTCTGGAACTGCCTTCGATACTGGCGACCTGGACCCAAGGAGAGGCGAGTGGAATTGCGA
```

GTGTAGAGGTGAAATTCGTAGATATTCGCAGGAACACCAGTGGCGAAGGCGACTCGCTGG
ACTTGTGGTGACGCTGAGATGCGAAAGCGTGGGGAGCAAACA
>217481 101B_2868
TGGGGAATATTGGACAATGGGCGAAAGCCTGATCCAGCAATGCCGCGTGAGTGATGAAGG
CCTTAGGGTTGTAAAGCTCTTTCGGGTGGGACGATGATGACGGTACCACCAGAAGAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGTTCGGAATT
ACTGGGCGTAAAGCGCACGCAGGCGGCTCGATAAATTAGAAGTGAAAGCCCCGGGCTTAA
CCTGGGAATTGCTTTTAAGACTGTCGAGCTAGAATCCAGAAGAGGGTAGTGGAATTCCGA
GTGTAGAGGTGAAATTCGTAGATATTCGGAAGAACACCAGTGGCGAAGGCGACTACCTGG
TCTGGCATTGACGCTCATGTGCGAAAGCGTGGGGAGCAAACA
>219226 107B_788
TGGGGAATCTTGCGCAATGGCCGAGAGGCTGACGCAGCGACGCCGCGTGGGGGATGAAGC
ATTTCGGTGTGTAAACCCCTGTTGCTCGGGACGAACGATCCTTTTCGAGGGATGTGACGG
TACCGAGTGAGGAAGCACCGGCTAACTCCGTGCCAGCAGCCGCGGTAATACGGAGGGTGC
GAGCGTTGTCCGGAATCACTGGGCGTAAAGGGCGCGTAGGTGGTTGGATGCGCCGGTGGT
GAAAGCGCAGGGCTCAACCCTGCGTCGGCCATCGGGACGGTCCGACTGGAGCACTGTAGA
GGCAGGTGGAATTCCGGGTGTAGCGGTGGAATGCGTAGAGATCCGGAAGAACACCGGTGG
CGAAGGCGGCCTGCTGGGCAGTTGCTGACACTGAGGCGCGACAGCGTGGGGAGCAAACA
>223618 101B_712
TGGGGAATATTGGACAATGGGCGAAAGCCTGATCCAGCAATGCCGCGTGTGTGAAGAAGG
TCTTCGGATTGTAAAGCACTTTCGGCGGGGACGATGATGACGGTACCCGCAGAAGAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGCTCGGAATG
ACTGGGCGTAAAGGGCGCGTAGGCGGTTTGCCAAGTTAGATGTGAAATTCCTGGGCTTAA
CCTGGGGGCTGCATTTGATACTGGCAGGCTTGAGTGTGGAAGAGGGTCGTGGAATTCCCA
GTGTAGAGGTGAAATTCGTAGATATTGGGAAGAACACCGGTGGCGAAGGCGGCGACCTGG
TCCATAACTGACGCTGAGGCGCGAAAGCGTGGGGAGCAAACA
>227434 101B_722
TGGGGAATCTTGCGCAATGGGCGAAAGCCTGACGCAGCCATGCCGCGTGGATGATGAAGG
TCTTAGGATTGTAAAATCCTTTCAGCGGGGACGATAATGACGGTACCCGCAGAAGAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGCTCGGATTT
ACTGGGCGTAAAGGGCGCGTAGGCGGACAGTTTAGTTGGGGGTGAAAGCCCGGGGCTCAA
CCTCGGAATTGCCTTCAATACTGGCTGTCTTGAGTATGGGAGAGGTGAGTGGAACTCCGA
GTGTAGAGGTGAAATTCGTAGATATTCGGAAGAACACCAGTGGCGAAGGCGACTCACTGG
CCCATTACTGACGCTGAGGCGCGAAAGCGTGGGGAGCAAACA
>254922 102B_22247
TGGGGAATATTGGACAATGGGCGAAAGCCTGATCCAGCAATGCCGCGTGTGTGAAGAAGG
TCTTCGGATTGTAAAGCACTTTTGGCAGGGACGATGATGACGGTACCTGCAGAATAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGCTCGGAATG
ACTGGGCGTAAAGGGCGCGTAGGCGGCCTACACAGTCAGATGTGAAATTCCTGGGCTCAA
CCTGGGGACTGCATTTGAGACGTGTAAGCTTGAGTGGAGAAGAGGGTCGTGGAATTACCA
GTGTAGAGGTGAAATTCGTAGATATTGGTAAGAACACCGGTGGCGAAGGCGGCGACCTGG
TCTTTAACTGACGCTGAGGCGCGAAAGCGTGGGGAGCAAACA
>271114 101B_445
TGGGGAATATTGGACAATGGGCGCAAGCCTGATCCAGCAATGCCGCGTGTGTGAAGAAGG
TCTTCGGATTGTAAAGCACTTTTGGCGGGGACGATGATGACGGTACCCGCAGAATAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGCTCGGAATG
ACTGGGCGTAAAGGGCGCGTAGGCGGCCTACACAGTCAGATGTGAAATTCCTGGGCTCAA
CCTGGGGACTGCATTTGATACGTGTGAGCTTGAGTGAAGAAGAGGGTCGTGGAATTTCCA
GTGTAGAGGTGAAATTCGTAGATATTGGAAAGAACACCGGTGGCGAAGGCGGCGACCTGG
TCTTTAACTGACGCTGAGGCGCGAAAGCGTGGGGAGCAAACA
>279138 101B_2878
TGGGGAATATTGGACAATGGGGGAAACCCTGATCCAGCGACGCCGCGTGTGTGAAGAAGG
CCTGCGGGTTGTAAAGCACTTTTAGTGGGGACAAAAAGCTACGGATTAATACTTCGTGGT
CTTGATTTAACCCAAAGAAAAAGCACCGGCTAACTCTGTGCCAGCAGCCGCGGTAATACA
GAGGGTGCGAGCGTTAATCGGAATTACTGGGCGTAAAGCGCGCGTAGACGGTTTTGTAAG
TCAGATGTGAAATCCCTGGGCTCAACCTGGGAACTGCATTTGAAACTGCATGGCTAGAGT
ATGGTAGAGGGAAGTGGAATTTCCGGTGTAGCGGTGAAATGCGTAGATATCGGAAGGAAC
ACCAGTGGCGAAAGCGACTTCCTGGACCAATACTGACGTTCATGTGCGAAAGCGTGGGGA
GCAAACA

>37406 101B_5900
TGGGGAATATTGGACAATGGGCGAAAGCCTGATCCAGCAATGCCGCGTGAGTGATGAAGG
CCTTAGGGTTGTAAAGCTCTTTCGGGTGGGACGATGATGACGGTACCACCAGAAGAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGTTCGGAATT
ACTGGGCGTAAAGCGCACGCAGGCGGCTCGATAAATTAGAAGTGAAAGCCTTGGGCTTAA
CCTGAGAATTGCTTTTAAGACTGTCGAGCTAGAATCCAGAAGAGGGTAGTGGAATTCCGA
GTGTAGAGGTGAAATTCGTAGATATTCGGAAGAACACCAGTGGCGAAGGCGACTACCTGG
TCTGGCATTGACGCTCATGTGCGAAAGCGTGGGGAGCAAACA
>4321318 103B_995
TGGGGAATATTGGACAATGGGCGCAAGCCTGATCCAGCAATGCCGCGTGTGTGAAGAAGG
TCTTCGGATTGTAAAGCACTTTCGACGGGGACGATGATGACGGTACCCGTAGAAGAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGCTCGGAATG
ACTGGGCGTAAAGGGCGCGTAGGCGGATGGCACAGTCAGATGTGAAATTCCCGGGCTTAA
CCTGGGGGCTGCATTTGATACGTGGTGTCTAGAGTGAGGAAGAGGGTTGTGGAATTCCCA
GTGTAGAGGTGAAATTCGTAGATATTGGGAAGAACACCGGTGGCGAAGGCGGCAACCTGG
TCCTTGACTGACGCTGAGGCGCGAAAGCGTGGGGAGCAAACA
>4355811 107B_7716
TAGGGAATATTGGACAATGGGCGAAAGCCTGATCCAGCCATGCCGCGTGAGTGAAGAAGG
CCTTAGGGTTGTAAAGCTCTTTTGGCGGGGAAGATAATGACGGTACCCGCAGAATAAGCT
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGTTCGGAATC
ACTGGGCGTAAAGCGCACGCAGGCGGATTGATAAGTCGGGGGTGAAATCCCGAGGCTCAA
CCTCGGAATTGCCTTCGATACTGTCTGTCTTGAGTCCGGGAGAGGTGAGTGGAATTCCTA
GTGTAGAGGTGAAATTCGTAGATATTAGGAAGAACACCAGTGGCGAAGGCGGCTCACTGG
CCCGGTACTGACGCTCATGTGCGAAAGCGTGGGGAGCAAACA
>4468101 103B_14348
TGGGGAATATTGGACAATGGGGGAAACCCTGATCCAGCGACGCCGCGTGTGTGAAGAAGG
CCTGCGGGTTGTAAAGCACTTTTAGTGGGGACAAAAAGCCATGGACTAATACTCTGTGGT
CTTGATTTAACCCAAAGAAAAAGCACCGGCTAACTCTGTGCCAGCAGCCGCGGTAATACA
GAGGGTGCGAGCGTTAATCGGAATTACTGGGCGTAAAGCGCGCGTAGACGGTTTTGTAAG
TCAGATGTGAAATCCCTGGGCTCAACCTGGGAACTGCATTTG
>534914 101B_75539
TGGGGAATCTTGCACAATGGACGAAAGTCTGATGCAGCGACGCCGCGTGAGCGATGAAGC
CCTTCGGGGTGTAAAGCTCTTTCGGCAGGGACGATAATGACGGTACCTGAAGAAGAAGCT
GCGGCTAACTACGTGCCAGCAGCCGCGGTAATACGTAGGCAGCGAGCGTTGTTCGGAATT
ACTGGGCGTAAAGAGTGTGTAGGCGGTGCTCTAAGTTTGGTGTGAAATCTCCCGGCTCAA
CTGGGAGGGTGCGCCGAAGACTGGAGTGCTCGAGTGTGGGAGAGGAAAGCGGAATTCCTG
GTGTAGCGGTGAAATGCGTAGATATCAGGAGGAACACCTGTGGTGTAGACGGCTTTCTGG
ACCATTACTGACGCTGAGACACGAAAGCGTGGGTAGCAAACA
>538111 101B_323
TGGGGAATATTGCACAATGGGCGAAAGCCTGATGCAGCGACGCCGCGTGAGGGATTAAGG
CCTTCGGGTTGTAAACCTCTTTCAGCAGGGAAGAAGCGAGAGTGACGGTACCTGCAGAAG
AAGCACCGGCTAACTACGTGCCAGCAGCCGCGGTAATACGTAGGGTGCAAGCGTTGTCCG
GAATTATTGGGCGTAAAGAGCTTGTAGGCGGTTTGTCGCGTCTGCTGTGAAATTTCGGGG
CTCAACCCCGAACTTGCAGTGGGTACGGGCAGACTAGAGTGTGGTAGGGGAGACTGGAAT
TCCTGGTGTAGCGGTGAAATGCGCAGATATCAGGAGGAACACCGATGGCGAAGGCAGGTC
TCTGGGCCACTACTGACGCTGAGAAGCGAAAGCATGGGGAGCGAACA
>53994 101B_227
TGGGGAATATTGGACAATGGGCGCAAGCCTGATCCAGCAATGCCGCGTGTGTGAAGAAGG
TCTTCGGATTGTAAAGCACTTTTGGCAGGGACGATGATGACGGTACCTGCAGAATAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGCTCGGAATG
ACTGGGCGTAAAGGGCGCGTAGGCGGCTGTCACAGTCAGATGTGAAATTCCTGGGCTCAA
CCTGGGGACTGCATTTGATACGTGGCGGCTTGAGTGGAGAAGAGGGTTGTGGAATTTCCA
GTGTAGAGGTGAAATTCGTAGATATTGGAAAGAACACCGGTGGCGAAGGCGGCAACCTGG
TCTTTAACTGACGCTGAGGCGCGAAAGCGTGGGGAGCAAACA
>557209 101B_4611
TGGGGAATATTGGACAATGGGCGAAAGCCTGATCCAGCCATGCCGCGTGAGTGATGACGG
CCTTAGGGTTGTAAAGCTCTTTCGCCCACGACGATAATGACGGTAGTGGGAGAAGAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGTTCGGAATT
ACTGGGCGTAAAGCGCGTGTAGGCGGGTCCTTAAGTCAGGGGTGAAATGCCAAGGCTCAA

CCTTGGAACTGCCTTTGATACTGGGGATCTTGAGTCCGGGAGAGGTGAGTGGAACTGCGA
GTGTAGAGGTGAAATTCGTAGATATTCGCAAGAACACCAGTGGCGAAGGCGGCTCACTGG
CCCGGAACTGACGCTGAGACGCGAAAGCGTGGGGAGCAAACA
>568398 103B_56704
TGGGGAATTTTGCGCAATGGGGGAAACCCTGACGCAGCAACGCCGCGTGGAGGATGAAAT
ATCTTGGTATGTAAACTCCTTTCGATGGGGAAGATTATGACGGTACCCATAGAAGAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAGGGGGGCAAGCGTTGTTCGGAATT
ATTGGGCGTAAAGGGTGCGTAGGCGGTTTGACAAGTCTTGTGTGAAATCTATGGGCTCAA
CCCATAGTCTGCACAGGAAACTGTCGGGCTTGAGTATGGGAGAGGTGAGTGGAATTTCCG
GTGTAGCGGTGAAATGCGTAGATATCGGAAGGAACACCTGTGGCGAAAGCGGCTCACTGG
ACCATAACTGACGCTGATGCACGAAAGCTAGGGGAGCAAACA
>572984 101B_4836
TGGGGAATATTGGACAATGGGCGAAAGCCTGATCCAGCAATGCCGCGTGGATGAAGAAGG
TCTTCGGATTGTAAAGTCCTTTCGGCGGGGACGATGATGACGGTACCCGCAGAAGAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGCTCGGAATG
ACTGGGCGTAAAGGGCGCGTAGGCGGTTTGTACAGTCAGATGTGAAATTCCCGGGCTTAA
CCTGGGGACTGCATTTGATACGTGCAGGCTTGAGTGTGGAAGAGGGTCGTGGAATTCCCA
GTGTAGAGGTGAAATTCGTAGATATTGGGAAGAACACCGGTGGCGAAGGCGGCGACCTGG
TCCATAACTGACGCTGAGGCGCGAAAGCGTGGGGAGCAAACA
>576231 106B_65974
TGGGGAATATTGCGCAATGGGCGGAAGCCTGACGCAGCGACGCCGCGTGAGGGATGAAGG
CCTTCGGGTCGTAAACCTCTTTCAGCAGGGAAGAAGCGAGAGTGACGGTACCTGCAGAAG
AAGCACCGGCTAACTACGTGCCAGCAGCCGCGGTAATACGTAGGGTGCAAGCGTTGTCCG
GAATTATTGGGCGTAAAGAGCTCGTAGGCGGTCTGTCGCGTCTGCTGTGAAAACTCAGGG
CTTAACCCTGAGCTTGCAGTGGGTACGGGCAGACTAGAGTGCGGTAGGGGAGACTGGAAT
TCCTGGTGTAGCGGTGAAATGCGCAGATATCAGGAGGAACACCGGTGGCGAAGGCGGGTC
TCTGGGCCGTAACTGACGCTGAGGAGCGAAAGCATGGGGAGCGAACA
>590450 101B_69181
TGGGGAATATTGCGCAATGGGGGAAACCCTGACGCAGCAACGCCGCGTGAATGATGAAGG
CCTTCGGGTTGTAAAGTTCTGTCTTCTGGGACGATAATGACGGTACCAGAGGAGGAAGCC
ACGGCTAACTACGTGCCAGCAGCCGCGGTAATACGTAGGTGGCAAGCGTTGTCCGGATTT
ACTGGGCGTAAAGGATGCGTAGGCGGACATTTAAGTCAGATGTGAAATACCCGAGCTTAA
CTTGGGTGCTGCATTTGAAACTGGGTGTCTAGAGTGCAGGAGAGGTAAGTGGAATTCCTA
GTGTAGCGGTGAAATGCGTAGAGATTAGGAAGAACACCAGTGGCGAAGGCGACTTACTGG
ACTGTAACTGACGCTGAGGCATGAAAGCGTGGGGAGCAAACA
>647790 101B_583
TGGGGAATATTGGACAATGGGCGCAAGCCTGATCCAGCCATGCCGCGTGAGTGATGACGG
CCTTAGGGTTGTAAAGCTCTTTCGCTAGGGACGATAATGACGGTACCTAGACAAGAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGTTCGGAATT
ACTGGGCGTAAAGCGCGTGTAGGCGGGCTTTTAAGTCAGGGGTGAAATGCCAAGGCTCAA
CCTTGGAACTGCCTTTGATACTGGAAGTCTTGAGTCCGGGAGAGGTGAGTGGAACTGCGA
GTGTAGAGGTGAAATTCGTAGATATTCGCAAGAACACCAGTGGCGAAGGCGGCTCACTGG
CCCGGAACTGACGCTGAGACGCGAAAGCGTGGGGAGCAAACA
>688259 107B_54008
TGGGGAATATTGCACAATGGGCGGAAGCCTGATGCAGCGACGCCGCGTGAGGGATGACGG
CCTTCGGGTTGTAAACCTCTTTCAGCAGGGACGAAGCGCAAGTGACGGTACCTGCAGAAG
AAGCGCCGGCCAACTACGTGCCAGCAGCCGCGGTAAGACGTAGGGCGCGAGCGTTGTCCG
GATTTATTGGGCGTAAAGAGCTCGTAGGCGGCTTGTCGCGTCGACTGTGAAAACCCGCGG
CTCAACCGCGGGCCTGCAGCCGATACGGGCAGGCTAGAGTTCGGTAGGGGAGACTGGAAT
TCCTGGTGTAGCGGTGAAATGCGCAGATATCAGGAGGAACACCGATGGCGAAGGCAGGTC
TCTGGGCCGATACTGACGCTGAGGAGCGAAAGCGTGGGGAGCGAACA
>798634 102B_123346
TGGGGAATTTTGGACAATGGGCGCAAGCCTGATCCAGCCATGCCGCGTGCGGGAAGAAGG
CCTTCGGGTTGTAAACCGCTTTTGTCAGGGAAGAAACGCTCCGGGCTAATACCCTGGGGT
AATGACGGTACCTGAAGAATAAGCACCGGCTAACTACGTGCCAGCAGCCGCGGTAATACG
TAGGGTGCAAGCGTTAATCGGAATTACTGGGCGTAAAGCGTGCGCAGGCGGTTATGCAAG
ACAGATGTGAAATCCCCGGGCTCAACCTGGGAACTGCATTTGTGACTGCATAGCTAGAGT
ACGGTAGAGGGGGATGGAATTCCGCGTGTAGCAGTGAAATGCGTAGATATGCGGAGGAAC
ACCGATGGCGAAGGCAATCCCCTGGACCTGTACTGACGCTCATGCACGAAAGCGTGGGGA

GCAAACA
>806916 101B_4741
TGGGGAATATTGGACAATGGGCGCAAGCCTGATCCAGCAATGCCGCGTGGGTGAAGAAGG
TCTTCGGATTGTAAAGCCCTTTCGGCGGGGACGATGATGACGGTACCCGCAGAAGAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGCTCGGAATG
ACTGGGCGTAAAGGGCGCGTAGGCGGCTGTTACAGTCAGGCGTGAAATTCCTGGGCTCAA
CCTGGGGACTGCGCTTGATACGTAGTGGCTTGAGTGCGGAAGAGGGTCGTGGAATTCCCA
GTGTAGAGGTGAAATTCGTAGATATTGGGAAGAACACCGGTGGCGAAGGCGGCGACCTGG
TCCGTGACTGACGCTGAGGCGCGAAAGCGTGGGGAGCAAACA
>818605 103B_26740
TGGGGAATATTGGACAATGGGGGCAACCCTGATCCAGCAATGCCGCGTGAGTGATGAAGG
CCTTAGGGTCGTAAAGCTCTTTTACCCGGGATGATAATGACAGTACCGGGAGAATAAGCC
CCGGCTAACTCCGTGCCAGCAGCCGCGGTAATACGGAGGGGGCTAGCGTTGTTCGGAATT
ACTGGGCGTAAAGCGCACGTAGGCGGTTACTCAAGTCAGAGGTGAAAGCCCGGGGCTCAA
CCCCGGAACTGCCTTTGAAACTAGGTGACTGGAATCTTGGAGAGGCGAGTGGAATTCCGA
GTGTAGAGGTGAAATTCGTAGATATTCGGAAGAACACCAGTGGCGAAGGCGACTCGCTGG
ACAAGTATTGACGCTGAGGTGCGAAAGCGTGGGGAGCAAACA
>870223 101B_45564
TGGGGAATATTGCGCAATGGGCGGAAGCCTGACGCAGCGACGCCGCGTGAGGGATGACGG
CCTTCGGGTTGTAAACCTCTTTCAGCTCTGACGAAGCGAGAGTGACGGTAGGAGCAGAAG
AAGCACCGGCCAACTACGTGCCAGCAGCCGCGGTAATACGTAGGGTGCAAGCGTTGTCCG
GAATTATTGGGCGTAAAGAGCTCGTAGGCGGTTTGTCGCGTCGAATGTGAAAACCCGGGG
CTCAACTCCGGGCCTGCATTCGATACGGGCAGACTAGAGTTCGGTAGGGGAGACTGGAAT
TCCTGGTGTAGCGGTGAAATGCGCAGATATCAGGAGGAACACCGGTGGCGAAGGCGGGTC
TCTGGGCCGATACTGACGCTGAGGAGCGAAAGCGTGGGGAGCAAACA
>979536 103B_1946
TGGGGAATCTTGCACAATGGGGGCAACCCTGATGCAGCGACGCCGCGTGAACGATGAAGC
CCTTCGGGGTGTAAAGTTCTTTCGGCAGGGACGATAATGACGGTACCTGAAGAAGAAGCT
GCGGCTAACTACGTGCCAGCAGCCGCGGTAATACGTAGGCAGCGAGCGTTGTTCGGAATT
ACTGGGCGTAAAGAGTGTGTAGGCGGTGCTGTAAGTTCGGTGTGAAATCTCCTGGCTTAA
CTGGGAGGGTGCGCCGGAAACTGCAGTGCTCGAGTGTGGGAGAGGAAAGCGGAATTCCTG
GTGTAGCGGTGAAATGCGTAGATATCAGGAGGAACACCTGCGGTGTAGACGGCTTTCTGG
ACCATTACTGACGCTGAGACACGAAAGCGTGGGTAGCAAACA
>New.ReferenceOTU10157 56B_63607
TGGGGAATATTGGACAATGGGCGCAAGCCTGATCCAGCAATGCCGCGTGAGTGAAGAAGG
TCTTAGGATTGTAAAGCTCTTTCGGTGGGGACGATGATGACGGTACCCACAGAAGAAGCC
CCGGCTAACGTCGTGCGAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGCTCGGAATG
ACTGGGCGTAAAGGGCGCGTAGGCGGCGGACATAGTCAGATGTGAAATTCCTGGGCTCAA
CCTGGGGACTGCATTTGATACGTGTTTGCTTGAGTGCGGAAGAGGGTCGTGGAATTCCCA
GTGTAGAGGTGAAATTCGTAGATATTGGGAAGAACACCGGTGGCGAAGGCGGCGACCTGG
TCCGTAACTGACGCTGAGGCGCGAAAGCGTAGGGAGCAAACA
>New.ReferenceOTU13914 114B_65949
TGGGGAATATTGGACAATGGGCGCAAGCCTGATCCAGCAATGCCGCGTGGGTGAAGAAGG
TCTTCGGATTGTAAAGCCCTTTTGGCGGGGACGATGATGACGGTACCCGCAGAATAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGCTCGGAATG
ACTGGGCGTAAAGGGCGCGTAGGCGGCATATACAGTCAGATGTGAAATTCCTGGGCTCAA
CCTGGGGACTGCATTTGAAACGTATGAGCTTGAGTGAAGAAGAGGGTCGTGGAATTTCCA
GTGTAGAGGTGAAATTCGTAGATATTGGAAAGAACACCGGTGGCGAAGGCGGCGACCTGG
TCTTTAACTGACGCTGAGGCGCGAAAGCGTGGGGAGCAAACA
>New.ReferenceOTU61761 10B_90312
TGGGGAATATTGCGCAATGGGCGGAAGCCTGACGCAGCGACGCCGCGTGAGGGATGAAGG
CCTTCGGGTCGTAAACCTCTTTCAGCAGGGAAGAAGCGAGAGTGACGGTACCTGCAGAAG
AAGCACCGGCTAACTACGTGCCAGCAGCCGCGGTAATACGTAGGGTGCAAGCGTTGTCCG
GAATTATTGGGCGTAAAGAGCTCGTAGGCGGTCTGTCGCGTCTGCTGTGAAATCTCAGGG
CTTAACCCTGAGCTTGCAGTGGGTACGGGCAGACTAGAGTGCGGTAGGGGAGACTGGAAT
TCCTGGTGTAGCGGTGAAATGCGCAGATATCAGGAGGAACACCGGTGGCGAAGGCGGGTC
TCTGGGCCGTAACTGACGCTGAGGAGCGAAAGCATGGGGAGCGAACA
>New.CleanUp.ReferenceOTU174212 101B_19979
TGGGGAATATTGGACAATGGGCGAAAGCCTGATCCAGCAATGCCGCGTGGGTGAAGAAGG

```
TCTTCGGATTGTAAAGCCCTTTTGGCAGGGACGATGATGACGGTACCTGCAGAATAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGCTCGGAATG
ACTGGGCGTAAAGGGCGCGTAGGCGGTTTATACAGTCAGATGTGAAATTCCTGGGCTCAA
CCTGGGGACTGCATTTGATACGTATGGACTTGAGTGGAGAAGAGGGTCGTGGAATTTCCA
GTGTAGAGGTGAAATTCGTAGATATTGGAAAGAACACCGGTGGCGAAGGCGGCGACCTGG
TCTTTAACTGACGCTGAGGCGCGAAAGCGTGGGGAGCAAACA
```

xvii. Additional supplement (S_endophytes_taxonomy; S_endophytes_fasta).

```
>1120868 10B_94140
TGGGGAATATTGGACAATGGGCGGAAGCCTGATCCAGCAATACCGCGTGTGTGAAGAAGG
CCTGAGGGTTGTAAAGCACTTTCAATGGGAAGGAATACCTAATGGCGAATACCCATTAGA
CTGACATTACCCATACAAGAAGCACCGGCTAACTCCGTGCCAGCAGCCGCGGTAATACGG
AGGGTGCAAGCGTTAATCGGAATTACTGGGCGTAAAGCGTGCGTAGGCGGTTATTTAAGT
CAGATGTGAAAGCCCTGGGCTTAACCTGGGAACTGCATTTGATACTGGATGACTAGAGTT
GAGTAGAGGAGAGTGGAATTTCAGGTGTAGCGGTGAAATGCGTAGAGATCTGAAGGAACA
CCAGTGGCGAAGGCGGCTCTCTGGACTCAAACTGACGCTGAGGTACGAAAGCGTGGGTAG
CAAACA
>535429 102B_10362
TGGGGAATATTGGACAATGGGCGCAAGCCTGATCCAGCCATGCCGCGTGAGTGATGAAGG
CCTTAGGGTTGTAAAGCTCTTTCGCCAGGGACGATAATGACGGTACCTGGATAAGAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGTTCGGATTT
ACTGGGCGTAAAGCGCACGTAGGCGGATCTTTAAGTCAGGGGTGAAATCCCGAGGCTCAA
CCTCGGAACTGCCTTTGATACTGGAGGTCTCGAGTCCGGGAGAGGTGAGTGGAAC
>588559 106B_124688
TGGGGAATATTGGACAATGGGCGAAAGCCTGATCCAGCAATACCGCGTGTGTGAAGAAGG
CCTGAGGGTTGTAAAGCACTTTCAATGGGAAGGAATACCTATCGGCGAATACCCGGTAGA
CTGACATTACCCATACAAGAAGCACCGGCTAACTCCGTGCCAGCAGCCGCGGTAATACGG
AGGGTGCAAGCGTTAATCGGAATTACTGGGCGTAAAGCGTGCGTAGGCGGTTCGTTAAGT
CAGATGTGAAAGCCCTGGGCTCAACCTGGGAACTGCATTTGATACTGGCGAACTAGAGTT
GAGTAGAGGAGAGTGGAATTTCAGGTGTAGCGGTGAAATGCGTAGAGATCTGAAGGAACA
CCAGTGGCGAAGGCGGCTCTCTGGACTCAAACTGACGCTGAGGTACGAAAGCGTGGGTAG
CAAACA
>701385 101B_18188
TGGGGAATATTGGACAATGGGCGCAAGCCTGATCCAGCCATGCCGCGTGAGTGATGAAGG
CCTTAGGGTTGTAAAGCTCTTTCGCCAGGGACGATAATGACGGTACCTGGATAAGAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGTTCGGATTT
ACTGGGCGTAAAGCGCACGTAGGCGGATCTTTAAGTCAGGGGTGAAATCCCGAGGCTCAA
CCTCGGAACTGCCTTTGATACTGGAGGTCTCGAGTCCGGGAGAGGTGAGTGGAACTGCGA
GTGTAGAGGTGAAATTCGTAGATATTCGCAAGAACACCAGTGGCGAAGGCGGCTCACTGG
CCCGGTACTGACGCTGAGGTGCGAAAGCGTGGGGAGCAAACA
>New.ReferenceOTU13163 60B_79910
TGGGGAATATTGGACAATGGGCGAAAGCCTGATCCAGCAATACCGCGTGTGTGAAGAAGG
CCTGAGGGCTGTAAAGCACTTTCAATGGGAAGGAATACCTATCGGCGAATACCCGGTAGA
CTGACATTACCCATACAAGAAGCACCGGCTAACTCCGTGCCAGCAGCCGCGGTAATACGG
AGGGTGCAAGCGTTAATCGGAATTACTGGGCGTAAAGCGTGCGTAGGCGGTTCGTTAAGT
CAGATGTGAAAGCCCTGGGCTCAACCTGGGAACTGCATTTGATACTGGCGA
>New.ReferenceOTU30099 98B_66480
TGGGGAATATTGGACAATGGGCGCAAGCCTGATCCAGCCATGCCGCGTGAGTGATGACGG
CCTTAGGGTTGTAAAGCTCTTTCGCTAGGGACGATAATGACGGTACCTAGACAAGAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGTTCGGAATT
ACTGGGCGTAAAGCGCACGTAGGCGGATCTTTAAGTCAGGGGTGAAATGCCAAGGCTCAA
CCTTGGAACTGCCTCTGATACTGGAGATCTTGAGTTCGAGAGAGGTGAGTGGAACTGCGA
GTGTAGAGGTGAAATTCGTAGATATTCGCAAGAACACCAGTGGCGAAGGCGGCTCACTAG
CTCGATACTGACGCTGAGGTGCGAAAGCGTGGGGAGCAAACA
```

```
>New.ReferenceOTU73174 10B_335428
TGGGGAATATTGGACAATGGGCGAAAGCCTGATCCAGCAATACCGCGTGTGTGAAGAAGG
CCTGAGGGTTGTAAAGCACTTTCAATGGGAAGGAATACCTATGGGCTAATACCCTGTAGA
CTGACATTACCCATAGAAGAAGCACCGGCTAACTCCGTGCCAGCAGCCGCGGTAATACGG
AGGGTGCGAGCGTTAATCGGAATTACTGGGCGTAAAGCGTGCGTAGGCGGTTCGTTAAGT
CAGATGTGAAAGCCCTGGGCTCAACCTGGGAACTGCATTTGATACTGGCGAACTAGAGTT
GAGTAGAGGAGAGTGGAATTTCAGGTGTAGCGGTGAAATGCGTAGAGATCTGAAGGAACA
CCAGTGGCGAAGGCGGCTCTCTGGACTCAAACTGACGCTGAGGTACGAAAGCGTGGGTAG
CAAACA
>New.ReferenceOTU890 118B_97537
TGGGGAATATTGGACAATGGGCGCAAGCCTGATCCAGCCATGCCGCGTGAGTGATGACGG
CCTTAGGGTTGTAAAGCTCTTTCGCACGCGACGATAATGACGGTAGCGTGAGAAGAAGCC
CCGGCTAACTTCGTGCCAGCAGCCGCGGTAATACGAAGGGGGCTAGCGTTGTTCGGATTA
ACTGGGCGTAAAGGGTGCGTAGGCGGGCTTTTAAGTCAGGGGTGAAATCCCAAGGCTCAA
CCTTGGAACTGCCTTTGATACTGGGAGTCTTGAGTCCGGGAGAGGTGAGTGGAACTGCGA
GTGTAGAGGTGAAATTCGTAGATATTCGCAAGAACACCAGTGGCGAAGGCGGCTCACTGG
CCCGGTACTGACGCTGAGGCACGAAAGCGTGGGGAGCAAACA
```

xviii. Supplementary Table S4: Methane oxidation and methane production rates.

	hours	MP ster.moss A_S0	MP ster.moss B_S0	MP ster.moss C_S0	MP ster.moss +I. A_S0	MP ster.moss +I B_S0	MP ster.moss +I C_S0	MP unster.moss A_S0	MP unster.moss B_S0	MP unster.moss C_S0
	0	0,78	0,54	0,50	4,76	5,57	6,29	1,94	2,42	1,68
	73							41,88	60,23	30,86
	94									
	99	0,49	0,51	0,46	4,69	5,45	6,26	49,98	64,72	34,40
	121							52,36	66,61	36,57
	143							53,85	69,70	37,87
	167							52,48	70,03	39,89
T (Kelvin) (22°C)		295	295	295	295	295	295	295	295	295
V bei VersuchsT		24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282
HS (Headspac		0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045
mol in HS		0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186
ppm in nmol	0	1,44549	1,00621	0,92774	8,84221	10,36305	11,69035	3,60232	4,50131	3,12435
	73	0,00000	0,00000	0,00000	0,00000	0,00000	0,00000	77,85210	111,98322	57,36396

9,82776	10,80206	10,10936	0,00000	0,00000	0,00000	0,00000	0,00000	0,00000	1881,125 86	4366,545 75
9,65252	10,63850	9,93453	5784,090 74	5663,166 37	6035,463 80	5920,442 30	5870,343 02	5711,209 81	5965,754 38	5840,645 02
0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186
0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045
24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82
295	295	295	295	295	295	295	295	295	295	295
			1636,46	1480,25	2050,68				52,76	670,64
5,51	5,93	5,47	1945,47	1880,18	2350,19	3195,40	3102,67	3135,87	92,99	995,11
5,45	5,97	5,52	2305,67	2227,08	2682,07	3299,47	3124,42	3154,84	228,41	1497,72
5,21	5,75	5,44	2474,13	2395,90	2799,78	3137,73	3115,11	2894,00	373,38	1837,79
									544,86	2058,76
5,29	5,81	5,44							1011,84	2348,73
5,19	5,72	5,34	3111,21	3046,17	3246,43	3184,56	3157,61	3072,01	3208,93	3141,63
MP unster.moss +l. A_S0	**MP unster.moss +l B_S0**	**MP unster.moss +l C_S0**	**MO ster.moss A_S0**	**MO ster.moss B_S0**	**MO ster.moss C_S0**	**MO ster.moss +l. A_S0**	**MO ster.moss +l B_S0**	**MO ster.moss +l C_S0**	**MO unster.moss A_S0**	**MO unster.moss B_S0**

3525,68810	5969,69181	5998,36044	5958,71508	0,00000	0,00000	0,00000	0,00000	0,00000	0,00000	4,63965
5771,57690	5937,06496	6103,65159	5869,52704	0,83055	0,94603	0,95267	8,58463	9,64655	9,82268	1,25166
0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186
0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045
24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282
295	295	295	295	295	295	295	295	295	295	295
265,00										5,72
460,32	3209,27	3255,43	3242,67							5,01
836,99	3245,94	3347,87	3238,33							4,33
1166,23	3116,21	3227,05	3276,31	0,41	0,67	0,61	4,66	5,34	5,48	3,35
1388,42										
1896,44	3211,05	3226,47	3205,14							2,50
3104,48	3193,50	3283,10	3157,17	0,45	0,51	0,51	4,62	5,19	5,28	0,67
MO unster.moss C_S0	**MO unster.moss +l. A_S0**	**MO unster.moss +l B_S0**	**MO unster.moss +l C_S0**	**MP ster.moss A_S8**	**MP ster.moss B_S8**	**MP ster.moss C_S8**	**MP ster.moss +l. A_S8**	**MP ster.moss +l B_S8**	**MP ster.moss +l C_S8**	**MP unster.moss A_S8**

MP unster.moss B_S8	MP unster.moss C_S8	MP unster.moss +l. A_S8	MP unster.moss +l B_S8	MP unster.moss +l C_S8	MO ster.moss A_S8	MO ster.moss B_S8	MO ster.moss C_S8	MO ster.moss +l. A_S8	MO ster.moss +l B_S8	MO ster.moss +l C_S8
4,45051	10,68261	9,93780	9,20801	9,53160	0,00000	0,00000	0,00000	0,00000	0,00000	0,00000
0,74674	1,56710	9,40492	8,97359	9,09815	5909,557 40	6038,694 76	5946,006 20	5756,029 61	5959,644 65	5876,609 91
0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186
0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045
24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82
295	295	295	295	295	295	295	295	295	295	295
5,50	26,03				3097,91	3262,03	3122,82			
4,75	18,79	5,28	4,95	5,05	3223,73	3234,01	3166,56	3188,90	3192,34	3175,52
4,15	13,24	5,25	4,94	5,10	3200,13	3251,65	3220,02	3282,98	3214,06	3160,68
3,34	9,03	5,14	4,86	5,06	3222,60	3226,41	3116,26	3148,87	3095,89	2851,47
2,39	5,75	5,35	4,95	5,13						
0,40	0,84	5,06	4,83	4,89	3178,70	3248,16	3198,31	3096,12	3205,64	3160,98

5481,608 18	5129,279 21	5489,097 01	6092,437 47	5715,075 96	5919,201 22	0,00000	0,00000	0,00000	0,00000	0,00000
5745,779 68	5915,484 08	5991,558 12	6021,377 86	5902,370 08	5875,334 21	1,11836	0,99870	0,91455	10,05353	9,68916
0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186
0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045
24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82
295	295	295	295	295	295	295	295	295	295	295
1837,49	1395,82	1390,58				13,24	12,80	18,97		
2257,07	1808,47	1858,26	3277,66	3188,78	3188,16	9,64	9,34	12,72	5,55	5,48
2602,21	2278,88	2355,32	3298,59	3228,77	3240,99	8,18	8,38	9,85	5,43	5,47
2716,38	2468,27	2579,71	3275,99	3174,76	3172,01	6,91	7,15	8,49	5,48	5,39
3028,65	2579,80	2724,26								
2948,51	2759,00	2952,54	3277,07	3074,09	3183,89					
3090,61	3181,89	3222,81	3238,85	3174,84	3160,29	0,60	0,54	0,49	5,41	5,21
MO unster.moss A_S8	**MO unster.moss B_S8**	**MO unster.moss C_S8**	**MO unster.moss +I. A_S8**	**MO unster.moss +I B_S8**	**MO unster.moss +I C_S8**	**MP ster.moss A_Glu**	**MP ster.moss B_Glu**	**MP ster.moss C_Glu**	**MP ster.moss +I. A_Glu**	**MP ster.moss +I B_Glu**

MP ster.moss +l C_Glu	MP unster.moss A_Glu	MP unster.moss B_Glu	MP unster.moss C_Glu	MP unster.moss +l. A_Glu	MP unster.moss +l B_Glu	MP unster.moss +l C_Glu	MO ster.moss A_Glu	MO ster.moss B_Glu	MO ster.moss C_Glu	MO ster.moss +l. A_Glu
0,00000	176,73687	33,14671	107,64807	9,96065	10,88516	10,78308	0,00000	0,00000	0,00000	0,00000
8,07793	13,37145	3,21907	9,70394	9,42301	10,65287	9,14768	5911,69406	5722,73458	5933,85028	5980,89410
0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186
0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045
24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282
295	295	295	295	295	295	295	295	295	295	295
	249,80	37,84	150,99				1977,80	1577,59	2953,07	
4,44	214,68	34,70	123,80	5,52	5,90	6,19	2346,92	1914,20	2977,69	3251,41
4,49	172,33	28,15	101,76	5,41	5,93	6,03	2611,74	2239,10	3126,75	3329,44
4,47	127,29	23,48	79,56	5,36	6,00	5,87	2695,85	2366,34	3082,96	3240,05
	95,07	17,83	57,90	5,36	5,86	5,80				
4,35	7,19	1,73	5,22	5,07	5,73	4,92	3179,85	3078,21	3191,77	3217,07

0,00000	0,00000	5975,17568	2243,66118	4266,30769	5904,87505	6098,27357	5940,81956	0,00000	0,00000	0,00000
5972,88408	6029,60042	5549,24015	5901,49505	5527,64300	5918,68613	5961,26483	5873,83906	1,19844	0,76415	0,76474
0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186
0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045
24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282
295	295	295	295	295	295	295	295	295	295	295
		89,64	281,03	256,61						
3238,20	3249,02	172,40	950,87	457,03	3269,53	3246,92	3209,11			
3369,07	3272,87	385,58	1383,28	779,71	3241,93	3269,62	3290,02			
3248,82	3248,82	610,26	1683,18	1048,99	3278,12	3261,41	2822,34	1,03	0,61	0,56
		747,42	1915,73	1236,03						
		3214,00	1206,85	2294,81	3176,18	3280,21	3195,52			
3212,77	3243,27	2984,89	3174,37	2973,27	3183,61	3206,52	3159,49	0,64	0,41	0,41
MO ster.moss +I B_Glu	**MO ster.moss +I C_Glu**	**MO unster.moss A_Glu**	**MO unster.moss B_Glu**	**MO unster.moss C_Glu**	**MO unster.moss +I. A_Glu**	**MO unster.moss +I B_Glu**	**MO unster.moss +I C_Glu**	**MP ster.moss A_Knu**	**MP ster.moss B_Knu**	**MP ster.moss C_Knu**

0,00000	0,00000	0,00000	32,39488	48,30089	47,87567	9,71939	9,10025	10,03834	0,00000	0,00000
10,01324	9,26250	8,29680	4,49983	5,11041	4,65081	9,16549	9,02133	10,19378	5928,120 88	5933,266 80
0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186
0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045
24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82	24,20512 82
295	295	295	295	295	295	295	295	295	295	295
			33,39	64,54	59,31				3055,03	2978,54
			30,00	55,56	53,46	5,17	5,03	5,51	3030,43	3053,06
			26,80	45,15	45,49	5,08	4,97	5,59	3090,68	3083,20
5,09	5,04	4,35	21,85	36,49	33,90	5,06	4,94	5,47	2895,31	3014,15
			17,42	25,98	25,75	5,23	4,89	5,40		
5,39	4,98	4,46	2,42	2,75	2,50	4,93	4,85	5,48	3188,69	3191,46
MP ster.moss +l. A_Knu	**MP ster.moss +l B_Knu**	**MP ster.moss +l C_Knu**	**MP unster.m oss A_Knu**	**MP unster.m oss B_Knu**	**MP unster.m oss C_Knu**	**MP unster.m oss +l. A_Knu**	**MP unster.m oss +l B_Knu**	**MP unster.m oss +l C_Knu**	**MO ster.moss A_Knu**	**MO ster.moss B_Knu**

0,00000	0,00000	0,00000	0,00000	1592,47445	851,12216	2142,05621	6386,50773	6285,39708	5872,48884
5829,17684	5923,39435	6027,18382	6019,51867	5412,86011	5321,36948	5633,47692	6048,76104	6225,60695	5869,43501
0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186	0,00186
0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045	0,045
24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282	24,2051282
295	295	295	295	295	295	295	295	295	295
3020,78				34,88	8,03	92,25			
3091,88	3226,49	3265,95	3252,16	83,04	20,25	190,78	3303,49	3217,68	3179,36
3100,60	3267,37	3322,11	3276,40	220,56	69,00	417,80	3321,41	3234,05	3191,01
3115,15	3195,11	3031,32	3220,10	257,98	144,30	575,44	3114,78	3204,45	3119,26
				477,23	210,25	748,82			
				856,58	457,81	1152,19	3435,25	3380,86	3158,76
3135,47	3186,14	3241,97	3237,85	2911,53	2862,32	3030,20	3253,58	3348,70	3157,12
MO ster.moss C_Knu	**MO ster.moss +l. A_Knu**	**MO ster.moss +l B_Knu**	**MO ster.moss +l C_Knu**	**MO unster.moss A_Knu**	**MO unster.moss B_Knu**	**MO unster.moss C_Knu**	**MO unster.moss +l. A_Knu**	**MO unster.moss +l B_Knu**	**MO unster.moss +l C_Knu**