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Aspects of microbial communities in peatland carbon cycling under changing climate and land use pressures

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SUMMARY

Globally, major efforts are being made to restore peatlands to maximise their resilience to anthropogenic climate change, which puts continuous pressure on peatland ecosystems and modifies the geography of the environmental envelope that underpins peatland functioning. A probable effect of climate change is reduction in the waterlogged conditions that are key to peatland formation and continued accumulation of carbon (C) in peat. C sequestration in peatlands arises from a delicate imbalance between primary production and decomposition, and microbial processes are potentially pivotal in regulating feedbacks between environmental change and the peatland C cycle. Increased soil temperature, caused by climate warming or disturbance of the natural vegetation cover and drainage, may result in reductions of long-term C storage via changes in microbial community composition and metabolic rates. Moreover, changes in water table depth alter the redox state and hence have broad consequences for microbial functions, including effects on fungal and bacterial communities especially methanogens and methanotrophs. This article is a perspective review of the effects of climate change and ecosystem restoration on peatland microbial communities and the implications for C sequestration and climate regulation. It is authored by peatland scientists, microbial ecologists, land managers and non-governmental organisations who were attendees at a series of three workshops held at The University of Manchester (UK) in 2019–2020. Our review suggests that the increase in methane flux sometimes observed when water tables are restored is predicated on the availability of labile carbon from vegetation and the absence of alternative terminal electron acceptors. Peatland microbial communities respond relatively rapidly to shifts in vegetation induced by climate change and subsequent changes in the quantity and quality of below-ground C substrate inputs. Other consequences of climate change that affect peatland microbial communities and C cycling include alterations in snow cover and permafrost thaw. In the face of rapid climate change, restoration of a resilient microbiome is essential to sustaining the climate regulation functions of peatland systems. Technological developments enabling faster characterisation of microbial communities and functions support progress towards this goal, which will require a strongly interdisciplinary approach.

KEY WORDS: archaea, bacteria, climate change, fungi, resilience



INTRODUCTION

Peatlands effectively remove carbon dioxide from the atmosphere and potentially store it for millennia. During the Holocene, peatlands are estimated to have absorbed 539 Gt of carbon (C) from the atmosphere into terrestrial pools at rates ranging from 21 to 83 Mt yr⁻¹ (Yu 2011). However, peatland systems are subject to considerable degradation through anthropogenic pressures that modify their C storage potential and can turn them from C sinks into sources of C to the atmosphere (Leifeld *et al.* 2019). Importantly, if restored, peatlands can become a vital tool in climate change mitigation strategies (Leifeld & Menichetti 2018). Understanding the stability of these ecosystems, their resistance and resilience to environmental change and human interventions, as well as the underpinning soil processes, is key to the management of global terrestrial carbon cycles.

Peatlands sequester C from the atmosphere because the rate of C input through primary production exceeds the rate of C loss, primarily through the decomposition of organic matter. Decomposition is facilitated by decomposer mesofauna (e.g. Briones *et al.* 2014) that break down and assimilate organic material (Frouz 2018). Further breakdown of the structural C compounds is driven primarily by the direct action of microbes (bacteria, fungi, archaea) and indirectly through their regulation by predators such as viruses (Emerson *et al.* 2018) and protists. Thus, complex interactions within diverse soil food webs play an important role in breaking down organic molecules to simpler compounds which are metabolised, releasing CO₂ and CH₄ to the atmosphere at rates that depend upon the prevailing environmental conditions. Primary production, although carried out mainly by macroscopic plants, is similarly facilitated by and linked to the myriad of activities of microorganisms in the soil that control C and nutrient cycling.

Aerobic respiration (including microbial and plant root respiration) drives CO₂ emissions from peatland soils. Anaerobic respiration by methanogenic archaea produces CH₄, of which an estimated 50–70 % is oxidised by methanotrophic bacteria (e.g. Raghoebarsing *et al.* 2005), primarily in the upper aerobic peat layers (Bodelier 2011, Nielsen *et al.* 2019) and in rhizospheres associated with some flooding-adapted plants. Because they ultimately control the production and cycling of greenhouse gases in soil, microbial processes are key to understanding the feedbacks between environmental change, C cycling, and global climate regulation by peatlands.

There has been a major focus on the role of peatlands in the C cycle for at least 30 years (e.g. Gorham 1991). Significant progress has been made in quantifying and modelling their key C fluxes (e.g. IPCC 2014) and, as of 2021, greenhouse gas emissions from peatlands are reported in the UK's emissions inventory (Evans *et al.* 2017). However, changes in the C cycle are understood mainly in terms of system response to changes in physical conditions such as temperature and water table depth (e.g. Strack & Waddington 2007), which are effectively proxies for microbially driven processes underpinning the functioning of the peatland C cycle. Such proxies have been proven reliable for modelling peatland responses to environmental change (Clark *et al.* 2010, Worrall *et al.* 2009), but are based on (only) recent periods of data collection and model development. This means they are applicable only within the existing climate envelope of current peatland distribution. As climate changes in the future, peatlands may be forced to exist in 'no analogue' conditions under which the established relationships between physical proxies and peatland functions will become unreliable.

Previous research on (natural and) disturbed peatland microbial communities was summarised in a review by Andersen *et al.* (2013). A key conclusion from this work was that, whilst some progress has been made towards understanding the structure of peatland microbial communities, much more needs to be done to relate the structure of microbial communities to the ecosystem functions of peatlands. Such a process-level understanding is key to assessing the role of peatland systems in the C cycle as climate and environmental changes increasingly modify system boundary conditions. It could also underpin efforts to maximise the resilience and recovery of peatlands and to potentially influence the net outcomes via targeted management.

During the nine years since the Andersen *et al.* (2013) review was published, there have been major advances in technological capability for analysis of the microbiome with respect to various community attributes, such as its diversity and structure, as well as its function. The authors of this article are peatland scientists, microbial ecologists, land managers and members of non-governmental organisations who attended a series of three workshops held at The University of Manchester in 2019–2020 on the subject of a microbial process-based understanding of the resilience of peatland systems. In a recent paper arising from this initiative, Ritson *et al.* (2021) laid out a research agenda that could help inform and guide peatland restoration in practice. In the present

work, we review additions to the science base over the last nine years with a view to assessing the degree to which the challenges laid down by Andersen *et al.* (2013) have been addressed. We focus on the effects of climate change (search criteria for references are given in the introduction to the section “Effects of climate change on peatland microbial communities”) and ecosystem restoration on peatland microbial communities and the implications for C sequestration and climate regulation; and on this basis attempt to describe the underlying microbial communities and processes that will drive the response of carbon exchange in natural, modified and restored peatlands to climate change. This knowledge will support the integration of microbial process understanding into our assessments of the response of peatlands to future climate change and their potential role in climate change mitigation.

PREDICTED CLIMATE CHANGE EFFECTS ON PEATLANDS

In this section we summarise how changes in temperature and rainfall brought about by climate change may affect peatlands, and how anthropogenic pressures may exacerbate this.

Peatlands form where primary production exceeds decomposition. This commonly occurs where high water tables occur, favouring anoxic conditions in the soil. Minerotrophic peatlands are groundwater fed, with water influx dependent on catchment characteristics; whereas ombrotrophic peatlands (bogs) are rain-fed and dependent on the balance between precipitation and evaporative and fluvial losses to sustain high water tables. Peatlands occur across a wide geographical range that spans the temperate, boreal and subarctic climate zones, as well as in the tropics if the appropriate climate conditions along with waterlogging are found (Xu *et al.* 2018).

Given this large latitudinal range, projections of future climate change are varied, with arctic peatlands potentially facing 4.6–5.3 °C of warming by the end of the century whereas temperate and southeast Asian peatlands could experience more moderate temperature rises of 2.3–3.2 °C and 1.6–1.7 °C, respectively (2 °C warming pathway SSP2 4.5 25th and 75th percentiles; IPCC 2021). Temperature increases where soil moisture is maintained have been shown to increase CH₄ production rates in peat soils, although this is due to enhanced degradation of relatively modern material rather than the larger and older carbon stores in the catotelm (Wilson *et al.* 2016).

Projected changes to soil moisture have a higher degree of uncertainty than temperature projections, with some models included in the IPCC assessment disagreeing on the sign of potential changes in soil moisture. For example, in Central Asia and the high northern latitudes, there is uncertainty on the sign of soil moisture changes, whereas there is high confidence of drying in the Mediterranean, northeast and southwest South America, southern Africa and southwestern USA, many of which do not contain significant peatlands. Soil moisture projections also vary by soil depth, with generally larger reductions in surface soil moisture than in total soil moisture (Berg *et al.* 2017). This presents challenges, both in attempting to understand the complex effects of climate change on peatlands as a whole, and in comparing results between studies on peatland microbial processes which may use very different temperature manipulations and often lack rigorous assessments of interactions with peat moisture changes (e.g. Abdalla *et al.* 2016). Furthermore, the outputs from models which do not account for the unique self-regulating hydrology of peatland systems may over-estimate the risk posed by drought to peatlands in the future (Nijp *et al.* 2017).

Climate-induced changes in precipitation will probably be an important factor altering peatland vegetation in temperate and boreal regions, with decreasing wetness during the growing season generally associated with a shift from a *Sphagnum* dominated to vascular plant dominated vegetation type and a general decline of carbon sequestration in the long term (Limpens *et al.* 2008). Mire ecosystems (i.e. bogs, transition bogs and fens) in central Europe face severe climate-induced risk, with increased summer temperatures being particularly important. For a complete review of the likely shifts in peatland vegetation with climate change, see Antala *et al.* (2022). Decreased dry season precipitation and longer dry seasons in major tropical peatland areas in southeast Asia are projected to result in lower water tables more often and for longer periods, with an increased risk of fire (IPCC 2021), a problem which is increasingly not confined to these areas.

The areas where bioclimatic conditions support the accumulation of carbon in peatlands are likely to change under conditions of climate change. For example, the current extent of blanket peatland is projected to shrink (Gallego-Sala & Prentice 2012); however, warming may increase the overall peatland carbon sink in the mid- to-high latitudes due to longer and warmer growing seasons if soil moisture is sufficiently maintained (Gallego-Sala *et al.* 2018). However, evidence of widespread drying across

European peatlands in the last 400 years, linked to their drainage for agricultural and forestry use, suggests that soil moisture might not be retained, risking carbon losses (Swindles *et al.* 2019). While these studies using global datasets miss much site-specific detail, they can identify broad trends that are likely to be observed as climate changes and, therefore, offer useful insights about factors which may or may not support continued C accumulation. Indeed, the response of peatland to climate change does not follow a direct cause-effect relationship, but instead involves causal feedback loops linking hydrological processes and peat accumulation, which may lead to large and rapid changes in C cycling (Belyea 2009).

Long-term palaeoecological records (e.g. Vitt *et al.* 2000) identify changing patterns of surface vegetation in response to climate change; however, the record of net peatland C accumulation commonly observed in stratigraphic studies points to significant resilience of the peatland carbon sink to regular patterns of climate change and underlines the important role of peatlands in climate regulation (Yu 2011). The scale of climate change predicted for the next century and the magnitude of human impacts on peatlands in the last century (Joosten *et al.* 2016) mean there is a risk that undrained peatland systems could cross a threshold to a modified system state. By this we mean an alternative state for the ecosystem which may have differing capacity to deliver ecosystem services. Feedbacks between hydrology, vegetation and the microbial community are likely to control the resilience (in the sense of Walker *et al.* 2004) of the system to transitions, and will be key to understanding these processes and the possibility of rapid transitions brought about by climate extremes (Turner *et al.* 2020).

Other anthropogenic pressures (drainage, atmospheric deposition chemistry, burning, grazing, peat cutting and afforestation) can contribute to peatland drying, erosion and shifts in vegetation (Swindles *et al.* 2019, Evans *et al.* 2006), and potentially large loss of C (Heinemeyer *et al.* 2019), exacerbating the impact of climate change. As these pressures are more likely to occur in the mid-to-lower latitudes where direct anthropogenic influence is greater, peatlands in this zone are likely to experience varied responses to future conditions. In the high latitude areas, where other anthropogenic impacts have been minimal, climate change will be the dominant force with larger changes in temperature and precipitation, whereas the temperate and tropical zones will have smaller changes in climatic conditions but are likely to suffer greater direct

anthropogenic pressures. Therefore, it is imperative to consider not just changes in temperature or precipitation, but how these interact with the many other drivers of change.

It is worth noting here that some degraded peatlands are apparently recovering spontaneously by switching from erosion to renewed C accumulation - a type of ecological regime shift observed in some UK peatlands that were once actively eroding and are now undergoing spontaneous revegetation (Hancock *et al.* 2019, Milner *et al.* 2020). Understanding the processes behind these regime shifts and subsequent application to management and restoration could deliver a huge potential net C benefit by reactivating peat formation on degraded peatlands (Heinemeyer *et al.* 2019). The processes which underlie changes in peatland soil C cycling under conditions of changing climate are predominantly microbial (with important linkages to vegetation) but until recently it has been difficult to precisely quantify the functional role of different microbial communities, or microbial diversity itself, in peatland processes.

In summary, climate change is likely to exacerbate existing anthropogenic pressures on peatlands. Whilst continued carbon sequestration and storage is possible under future higher temperatures, this is predicated on soil moisture levels being maintained. This may not be possible given future changes in rainfall patterns, continued drainage of peatlands for agricultural and forestry use, and other pressures. Given the diverse pressures on global peatlands, geographically variable pressures of climate change act across a spectrum of intact, degraded, regenerated and restored peatland systems. Simple proxies calibrated under current conditions may not be appropriate for future no-analogue conditions (Ritson *et al.* 2021). A process based understanding of peatland function rooted in knowledge of microbial communities and processes is essential to a proper analysis of changing peatland function in a warming world.

EFFECTS OF CLIMATE CHANGE ON PEATLAND MICROBIAL COMMUNITIES

Peatlands support taxonomically and functionally diverse microbial communities. Saprotrophic and ericoid mycorrhizal fungi and bacteria play major roles in litter decay. Methanogenic archaea are found in deeper anoxic layers and methanotrophic bacteria in the overlying layers can oxidise some of the methane they form. The vertical stratification of

species and the diversity of taxa means that the effects of changing temperature and moisture conditions are experienced differently. In this review, which draws on literature post-2012 (not reviewed by Andersen *et al.* 2013), we consider separately the effects of climate change (increases in temperature and decreases in peat moisture content) on fungi, and on bacteria and archaea. We also draw on evidence from studies concerning peatland drainage, as these offer insight into microbial communities which may occur if water tables are lowered due to climate change. Three separate searches in Web of Science were carried out: (1) peat* AND fung* AND climate change; (2) peat* AND bacteri* AND climate change; (3) peat* AND archaea* AND climate change. From each of these searches post-2012, a study was chosen as relevant if it had fungal, bacterial or archaeal community structure data (with functional data if available) in response to increases in peat temperature and decreases in peat moisture. The chosen studies were supplemented by extensive review by the authors. Studies of predominantly freshwater environments in peatlands were not included.

Effects of increased temperature on fungal communities in peatlands

Table A1 in the Appendix shows a summary of the effects of increased temperature on fungal communities in peatlands. Asemaninejad *et al.* (2018) hypothesised temperature-induced shifts in structure of fungal communities in favour of recalcitrant compound decomposers observed across a depth gradient (Table A1), which may reduce long-term C storage of boreal peatlands under (warmer) future climate change scenarios. Similarly, organic matter (fungal necromass) stabilisation in peatland hollows was reduced by ~39 % and ~45 % under +4.5 °C and +9 °C increases in temperature resulting in a reduction in long-term C storage (Fernandez *et al.* 2019). In minirhizotron tubes installed in a forested bog, a loss of fungal functional diversity (which may reduce peat carbon accumulation) was found between the warm (+9 °C, elevated CO₂) and cold (0 °C, elevated CO₂) ends of the experimental temperature gradient; and the below-ground active season for both plant roots and fungi was extended by 62 days at the warm end compared with the cold end of the gradient, with implications for below-ground C fluxes (Defrenne *et al.* 2021). Soil fungal abundance increased after warming in several studies (Binet *et al.* 2017, Jiang *et al.* 2020, Song *et al.* 2021a, 2021b; Gao *et al.* 2022), although Peltoniemi *et al.* (2015) found that fungal biomass decreased in

response to increased temperature (Table A1). Ericoid shrub removal had cascading effects on soil fungal community composition but there was no effect of warming on the fungal community (Ward *et al.* 2015; Table A1).

Effects of water level drawdown / drought on fungal communities in peatlands

Table A2 contains information from studies of the effects of water table drawdown / drought on fungi in peatlands. As with the response to warming, variation of peatland fungal communities and experiments in differing peatland types with different vegetation complicate our understanding of the fungal communities' response to drought. For example, fungal biomass increased with water level drawdown in a 28-day drought experiment (Kwon *et al.* 2013) in samples from a tropical peatland, yet was found to be reduced in a comparison of near-natural sites and those that had been drained for 51 years in an ombrotrophic bog in Finland (Mpamah *et al.* 2017) (Table A2). These differences can perhaps be explained by the multiple effects caused by water table drawdown and the timescales over which they occur. Drawdown creates oxic conditions that drive increased decomposition in the short term, and changes vegetation with associated shifts in litter chemistry and root exudation in the longer term. Comparing these two contrasting results perhaps shows the difference in short vs. longer term effects of oxic conditions, which at first increase the abundance of fungi (Kwon *et al.* 2013) and later lead to decreases as peat chemistry, vegetation and pH change (Mpamah *et al.* 2017). Evidence for this hypothesis can be drawn from the fact that sites which had been drained in the study of Kwon *et al.* (2013) had lower abundance of fungi (i.e. showed the same effect as in Mpamah *et al.* (2017)) before increasing when exposed to an extreme drought. Contrasting results were also observed where fungal-derived membrane fatty acid abundance was highest in the upper part (0–30 cm) of the drained layer (Groß-Schmolders *et al.* 2021) whereas soil fungal PLFAs in the oxic zone of the drained site were lower than in the natural peatland (Xue *et al.* 2021; Table A2). In terms of fungal community structure, fungal lignocellulose degraders were enriched in the lowered water table treatment (Rupp *et al.* 2021) and water-table drawdown increased fungal diversity favouring Basidiomycota and Zygomycota with detrimental effects for Ascomycota.

In a non-manipulation study, the level of the water table was shown to potentially shape the structure of fungal communities at the micro-scale in boreal

peatlands (Asemaninejad *et al.* 2017a). Hollows contained a more diverse fungal community than hummocks, although fungal diversity was equally high at the same distance from the water table (Asemaninejad *et al.* 2017a). Consequently, it is expected that, following potential water table drawdown under future climate change scenarios, the zones of high fungal diversity would be most affected in boreal peatlands and possibly shrink or move downwards in the soil profile.

Multi-year experimental drought manipulations in nutrient poor acidic *Sphagnum* peatlands (Lamit *et al.* 2021) revealed that fungi were sensitive to both drought and changes in plant functional groups. Drought affected the abundance of ericoid mycorrhizal fungi, with negative effects on relative abundance in the shallowest peat (0–10 cm). The plant functional group effects arose largely from the dominance of ericoid mycorrhizal fungi in the oxic peat layers. When Ericaceae were removed, lignocellulose degraders (especially *Galerina* species) became dominant, suggesting that Ericaceae might suppress decomposers via their root-inhabiting ericoid mycorrhizal fungi. Since shrubs typically respond positively to water table drawdown (Potvin *et al.* 2015), it is possible that peatland drying could lead to greater ericoid mycorrhizal suppression of saprotrophs and pathotrophs, altering decomposition pathways and rates.

Effects of increased temperature on bacterial and archaeal communities in peatlands

A variety of approaches has been used to study the effects of increasing temperature on bacterial and archaeal communities in peatlands (Table A3), including small open-top chambers (e.g. Delarue *et al.* 2015, Peltoniemi *et al.* 2016, Weedon *et al.* 2017, Song *et al.* 2019), peat monoliths inserted in perfusion systems in solar domes (Kim *et al.* 2012), mesocosms (Weedon *et al.* 2013) and anoxic microcosms (Cui *et al.* 2015, Tveit *et al.* 2015; Table A3). In microcosms containing anaerobic deep (1.5–2 m) peat, the production of CO₂ and CH₄ was significantly greater in 15 °C treatments than in 6 °C treatments, although microbial community structure did not differ between the two temperatures (Kluber *et al.* 2020). Several experiments have additional treatments e.g. moisture regimes (Peltoniemi *et al.* 2016) and substrate additions (dead microbial cells, roots; Weedon *et al.* 2013). Methanogen abundance decreased (e.g. Kim *et al.* 2012, Peltoniemi *et al.* 2016) and increased (Song *et al.* 2019, 2021a, 2021b; Jiang *et al.* 2020) under warming. Methanotroph abundance increased after warming (Song *et al.*

2021a, 2021b; Jiang *et al.* 2020). The abundance of bacteria increased after warming (Delarue *et al.* 2015, Jiang *et al.* 2020, Gao *et al.* 2022) with temperature positively correlated with copiotrophic bacterial abundances and negatively with oligotrophic bacterial abundances in the hollows (Maillard *et al.* 2022).

The ongoing expansion of shrub cover in response to climate change presents an opportunity to explore the link between soil microbial communities and vegetation changes (Bragazza *et al.* 2013, 2015). This link is particularly important in peatlands where shrub expansion is expected to feed back negatively on the C sink capacity of these ecosystems (e.g. Gavazov *et al.* 2018, Street *et al.* 2020). Microbial community structure and function were measured seasonally in four peatlands located along an altitude gradient representing a natural gradient of climate and associated vascular plant abundance (Bragazza *et al.* 2015). The authors showed that increased soil temperature and reduced water content were associated with greater vascular plant biomass, in particular that of ericoid shrubs. This increased vascular plant biomass was correlated with greater microbial biomass and with microbial community structure characterised by an increasing dominance of fungi over bacteria with improved soil oxygenation. Bragazza *et al.* (2015) found that the C and nitrogen (N) stoichiometry of microbial biomass differed in relation to soil microbial community structure and that this was ultimately associated with a different investment in extracellular enzymatic activity of potential importance to carbon mineralisation.

Effects of water level drawdown / drought on bacterial and archaeal communities in peatlands

Table A4 contains information from studies of the effects of water table drawdown / drought on bacteria and archaea in peatlands. Archaeal communities were changed strongly by drainage (Kwon *et al.* 2013, Tian *et al.* 2015, Urbanová & Barta 2016; Table A4). Drainage significantly increased the biomass of methanotrophs (Cao *et al.* 2018). Drainage increased the abundance of bacteria (Mpamah *et al.* 2017, Cao *et al.* 2018, Groß-Schmölders *et al.* 2021). “Drought responsive OTUs” were disproportionately drawn from Bacteroidetes and Proteobacteria (Potter *et al.* 2017), Acidobacteria became dominant in drained sites (Urbanová & Barta 2016) and Xue *et al.* (2021) found an increase in the relative abundance of Proteobacteria and a decrease in the abundance of Firmicutes. In a non-manipulation study, Asemaninejad *et al.* (2019) examined the diversity and composition of

prokaryotic communities across a micro-topographical hummock-hollow gradient in a boreal peatland. There was an overlap in functional groups at lower layers (30–35 cm depth) of the hummocks and upper layers of the hollows (0–5 cm depth); however, significantly different prokaryotic communities were found in hollows compared with hummocks. Surfaces of hummocks (0–5 cm depth) were typified by aerobic chemoorganotrophs, methanotrophs and chemoheterotrophs, mid-depths were typified by aerobic chemoorganotrophs, N-fixing bacteria and anaerobic nitrate reducers, while lower depths (30–35 cm depth) in hollows were typified by anaerobic and facultative anaerobic chemoorganotrophs, nitrate reducers and methanogenic archaea.

A multi-year drought experiment found that lower water tables led to lower relative abundance of methanogens at 0–10, 10–20 and 30–40 cm depth (Lamit *et al.* 2021). By contrast, methanotrophs were responsive to the presence of sedges, the interactions of Ericaceae with water table, and the interactions of water table and depth. When sedges alone were present, the relative abundance of methanotrophs declined with lowered water table whereas, when Ericaceae were present, this water table effect was lessened or reversed depending on depth. Hence it appears that the complex interactions of plant functional groups and water table depth can drive the relative importance of methanogens and methanotrophs in ways that could alter methane efflux (e.g. Robroek *et al.* 2015).

Effects on microbes of nutritional gradients in relation to climate change in peatlands

Climate change can lead to shifts in the dominant vegetation present in northern peatlands, including changes from *Sphagnum* to vascular plant domination (Haynes *et al.* 2015). Such shifts in vegetation can result in changes to the chemical properties of C substrates for soil microbial decomposers (e.g. Robroek *et al.* 2016) with leaves and roots deposited at the peat surface and subsurface typically decomposing faster than *Sphagnum*. Haynes *et al.* (2015) characterised bacterial and fungal communities by T-RFLP along a nutrient gradient from rich to poor fen peatlands and assessed the metabolic potential of these communities to respire a variety of organic matter substrates of varying chemical complexity using substrate-induced respiration (SIR) assays. The rich and intermediate fen sites were dominated by non-tussock-forming sedges (*Eriophorum vaginatum* and *Carex* sp.) and sweet gale (*Myrica gale*), with some *Sphagnum*

mosses and sparse ericaceous shrubs present at the intermediate fen site. The poor fen was dominated by *Sphagnum* hummocks with leatherleaf (*Chamaedaphne calyculata*) and bog laurel (*Kalmia polifolia*) shrubs and a sparse overstorey of trees containing *Larix laricina* and *Picea mariana*. Distinct microbial communities existed in the rich, intermediate and poor fens, but SIR in each of the three sites exhibited the same pattern of C release, providing support for the concept of functional redundancy (e.g. Deacon *et al.* 2006), at least under standardised in vitro conditions. Preferential C release of simple organic substrates in the rich fen and complex compounds in the poor fen was not observed. Similarly, no preference was given to “native” organic matter extracts derived from each fen, with microbial communities opting for the most bioavailable substrate. This study suggests that soil microbes might be able to respond relatively rapidly to shifts in vegetation and subsequent changes in the properties of C substrate additions to peatlands associated with climate change. Functional redundancy in this case ensured stability (resilience) in carbon cycling.

There are examples of the effects of peatland nutritional gradients on populations of methanogens and methanotrophs. Increasing soil mineral nutrient content, on a gradient of minerotrophic, mixed and ombrotrophic categories of tropical peatlands, provided favourable habitats for *Methanobacteriaceae* (methanogens) while *Methylocystaceae* (methanotrophs) populations seemed to broadly distribute independent of nutrient content (Finn *et al.* 2020). Zhang *et al.* (2021) studied 14 peatlands in Finland located between latitudes of 60 °N and 70 °N on a gradient representing bogs, poor fens and rich fens. The abundance of all methanogens, except *Methanospirillaceae*, increased from bog to rich fen. The two methanotroph families (*Methylocystaceae*, *Methylococcaceae*) were concentrated towards opposite ends of the bog–fen gradient, with *Methylocystaceae* showing a distinct predominance in *Sphagnum*-dominated habitats. In a further gradient study, soil *mcrA* (methanogen) and *pmoA* (methanotroph) gene abundances in 0–15 cm depth of soil were high in continuous and discontinuous island permafrost peatlands, respectively (Y. Song *et al.* 2020). Soil *mcrA* and archaea were positively correlated with soil water content, TC, TN and DOC but negatively correlated with soil nitrate content. Soil *pmoA* gene abundances were positively correlated with TN, TC, soil water content, ammonia-N and TP but negatively correlated with soil nitrate content.

Effects of climate-driven shifts in vegetation on mycorrhizal fungi and fungal inter-guild interactions

In addition to shifts in the nutritional inputs of litter, changes in peatland vegetation driven by climate change are also associated with shifts in the presence and/or type of plant-associated mycorrhizal fungi. Whilst mosses and sedges do not form ‘typical’ mycorrhizal associations, grasses, ericaceous shrubs and invading trees (such as birch, spruce and larch) associate with arbuscular, ericoid and ectomycorrhizal fungi, respectively. These different functional groups can have substantially different below-ground C allocation (Ward *et al.* 2013) affecting the quality and quantity of soil organic matter and exudates released from roots and mycorrhizal fungi. Changes in this below-ground labile C, which can represent a significant proportion of total soil C inputs (Clemmensen *et al.* 2013), can in turn alter the composition and activity of wider microbial communities (Bardgett *et al.* 2013).

Distinct mycorrhizal guilds contribute differentially to organic matter decomposition, with many ericoid and ectomycorrhizal fungi capable of decomposing complex organic matter, and arbuscular mycorrhizal fungi having more limited degradation abilities (Frey 2019). While the presence of particular mycorrhizal fungal taxa may contribute to increases in decomposition rates (Zak *et al.* 2019), competitive

interactions with saprotrophic fungi can also reduce overall rates of decomposition (Fernandez & Kennedy 2015). For example, the presence of ericoid (Figure 1) or ectomycorrhizal fungi is associated with a wider C:N ratio in litter and inhibition of decomposition processes by saprotrophic fungi (Averill *et al.* 2014). This mechanism may partly explain observations that increases in the dominance of ericaceous shrubs in peatlands led to significant declines in decomposition rates (Ward *et al.* 2015) and their experimental removal can stimulate decomposition of some complex substrates (Wiedermann *et al.* 2017). Shifts in mycorrhizal guilds can also contribute to altered recalcitrance of soil organic matter directly, as some fungal species, particularly root associated ascomycetes, have highly melanised hyphae that are hard to decompose (Fernandez & Kennedy 2018). Hence, it is important to understand the mycorrhizal guild dynamics and inter-guild community structural response to climate change.

Other effects of climate change on microbes in peatlands - effects of alterations in snow cover and effects of permafrost

Alterations in snow cover driven by climate change may affect ecosystem functioning, including soil microbial processes (Robroek *et al.* 2013). In a Swiss mountain peatland, Robroek *et al.* (2013)

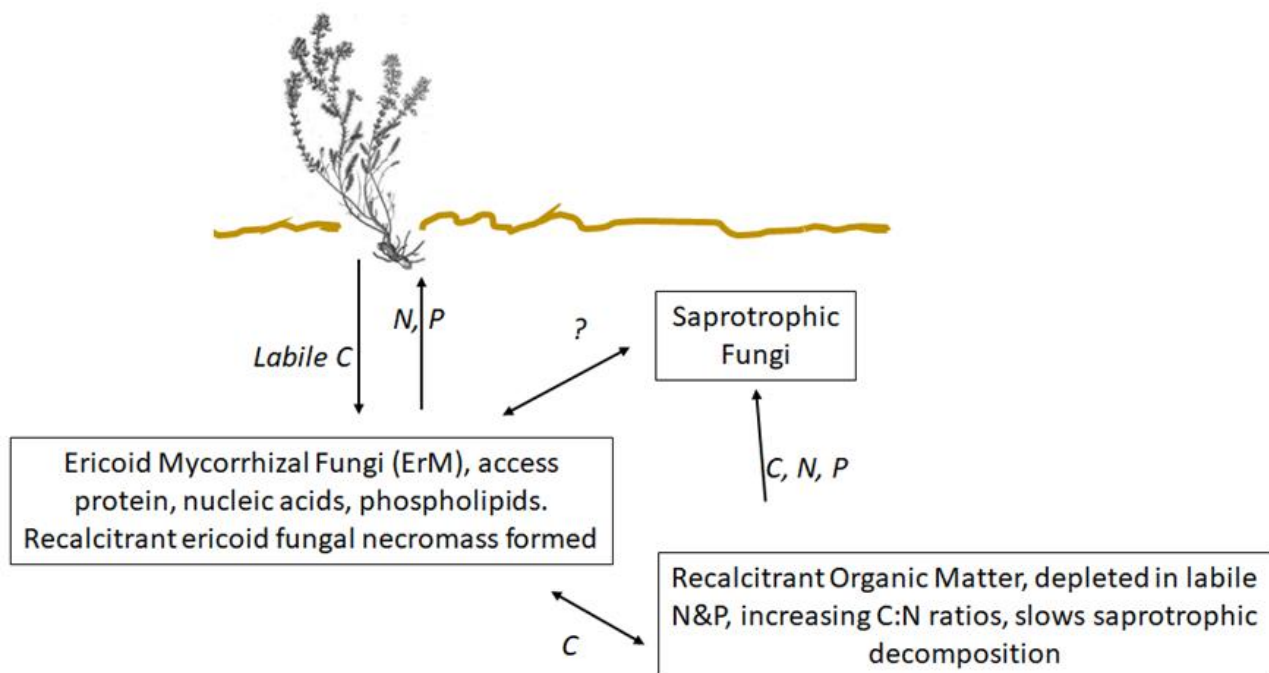


Figure 1. Conceptual model of ErM-saprotroph and ErM-plant interactions.

manipulated snow cover (addition, removal and control) and assessed the effects on soil microbial structure by phospholipid fatty acid (PLFA) analysis. Reduced snow cover produced warmer soils while increased snow cover kept soil temperatures close to freezing. Snow cover manipulation had a major influence on the microbial community, and prolonged ‘close-to-freezing’ temperatures caused a shift toward fungal dominance. Soil temperature largely explained soil microbial community structure. The authors envisaged that changes in composition of the microbial community driven by snow cover could lead to substantial changes in trophic fluxes and associated ecosystem processes.

Many key processes relevant to decomposition of C in soils are missing in models, particularly for permafrost C (IPCC 2021). Permafrost thaw is leading to rapid shifts in the ecosystem function of boreal peatlands. For example, fungal community composition differed significantly between thawed and intact permafrost sites (Schütte *et al.* 2019). Relative abundance of mycorrhizal fungal taxa decreased while relative abundance of putative fungal pathogens increased with permafrost thaw. In the greenhouse, ecto- and arbuscular-associated host plants had higher productivity in permafrost intact soils relative to thawed soils (Schütte *et al.* 2019). The results suggest that fungal communities are crucial in mediating plant community response and consequently C cycling to permafrost thaw.

Thawing permafrost could promote degradation of frozen and new C leading to biogenic production of methane, creating a positive feedback to climate change (Mondav *et al.* 2014). Characterisation of microbial community composition along a permafrost thaw gradient showed that partially thawed sites were frequently dominated by the single archaeal phylotype ‘*Candidatus Methanoflorens stordalenmirensis*’, which is widespread in high-methane-flux habitats suggesting it is a key mediator of methane-based positive feedback to climate warming (Mondav *et al.* 2014). The abundance of this phylotype is a key predictor of methane stable isotope composition, which is also linked to the ratio of methane to carbon dioxide emissions and, therefore, the strength of potential climate feedbacks driven by permafrost thaw (McCalley *et al.* 2014).

Summary of the effects of climate change on peatland microbial communities

In the years since the original Andersen *et al.* (2013) review there has been significant progress in understanding the interaction of peatland microbiota with changes in peatland condition. However, there

are still relatively few studies which combine the study of peatland microbial community structure with direct measurement of carbon cycling. Despite this caveat, current understanding suggests that increased soil temperature occurring because of climate warming (or disturbance of the natural vegetation cover and drainage) may result in reductions of long-term C storage via changes in microbial community composition and metabolic rates. Moreover, changes in water table alter the redox state and hence have broad consequences for microbial functions, including effects on fungal and bacterial communities, with the clearest effects seen in the balance of methanogens and methanotrophs.

PEATLAND RESTORATION, CLIMATE CHANGE AND MICROBIAL COMMUNITIES

The main effects of restoration on the peatland microbiome reported thus far are summarised in the recent review by Kitson & Bell (2020). In this work we focus on explaining the large microbially driven differences observed in methane emissions after restoration measures, a greater understanding of which is needed to garner both policy support and carbon financing for peatland restoration.

Peatlands will not continue to sequester carbon under climate change unless soil moisture can be maintained (Swindles *et al.* 2019), and for many peatlands this will require the reversal of drainage. As outlined in our recent commentary (Ritson *et al.* 2021), there is a need for a greater understanding of the role of microbial communities in determining peatland resilience to perturbations brought about by management and climate change. This is required to assess how these systems will respond outside the currently more well-studied conditions of water table, temperature and land use. Furthermore, there is an increasing trend for restoration projects aiming to increase peatland resilience to be dependent on carbon financing. Therefore, an understanding of the factors determining, e.g., the balance of GHG emissions post-restoration and how the microbial community controls the extent and resilience of these changes, is needed.

Peatlands have been subject to anthropogenic pressures for centuries, mainly through attempts at improvement for pasture, arable or forestry production, the harvesting of peat for fuel or horticultural purposes, sport shooting and development (mining, oil exploration, wind farms, infrastructure). Restoration commonly involves raising the water table by blocking drainage features

or erosion gullies, but can also include the introduction of native vegetation, removal of tree plantations, reprofiling of surfaces and other measures (Andersen *et al.* 2017, Chimner *et al.* 2017). While many indicators of successful restoration have been established, such as water table depth and other hydrological responses, vegetation establishment (Alderson *et al.* 2019) and GHG emissions, much less is known about the effect of restoration on the bacterial, fungal and archaeal communities which are fundamental to ecosystem services provision.

The drainage of peatlands has been shown to reduce methanogen abundance and diversity because oxic conditions prevail once the water table has been lowered, removing the habitat niches of anaerobic archaea (Juottonen *et al.* 2012) with fens being more sensitive to this than bogs (Urbanová *et al.* 2013). On rewetting, anaerobic conditions return with a lagged re-establishment of methanogens (Wen *et al.* 2018, Weil *et al.* 2020). This re-establishment has mixed effects on methane emissions, with some authors observing low methane emissions post-restoration (Juottonen *et al.* 2012, Urbanová *et al.* 2013, Urbanová & Bárta 2020) while others have noted large spikes in methane emissions (Hahn *et al.* 2015, Reumer *et al.* 2018, Weil *et al.* 2020) and some lasting impacts (Vanselow-Algan *et al.* 2015). As an example, Juottonen *et al.* (2012) found methane emissions in the growing season to be around 26 times higher in near-natural boreal mire sites compared to restored sites, whereas Hahn *et al.* (2015) found a 190-fold increase in methane emissions on re-flooding of a coastal fen.

The majority of methane emissions post-restoration have been shown by stable isotope and radiocarbon analysis to be from young sources, although increased methane production from older peat has also been demonstrated during the growing season, suggesting the possibility of priming of peat decomposition by vegetation (McNicol *et al.* 2020). High methane emissions have also been noted where the re-flooding of peatlands has caused dieback of the existing vegetation, providing a source of labile carbon for methanogenesis (Hahn *et al.* 2015). Furthermore, sites where methane emissions are low have been shown to be substrate limited (Urbanová & Bárta 2020), highlighting the importance of vegetation in methanogenesis and perhaps explaining why heavily degraded sites without vegetation cover can have low methane emissions after rewetting (Figure 2).

Variation in methanogen activity across restored sites is also dependent on the absence of more

thermodynamically favourable terminal electron acceptors. In a study across the chemical gradient of a reflooded fen, He *et al.* (2015) noted a negative correlation between methanogen abundance and that of nitrate-, sulphate- and metal-reducing bacteria, with methane production being highest where there was low availability of electron acceptors. Similar results have been found when comparing methane emissions between a percolation fen and a brackish coastal fen. In this instance, the brackish site showed higher abundance of sulphate reducers and lower abundance of methanogens, with consequently lower methane emissions than the other sites (Weil *et al.* 2020). Given the importance of organic electron acceptors in peat for regulating methane emissions (e.g. Klüpfel *et al.* 2014) and the effect of peatland drainage on the chemical character of peat (e.g. Kane *et al.* 2019), differential abundance and character of organic electron acceptors could also play a part in regulating the methane efflux from rewetted peatlands.

A further explanation for differences in methane emissions across sites is the presence of an aerobic methanotroph community where both O₂ and CH₄ are available (Wen *et al.* 2018). This important habitat niche for methanotrophs is quite vulnerable to destruction, for example in rewetted fens where the water table is maintained well above the peat surface all year round and where peat bulk density near the surface is much higher than in natural peatlands because of drainage-induced subsidence and decomposition. Vegetation re-establishment can aid development of the methanotrophic community by making O₂ available in the rooting zone (He *et al.* 2015); but methanotrophs can be outcompeted for O₂ by heterotrophs such as *Hyphomicrobiaceae*, which was shown to be the most abundant microbial family at two fen sites by Wen *et al.* (2018). There is growing evidence that the re-establishment of *Sphagnum* at restoration sites will aid methane oxidation due to the role of associated endophytic methanotrophic bacteria (Stępniewska *et al.* 2018).

Whilst the number of studies concerning the effect of restoration on the peatland microbiome is still limited, there is growing evidence that water table position and variability (and thus prevalence of niches containing O₂ and CH₄), as well as vegetation, are the main factors controlling methane emissions and, therefore, short-term GHG balances, with water table position governing the longer term (Evans *et al.* 2021, Huang *et al.* 2021). Further to this, the availability of alternative electron acceptors strongly affects microbial community structure and methane cycling, as does the site's history of land use and

deposition chemistry. As restoration sites transition towards higher steady state water tables, methane flux is likely to be controlled by the response of the microbiome to changing site conditions, so an understanding of these interactions is critical to assessing and potentially controlling any transition effects.

More research is needed into the interaction between climate change and different management practices with respect to microbiology, particularly given the large scope for variation between types of peatland, land-use history, deposition chemistry and

current management. Developing this knowledge can build confidence in the assessment of the GHG balance of restoration projects, which can be adversely affected by high methane fluxes in the years after restoration but which, in the longer term, may avoid CO₂ emissions via the oxidation of peat (Evans *et al.* 2021, Huang *et al.* 2021). Microbial process understanding is needed to assess this balance of methane and CO₂ emission over time. With this understanding, it may be possible to secure further policy support and carbon financing to increase the resilience of peatlands to climate change.

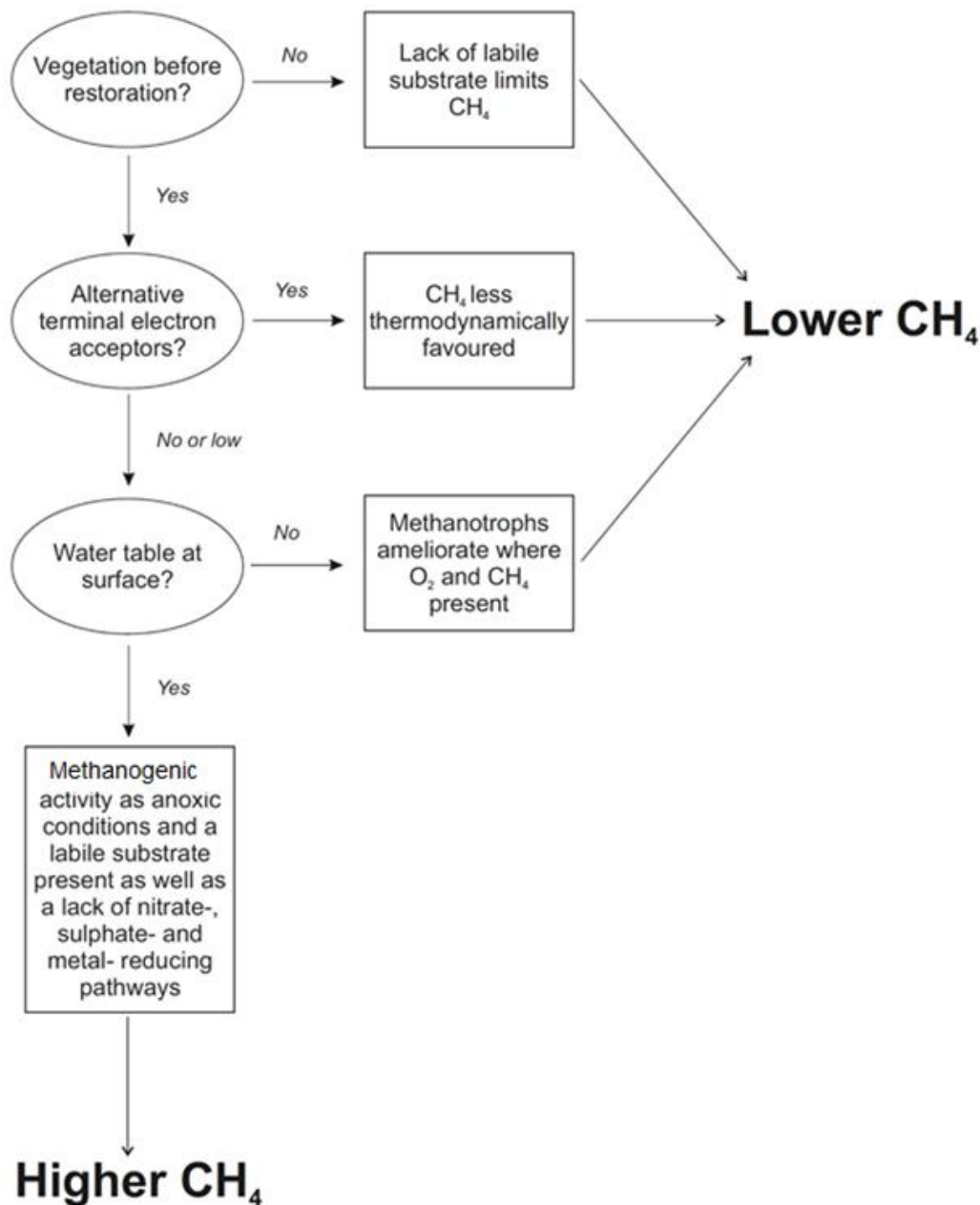


Figure 2. Flow diagram explaining when methane spikes might be expected post-restoration.

GAPS IN RESEARCH

Progress and gaps since the review of Andersen *et al.* (2013)

In the review by Andersen *et al.* (2013), one of the final questions asked was “Peatland microorganisms - what are they?” Subsequent to the Andersen *et al.* review, a range of methods has been used to identify microbes in peatlands (e.g., reviewed for fungi by Juan-Ovejero *et al.* 2020). This range of techniques includes molecular approaches, particularly the use of 16S rRNA genes for identifying bacteria and archaea. Anaerobic methane oxidation, shown to oxidise up to 30 % of the methane produced in some peatlands, has been found (Miller *et al.* 2019). Through whole genome sequencing approaches we are beginning to learn more about the microbial genes and pathways playing key roles in peat biochemistry, as well as determining the identities and ecology of organisms possessing these functions.

For example, in their study of high-arctic peatlands, Tveit *et al.* (2013) were able to define the identities of dominant bacteria and archaea involved in anaerobic and aerobic degradation of plant polymers. These authors additionally found genetic evidence for increased anaerobic respiratory and fermentative degradation pathways with peat depth, also consistent with depth-related increases in methanogenic pathways. Lin *et al.* (2014) contrasted several ombrotrophic peatlands in the Marcell Experimental Forest, Minnesota (USA), and found similar depth relationships with anaerobic pathways, but also identified that these *Sphagnum* dominated soils had high levels of N₂ fixation genes compared with non-peat soils. The finding that N fixation genes are elevated in peat soils has been replicated independently in a range of other studies (e.g. Malik *et al.* 2017, Warren *et al.* 2017), with the Bradyrhizobiaceae and Beijerinckiaceae identified as dominant diazotrophs, the latter also possibly involved in methanotrophy (Vile *et al.* 2014; but see Leppanen *et al.* 2015, Kox *et al.* 2018). These findings potentially indicate a reliance on gaseous N (as opposed to plant-derived N) to sustain the microbial community in peat systems.

Key insights come from from metagenomics (Woodcroft *et al.* 2018), metagenomics / transcriptomics (Singleton *et al.* 2018) and metabolomics (Wilson *et al.* 2021). Metagenomic sequencing of 214 samples from a permafrost thaw gradient was carried out to recover 1,529 metagenome-assembled genomes, including many from phyla with poor genomic representation (Woodcroft *et al.* 2018). Metagenomics revealed key

populations involved in the degradation of organic matter, including bacteria whose genomes encode a previously undescribed fungal pathway for xylose degradation. Microbial and geochemical data highlighted lineages that correlate with the production of greenhouse gases and indicate novel syntrophic relationships (Woodcroft *et al.* 2018), linking microbial community taxonomy to function. Metagenomics and transcriptomics, paired with *in situ* biogeochemical data, were used to gain a view of methanotroph community structure and function in the active layer of a thawing permafrost gradient by Singleton *et al.* (2018). Thirteen methanotroph population genomes were recovered, including two novel genomes belonging to the uncultivated upland soil cluster alpha (USCalpha) group and a novel potentially methanotrophic Hyphomicrobiaceae. Combined analysis of porewater delta¹³C-CH₄ isotopes and methanotroph abundances showed methane oxidation was greatest below the oxic-anoxic interface in the bog. Using metabolomics, Wilson *et al.* (2021) observed an increase in abundance of methanogenic genes in response to the increase in abundance of labile substrates occurring because the vascular plant cover of peatland tends to increase during warming, accompanied by a shift toward acetoclastic and methylotrophic methanogenesis. These authors stated that, with a warming-induced increase in vascular plant cover, a concomitant shift towards increasingly methanogenic conditions and amplified climate–peatland feedbacks is expected.

Since the review by Andersen *et al.* (2013), a rapidly expanding *Sphagnum* microbiome database has been set up (Kostka *et al.* 2016), indicating that a diverse community of microorganisms is intimately associated with *Sphagnum*, inhabiting the tissues and surface of the plant. More generally, through molecular sequencing approaches it is becoming clear that acidic peats have characteristic communities composed predominantly of *Acidobacteria*, *Alpha-* and *Deltaproteobacteria*. The acidobacteria have few cultured representatives, but with the ability to reconstruct genomes (MAGs) from whole genome sequencing datasets, we are now beginning to understand more about their function. For example, Hausmann *et al.* (2018) recently constructed Acidobacterial MAGS from an acidic peat and revealed that their genomes comprised potential for facultative anaerobic metabolism, oxygen respiration, fermentation, polymeric carbohydrate degradation and hydrogen metabolism, which demonstrates versatile metabolic capability for conserving energy required for life in peat systems.



Doubtless the continued progress in understanding the genetic features of peatland microorganisms, coupled with greater understanding of their ecology and sensitivity to change, will provide new avenues for linking with biogeochemical analyses to better understand the functionality of peat in a changing environment.

Another question asked in the review by Andersen *et al.* (2013) was “What happens to microbial diversity, function and their interaction when a peatland is disturbed?” Andersen *et al.* (2013) suggested that microbial species sorting (Van der Gucht *et al.* 2007) occurs, whereby in a given community only part of the pool of organisms present is active at any given time depending on, for example, substrate availability or redox status. Additionally, Andersen *et al.* (2013) proposed that functional redundancy, where different microorganisms carry out the same function, may be an important mechanism which controls diversity and maintains the function of peatland microbial communities. This is an area where less progress has been made. A key absence from peatland literature is the analysis of fungal communities using RNA, which identifies the ‘active’ microbial community and its enzymatic functions, in contrast to approaches using DNA which identify the ‘total’ fungal community (e.g. Cox *et al.* 2019). However, polysaccharide hydrolysis, fermentation, methanogenesis and methanotrophy in peatlands have been characterised using RNA techniques (e.g. Tveit *et al.* 2014, Singleton *et al.* 2018, Täumer *et al.* 2022); and our current review, which uses climate change as an example cause of peatland disturbance, does contain support for functional redundancy from the study of Haynes *et al.* (2015) above.

Our further review of the literature reveals relatively few studies that assess both microbial diversity and function. This paucity may be because the complexity of rapidly advancing genetic approaches and developing approaches to monitoring peatland carbon fluxes mean that such work requires multidisciplinary teams to understand the result of climate change for microbial community diversity and function in peatlands. Field experiments and *in situ* approaches could improve our understanding of the functional roles of microbes under more realistic climate change conditions (Juan-Ovejero *et al.* 2020). However, *ex situ* experiments are also insightful in reducing system complexity and isolating individual factors to understand key microbial process mechanisms. Further, a long-term perspective is needed to assess the possible shifts in microbial and plant communities under projected temperature

increases and lower water tables (and their interaction) in peatlands (Juan-Ovejero *et al.* 2020) as well as responses to restoration. Such long-term approaches are needed to contextualise short-term studies looking at effects of climate-induced extreme events (wildfires, droughts, flooding) and management (e.g. rewetting), particularly under a range of land uses or landscape settings. These themes constitute a future research agenda which is developed further in the complementary commentary by Ritson *et al.* (2021).

Gaps in research for peatland restoration related to microbial communities

We now have an increased understanding of how degradation and restoration affect the microbial community and methane cycling in northern peatlands. Rewetting of peatlands as part of restoration does not necessarily (but potentially could) lead to large methane emissions. Instead, spikes in methane during restoration are likely where labile carbon sources are present and alternative terminal electron acceptors are limited. Further work is needed to develop long-term understanding, and to disentangle the contributions of the many combinations of peatland type, land use history, deposition chemistry and severity of degradation. There is also currently a paucity of studies from tropical peatlands. With the knowledge gained so far there have been some successful attempts at interventions to nudge microbial community function in the desired direction through methods such as inoculation with favourable fungi (Tawarayama & Turjamam 2014) and the removal of nutrient-rich topsoil prior to restoration (Huth *et al.* 2020). This management of the microbial community for beneficial outcomes remains an avenue for further research and translation of microbial understanding into peatland restoration practice, including the development and use of microbial techniques to monitor restoration success. The notional definition of “success” itself may need to be revisited, and may differ for different sites and regions. From a microbial perspective, structural convergence towards “reference” conditions may not be achievable, but may also not be necessary to return key functions and reinstate feedback loops essential to long-term resilience.

Gaps in incorporating microbial processes into peatland models

Ecosystem models projecting changes in carbon stocks in soils in response to changes in future climate and management strategies often do not

explicitly consider microbial functions (Allison *et al.* 2010, Wieder *et al.* 2013). Incorporating microbial processes into peatland models has also been challenging, partly due to the mismatch in the timescales and spatial scales over which many key processes occur. Whilst many peatland models are developed using monthly or annual timesteps to understand peat accretion at high spatial resolution, microbial processes can be responsive to daily changes in temperature and water table position. It may be possible, however, to start incorporating microbial understanding into large scale earth system models such as JULES (Joint UK Land Environment Simulator) which run on a daily timestep (e.g. Gedney *et al.* 2019), and incorporating microbial processes could improve modelling of the seasonal dynamics of methane production (Chadburn *et al.* 2020). Further results have also been reported in incorporating microbial processes into the Integrated Biosphere Simulator model to examine wetland methane production (C. Song *et al.* 2020).

Newer decomposition models generally pertaining to soils have incorporated microbial functions with promising results (Allison *et al.* 2010, Wieder *et al.* 2013) but their inclusion increases uncertainties in predictions (Bradford *et al.* 2016, Sulman *et al.* 2018). This is largely due to the lack of mechanistic understanding of the feedback responses of complex microbial communities (Bardgett *et al.* 2008). The models may also struggle to describe microbial processes in response to changes in water table and vegetation cover in peatlands, as these processes are not well understood. Earlier decomposition models with microbial components coupled organic matter turnover to microbial biomass and physiology, with inclusion of extracellular enzymes that catalyse the breakdown of polymeric substrates into dissolved organic matter (Schimel & Weintraub 2003, Allison *et al.* 2010). In peatlands, degradation is largely driven by the loss of waterlogged anoxic conditions, which is likely to stimulate microbial growth and enzyme activity. Incorporating these fundamental processes in models predicting CO₂ emissions could be a first step towards coupling microbial physiology into predictions of large-scale processes. This advance could be made without incorporating taxonomic and functional diversity as it is difficult to distil the complexity of microbial communities into ecologically meaningful groups.

One way of reducing this complexity, while including some details of microbial processes into models, is to incorporate functionally relevant microbial groups. One such approach is the

Microbial-Mineral Carbon Stabilization (MIMICS) model (Wieder *et al.* 2014) that incorporates microbial functional groups based on life-history strategies that are optimised for different resource environments (copiotrophic and oligotrophic). However, quantifying the shifts in these groups in soils is challenging as this categorisation has been based largely on coarse-level taxonomic classification and assumes that organisms within a phylum have similar physiological characteristics (Ramirez *et al.* 2012, Thomson *et al.* 2013). While some of the microbial functional traits like growth efficiency and turnover rates exhibit evolutionary pressures, the copiotroph-oligotroph dichotomy is difficult to establish in complex microbial communities (Morrissey *et al.* 2016, Roller & Schmidt 2015). There is a need to develop observationally based tools to better capture their physiology. One way to achieve this is to use a trait-based approach, which is gaining popularity in microbial ecology and is already widely used for other taxonomic groups in peatland research, including testate amoebae (e.g. Marcisz *et al.* 2016, Zhang *et al.* 2020), plants (e.g. Goud *et al.* 2017, Konings *et al.* 2019, Lin *et al.* 2020) and arthropods (e.g. Neoh *et al.* 2017, Pravia *et al.* 2019). Quantification of traits, or phenotypic characteristics, will enable direct assignment of function to meta-communities under different change scenarios, with the long-term goal of informing carbon cycle projections made by terrestrial ecosystem models in response to environmental change. Defining life history strategies based on traits into high yield (Y), resource acquisition (A) and stress tolerance (S) (the Y-A-S framework) is one available approach which can incorporate key microbial processes in peatlands including stress, which is likely to be a big factor (Malik *et al.* 2020). Integrating these trait-based insights along with some community-aggregated process rate measurements into spatial modelling tools will help upscale the projections to ecosystem and global scales (Wieder *et al.* 2015).

Further experimental work is needed to understand the functional response of peatlands outside the envelope of previously observed conditions to ensure better model parameterisation and greater predictive power under future climate conditions. In this, process-based models may offer a way forward for understanding non-analogue resilience. Collaboration between peatland scientists and the modelling community will be essential to ensure that results from observation and manipulation experiments can allow incorporation of microbial process understanding into peatland models and wider earth system models.

CONCLUSIONS AND IMPLICATIONS FOR FURTHER WORK

Our review reveals four key aspects on which our understanding of peatland microbiology has advanced in the past nine years:

- (i) the importance of ericaceous mycorrhizas versus saprotrophic fungal competition in potential peatland carbon sequestration;
- (ii) the importance of the re-establishment and resilience of methanotroph communities in mitigating CH₄ flux;
- (iii) the potential of microbial-trait-based approaches in modelling C cycling in peatlands; and
- (iv) the possibility that drying of peatlands (leading to more ericaceous shrubs in temperate peatlands) is partly mitigated by lower decomposition rates caused by competition between ericaceous mycorrhizas and saprotrophic fungi resulting from this vegetation change.

However, it is important to note that most studies to date have focused on northern peatlands while the microbial communities of tropical peatlands, and the likely impact on them of anthropic change/climate change, remain largely unknown. Given their large C stocks, extent of land use change, and potential for rehabilitation/restoration, this should be a priority for future research effort. There is some work in this direction e.g. Mishra *et al.* (2021).

Microbial community structure, function and peatland resilience

The long-term persistence of peatlands in the landscape and their role in C cycling at Holocene timescales demonstrates that undamaged peatlands' C sequestration and climate regulation functions are resilient to changes in climatic conditions. Understanding the process basis of this resilience requires progress on the links between microbial community structure and function and the ways in which microbial processes respond to changes in the peatland environment. Functional redundancy in microbial communities, and the capacity for elements of the microbiome to persist in inactive or dormant states in peat, are potentially important components of peatland resilience to climate change. In addition to functional redundancy and dormancy, other factors such as phenotypic plasticity and rapid temporal changes make it harder to link specific groups within the microbiome to ecosystem service provision during peatland restoration. Thus, the decoupling of microbial taxonomic identity and function poses an

immense challenge in linking microbiome to ecosystem processes. It can also be argued that diversity measurements may be less useful than functional analysis when studying system-level processes. Microbial phenotypic characteristics or traits could be a better indicator of key ecosystem processes like C storage or degradation. Understanding the system-level implications of microbial processes therefore needs an integrated understanding of taxonomy, function and process rate. There is an urgent need for integrated studies to support this aim.

There is much to be done to understand the detail of these interactions between peat microbiome, environment and functions. Since the review by Andersen *et al.* (2013) there have been considerable advances in gene and metagenome sequencing which allow analysis of the microbiome at higher speed and lower cost; and progress on metatranscriptomic, metaproteomic and metabolomic approaches which target microbial activity. A growing body of work is beginning to unpick the fundamental processes which underpin carbon sequestration in peatlands (e.g. St. James *et al.* 2020) but, in the context of a rapidly changing climate, further progress is urgently required to understand the potentially synergistic effects of climate-induced and land-use changes. Such progress is likely to require stronger collaborations between peatland scientists, microbiologists, palaeo researchers and climate modellers. Peatlands are highly compartmentalised systems; do we study them at the correct scale(s), and how can different scales be integrated adequately? How do new molecular methods enable better insight into spatially variable processes and how do we upscale towards global predictions? Management and restoration of peatland systems represents a form of green geoengineering with potential to provide long term drawdown of atmospheric carbon. At one extreme this may include engineering a resilient microbiome through inoculation but it is clear that, for any attempt to manage peatland carbon sequestration, the toolkit to undertake the work must include a process-based understanding of peatland function rooted in an understanding of peatland microbial communities.

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AUTHOR CONTRIBUTIONS

CHR, MGE: acquisition of funding; CHR, MGE, JPR, DMA, AAM, RIG: conceptualisation, writing original draft, review and editing of subsequent versions; all other authors: review and editing.

CONFLICTS OF INTEREST

A number of the authors work for, or have received research funding from, organisations undertaking peatland restoration. Otherwise the authors declare no conflicts of interest.

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Appendix

Table A1. Studies of the effects of increases in temperature on fungal communities in peatlands.

Latitude, longitude	Type of peat	Type of manipulation	Results	Reference
Northern fen 67° 60' N, 24° 12' E; Finland. Southern fen 61° 48' N, 24° 19' E; Finland.	Sedge fens.	Lowered water levels by ~3 cm. Seasonal artificial warming with small open-top chambers (OTCs). +0.8 °C immediately below moss layer, +0.3 °C at 5 cm depth. Lowered water levels by ~6 cm. Seasonal artificial warming with small OTCs.	Fungal biomass decreased by 20 nmol PLFAs g ⁻¹ (dry weight of soil) in response to warming. ITS copy number at 10–20 cm depth decreased in water level drawdown conditions, warming dampened the effect. OTUs representing <i>Tomentella</i> and <i>Lactarius</i> in drier regime and <i>Mortierella</i> in wet regime after warming.	Peltoniemi <i>et al.</i> (2015)
54° 65' N, 2° 45' W; northern England, UK.	Ombrotrophic blanket bog.	Warming by OTCs, increased mid-day air temperatures by about +1 °C. Plant functional group removals.	Ericoid shrub removal had cascading effects on soil fungal community composition. No effect of warming on fungal community.	Ward <i>et al.</i> (2015)
53° 11' 15" N, 18° 18' 34" E; Linje peatland, northern Poland.	<i>Sphagnum fallax</i> , <i>Eriophorum vaginatum</i> , <i>Oxycoccus palustris</i> , <i>Andromeda polifolia</i> , <i>Aulacomnium palustre</i> , <i>Drosera rotundifolia</i> , <i>Betula nana</i> , <i>Pinus sylvestris</i> .	OTCs; water table depth manipulated by adding or removing peat. Two temperature treatments: ambient or ~1.2–1.8 °C increase in mean temperature. Three water table treatments: control, wet, dry. Sampled top 3 cm of <i>Sphagnum</i> stems.	96 micro-eukaryotic OTUs as indicators of the dry treatment, 28 of which were assigned to fungi. Highest indicator value was for <i>Cortinarius</i> spp. 18 micro-eukaryotic OTUs as indicators of warming, 11 of which were assigned to fungi.	Reczuga <i>et al.</i> (2020)
52° 56' N, 122° 51' E; Da Xing'anling Mountain, China.	Permafrost peatland, maximum thaw depth 50–70 cm. Tussocks dominated by <i>E. vaginatum</i> with mosses and small shrubs predominant in microsites between tussocks. <i>Ledum palustre</i> , <i>Betula fruticosa</i> , <i>Vaccinium uliginosum</i> , <i>Chamaedaphne calyculata</i> , <i>Rhododendron parvifolium</i> . Soils are Glacial Historthels.	Cuboidal OTCs for 6 growing seasons. Mean air temperature increased by 0.47 °C. Soil temperature at 5 cm depth increased by 0.6 °C and at 15 cm depth by 0.53 °C. Warming did not change soil water content. Tussock soils sampled at 0–15 cm and 15–30 cm below the plant litter layer; rhizosphere and non-rhizosphere soils sampled under shrubs at 0–15 cm and 15–30 cm. Real-time PCR for fungi.	Soil fungal abundance from shrub non-rhizosphere was lower than that from shrub rhizosphere and under tussock but increased significantly under warming.	Song <i>et al.</i> (2021a)

Latitude, longitude	Type of peat	Type of manipulation	Results	Reference
52.94 °N, 122.86 °E; Da Xing'anling Mountains, northeast China.	Continuous permafrost peatland, depth of active layer 45–65 cm. <i>Eriophorum vaginatum</i> , <i>Vaccinium uliginosum</i> , <i>Chamaedaphne calyculata</i> , <i>Ledum palustre</i> , <i>Sphagnum palustre</i> .	Incubated litter of <i>E. vaginatum</i> and <i>Sphagnum</i> for 54 d at 10 °C or 20 °C.	Increase in temperature significantly promoted litter decomposition and CO ₂ emission. Increase in temperature resulted in more fungal ITS gene copies.	Gao <i>et al.</i> (2022)
52° 44' N, 122° 39' N; Great Hing'an Mountains, China.	Glacial Histoturbels, poor fen on continuous permafrost, active layer 0–60 cm. <i>Vaccinium uliginosum</i> , <i>Eriophorum vaginatum</i> , <i>Chamaedaphne calyculata</i> , <i>Sphagnum</i> spp., <i>Ledum palustre</i> .	Incubation at 5 °C or 15 °C under anaerobic conditions. 8 soil depths: 0–20, 20–40, 40–60, 60–80, 80–100, 100–120, 120–140, 140–150 cm, in 4 locations.	Cumulative emissions of CO ₂ at 15 °C across all soil depths was higher than at 5 °C. High fungal gene abundances were observed in 0–20 cm and 20–40 cm layers and abundances increased with temperature increasing.	Jiang <i>et al.</i> (2020)
Seven permafrost peatlands, northeastern China.	Continuous permafrost, discontinuous island permafrost, sporadic island permafrost. Soils are Glacial Histoturbels.	Incubation for 90 days at 5 °C or 15 °C for each soil layer (0–15 and 15–30 cm). Q-PCR for fungal ITS.	Topsoil of Youhao peatland had increase in fungi of 35.96 % with an increase in temperature.	Song <i>et al.</i> (2021b)
48° 21' N, 85° 21' W; northern Ontario, Canada.	Nutrient-poor fen.	Mesocosm experiment. Warming at +4 °C, +8 °C; elevated CO ₂ 750 ppm; lowered water table 20 cm from peat surface.	After 18 months, warming was the main driver of changes in fungal communities at 3 depths (0–5 cm, 10–15 cm, 30– 35 cm). Ascomycota- and Basidiomycota-dominated groups became more homogenous under warming conditions. Potential cellulose decomposers and mycorrhizal root-associated fungi from Basidiomycota were dominant under +4 °C warming, whereas prevalence of potential lignocellulose decomposers and mycorrhizal root-associated fungi from Ascomycota under +8 °C warming.	Asemaninejad <i>et al.</i> (2018)

Latitude, longitude	Type of peat	Type of manipulation	Results	Reference
48° 21' N, 85° 21' W; northern Ontario, Canada.	Nutrient-poor fen.	Peat litterbags placed at 10–15 cm depth in mesocosms as in Asmaninejad <i>et al.</i> (2018).	General fungal richness reduced under warming conditions, Ascomycota exhibited higher diversity under increased temperature treatments. Both increased temperature and lowered water table position drove shifts in fungal community composition, with a strong positive effect on endophytic and mycorrhizal fungi and different groups of saprotrophs <i>Mortierella</i> , <i>Galerina</i> and <i>Mycena</i> .	Asemaninejad <i>et al.</i> (2017b)
47° 30.4760' N, 93° 27.1620' W; northern Minnesota, USA.	Forested, weakly ombrotrophic peatland with perched water table.	Ecosystem climate manipulation. Addition of fungal necromass to hummocks and hollows in five (+0, +2.25, +4.5, +6.75, +9 °C) and two CO ₂ (0 ppm, 900 ppm) treatment levels in large (12 m diameter) OTCs.	Based on decay model, necromass organic matter stabilisation in hollows reduced by about 39 % and 45 % under the +4.5 °C and +9.0 °C scenarios. Water table drawdown occurred in hollows in warming treatments.	Fernandez <i>et al.</i> (2019)
47° 30.4760' N, 93° 27.1620' W; Marcell Experimental Forest, northern Minnesota, USA.	Weakly ombrotrophic peatland with perched water table. <i>Picea marina</i> , <i>Larix laricina</i> , <i>Rhododendron groenlandicum</i> , <i>Chamaedaphne calyculata</i> , <i>Sphagnum angustifolium</i> , <i>S. fallax</i> in hollows, <i>S. magellanicum</i> in hollows.	Decaying mycorrhizal fungal necromass incubated within mesh bags across a 9 °C whole ecosystem temperature enhancement.	Major taxonomic and functional shifts in fungal communities in response to warming. Changes most pronounced in hollow microsites, which showed convergence towards the necromass-associated fungal communities present in unwarmed hummocks. High colonisation of ericoid mycorrhizal fungal necromass by fungi from the same genera as the necromass.	Maillard <i>et al.</i> (2022)
46° 50' 38" N, 6° 10' 29" E; Jura Mountains, France.	Undisturbed ombrotrophic <i>Sphagnum</i> -dominated mire.	Two areas: Hummocks and Lawns. Hexagonal OTCs as warming treatment all year round, significantly increased ambient air temperature by around +1 °C in Hummocks and Lawns plots.	Second, third and fourth year of warming. Dark septate endophyte (DSE) colonisation of <i>Andromeda polifolia</i> increased and rhizosphere peroxidase activities decreased in warmed Hummocks while they remained stable in warmed Lawns. Significant negative correlation was observed between <i>A. polifolia</i> and moss litter phenolics recovered in warmed plots while no relationship was found in control plots. Significant positive correlation between DSE root colonisation and moss litter phenolics recovered in both microhabitats but only under ambient conditions.	Binet <i>et al.</i> (2017)

Table A2. Studies of the effects of water-table drawdown and drought on fungal communities in peatlands.

Latitude, longitude	Type of peatland	Type of manipulation	Results	Reference
Alaska Peatland Experiment, southwest of Fairbanks, Alaska.	Rich fen (pH 5.6–5.9); <i>Carex atherodes</i> , <i>Calamagrostis</i> sp., <i>Comarum palustre</i> , <i>Equisetum fluviatile</i> .	Lowered, raised and control water table manipulation maintained during growing season 2015 and first half of growing season 2016. Cores subsampled at 1–10 cm, 10–20 cm, 30–40 cm, 60–70 cm. Fine roots of each dominant plant species were collected.	Fungal community affected largely by plant functional group, especially <i>Comarum palustre</i> . Fungal endophytes (particularly <i>Acephala</i> spp.) were enriched in <i>Carex</i> and <i>Calamagrostis</i> roots, which may have underappreciated implications for organic matter breakdown and cycling. Fungal lignocellulose degraders were enriched in the lowered water table treatment.	Rupp <i>et al.</i> (2021)
61° 47' N, 24° 18' E; central Finland.	Natural minerotrophic tall sedge fen; natural ombrotrophic cotton grass pine bog with <i>Sphagnum fuscum</i> hummocks.	Ditch drained in 1961 (51 years before sampling); adjacent natural and drained sides of different fertility along a border ditch. Water table -8.0 cm and -34.9 cm for the natural and drained fens. Water table -12.0 cm and -16.4 cm for the natural and drained bogs.	Amount of fungal fatty acid did not differ between the drained and natural fen sides, but was lower in the surface layer (0–25 cm) of the drained bog side than the natural bog side.	Mpamah <i>et al.</i> (2017)
Lakkasuo, central Finland.	Fibric Histosol, ombrotrophic bog. Undrained site, pH 4.1, <i>Sphagnum angustifolium</i> is main species, water table is < 5 cm from surface. Drained site, pH 3.8, <i>Pleurozium</i> spp., is main moss species, high number of pine trees.	Ditches installed in 1961 (70 cm depth, spacing of 40–60 m). Four cores drilled with a Russian peat corer in each of drained and undrained sites.	Fungal-derived membrane fatty acid abundance was highest in the uppermost part (0–30 cm) of the drained layer.	Groß-Schmölders <i>et al.</i> (2021)
53° 11' 15" N, 18° 18' 34" E; northern Poland.	Poor fen with ombrotrophic vegetation.	Water table manipulation (Wet, Ambient, Dry). 1 m ² plots.	Substantial changes in ecosystem respiration, plant and fungal communities when the water table level fell below -24 cm. Ecosystem respiration was greatest when graminoids and saprotrophic fungi became prevalent as a response to extreme drought.	Jassey <i>et al.</i> (2018)

Latitude, longitude	Type of peatland	Type of manipulation	Results	Reference
42° 09' 5.8" N–42° 10' 9.2" N, 126° 43' 49.4" E–42° 10' 9.2" E; Baijinghe Peatland, Changbai Mountains, northeast China.	Natural part: pH 5.8, treeless poor fen; <i>Carex rostrata</i> , compact moss layer of <i>Sphagnum flexuosum</i> , very few shrubs. Drained part: pH 5.4; more shrubs, <i>Dasiphora fructicosa</i> with <i>Betula ovalifolia</i> , <i>Rhododendron capitatum</i> , <i>Ledum palustre</i> .	Western part of peatland drained in the 1970s. Ditches 0.5 m deep, 10 m spacing. Water table level 0.65 to 10.65 cm in natural peatland, -24.72 to -4.20 cm (i.e. below the soil surface) in drained peatland. Soil samples taken at 0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, 40–50 cm.	Soil fungal PLFAs in the oxic zone were lower in the drained peatland than in the natural peatland. The soil fungal : bacterial ratio was lower in the drained peat than in the natural peat at all sampling depths.	Xu <i>et al.</i> (2021)
33° 04' N, 102° 34' E; Zoige Plateau, Qinghai-Tibetan Plateau.	Moderately rich fen, dominated by grasses and sedges.	Long-term (48 years) drainage site used as a grazing pasture in 1970s. Drainage ditch 0.3–0.5 m deep and 1–1.5 m wide. Short-term (3 years) drainage site, drainage ditch 0.3–0.5 m deep and 0.5 to 1.0 m wide.	Duration of drainage and water table drawdown had significant effects on the diversity and composition of fungal communities. Water-table drawdown increased fungal diversity, with distinct benefits for Basidiomycota and Zygomycota and detrimental effects for Ascomycota. Duration of drainage affected the structure of fungal communities more than that of bacterial communities, and interactions between microbial species were more complex under long-term drainage. Fungal communities explained a larger part of microbial activity than bacterial communities.	Xue <i>et al.</i> (2021)
1° 53' 25" S, 113° 32' 09" E; Central Kalimantan, Indonesia.	Dominant vegetation: <i>Combretocarpus rotundatas</i> , <i>Cratoxylum glaucum</i> at Sites (1) and (2); <i>Palaquium leiocarpus</i> , <i>Syzygium creaghii</i> at Site (3). At Sites (1) and (2), peat at 0–5 cm depth almost completely decomposed with indistinct plant structure; at Site (3), weakly decomposed peat with distinct plant structure.	Site (1) ditched, with at least 6-yr drainage history; Site (2) in margin of a pristine area with intermediate water regime; Site (3) undisturbed, near the centre of a pristine peatland. Incubation in darkness of 10 g peat collected from depth 0–5 cm, for 28 days at 26 °C “drought treatment”.	Peat soil from Site (3) released DOC with high aromaticity; peat from Sites (1) and (2) released labile DOC. Fungal community structures from Site (3) were distinct after the incubation. Gene copy numbers of fungi in Sites (1) and (2) increased after incubation. Larger amount of CO ₂ released from Site (1).	Kwon <i>et al.</i> (2013)

Table A3. Studies of the effects of increases in temperature on bacterial and archaeal communities in peatlands.

Latitude, longitude	Type of peatland	Type of temperature manipulation	Results	Reference
78° 56.544', 11° 49.055' E; Knudsenheia, Ny- Aalesund, Svalbard.	Dominant peat-forming moss is <i>Callirgeron richardsonii</i> . Peat is 40 cm deep.	Anoxic microcosms incubated over a temperature gradient from 1 °C to 30 °C.	CH ₄ production at 4 °C was 25 % of that at 25 °C. Below 7 °C, syntrophic proprionate oxidation was rate-limiting; above this threshold temperature, polysaccharide hydrolysis became rate-limiting. Associated with Firmicutes being replaced by Bacteroidetes. Shift from the formate- and H ₂ -using Methanobacteriales to Methanomicrobiales and from the acetotrophic Methosarcinaceae to Methanosaetaceae. Methanogenesis from methylamines, probably stemming from degradation of bacterial cells, became more important with increasing temperature and corresponded with an increased relative abundance of predatory protists of the phylum Cercozoa.	Tveit <i>et al.</i> (2015)
78° 56.544' N, 11° 49.055' E; Knudsenheia, Ny- Aalesund, Svalbard.	Active layer is 40 cm deep. Dominant peat-forming moss is <i>Callirgeron richardsonii</i> .	Peat blocks obtained at 10–20 cm depth, upper 4 cm vegetation removed, made into slurry under anoxic conditions, pre-incubated for 171 d at 4 °C. Incubation in darkness to prevent photosynthesis. Temperature gradient 1 to 30 °C in single degree steps for approx.. 1 month.	Over high resolution temperature gradient (1–30 °C), microbial communities changed discretely, but not continuously or stochastically, in response to rising temperatures. Taxonomic variability may in part reflect the varied temperature responses of individual taxa and the competition between these taxa for resources. These taxonomic responses contrast the stable functional potential (metagenomics-based) across all temperatures or the previously observed metabolic or trophic shifts at key temperatures. Progressive decrease in species diversity with increasing temperature and increased variation of GHG production rates. Conclude that taxonomic variation is decoupled from both the functional potential of the community and the previously observed temperature-dependent changes in microbial function.	Yang <i>et al.</i> (2021)
68° 21' N, 18° 49' E; Abisko, sub-arctic Sweden.	Gently sloping ombrotrophic peat bog.	OTCs increase daily mean air temperature by 0.3–1.0 °C in spring and by 0.2–0.9 °C in summer. Peat cores taken to a depth of 20 cm, 2 cm diameter.	Bacterial community is stable under changing conditions.	Weedon <i>et al.</i> (2017)

Latitude, longitude	Type of peatland	Type of temperature manipulation	Results	Reference
Northern fen: 67° 60' N, 24° 12' E; Southern fen: 61° 48' N, 24° 19' E; Finland.	Boreal fen.	Small OTCs. Average daily temperature below the moss layer was 0.8 °C higher and at 5 cm depth 0.3 °C higher under the OTCs compared with controls. Two moisture regimes: an undisturbed wet regime and a drier regime with lowered water level achieved with a shallow drainage ditch 30 cm deep. Shallow ditch lowered water levels by, on average, 6 cm and 3 cm in the southern and northern fens, respectively.	After three years of experimental warming. Methanogenic community remained similar although methanogen abundance decreased after warming. Wet regime showed a significant small reduction in potential CH ₄ production with warming. Drying alone reduced potential CH ₄ production more than warming. Warming did not affect methane-oxidising bacteria (MOB) or the potential CH ₄ oxidation in wet regime; however, type 1b MOB abundance decreased and MOB related to <i>Methylocapsa</i> became typical after warming in the drier regime of the southern fen. CH ₄ fluxes measured <i>in situ</i> : warming and drying reduced methane emissions, drying more than warming. Methanogens and MOB may have different controlling patterns on CH ₄ fluxes when facing global warming.	Peltoniemi <i>et al.</i> (2016)
68° 21' N, 19° 02' E; Stordalen mire complex near Abisko, sub-arctic Sweden.	<i>Sphagnum fuscum</i> dominated area with scattered vascular plants.	Sixty day mesocosm experiment, factorial combination of three temperature (9 °C, 11 °C, 14 °C) and three substrate (no substrate added, dead microbial cells, roots) treatments.	Temperature-only effect was not sufficient to account for the increases in respiration observed in previous field experiments. Additions of dead microbial cells led to 83 % increase in organic N pool sizes, 16–64 % increases in potential activities of most soil enzymes, a transient increase in the relative abundance of beta-proteobacteria and a decrease in the relative abundance of alpha-proteo-, Actino- and Acidio-bacteria.	Weedon <i>et al.</i> (2013)
UK Grid Reference SN820866; Plynlimon catchment, north Wales, UK.	Mesotrophic peatland dominated by <i>Sphagnum</i> spp. (~ 60 %) and <i>Festuca</i> spp.	Warming (+ 3 °C tracked continuously above ambient) and control (ambient temperature) in solar domes. Peat monoliths (11 cm diam. × 25 cm depth) inserted in perfusion systems that allow both fine control of the water table and lateral water movement. Peat monoliths incubated for three growing seasons. Water levels were kept close to the soil surface by adding water collected from the sampling sites. Peat removed from different depths: surface (1–3 cm), middle (9–11 cm) and deep (17–19 cm).	Warming increased CO ₂ and CH ₄ but not significantly. Warming caused a shift in the composition of bacterial communities in the surface and middle layers but not in the deep layer. Few changes in diversity indices and quantity of bacterial communities due to warming treatments. Warming significantly decreased richness, Shannon diversity index and quantity of methanogens. However, the composition was hardly related to temperature. The ratios of methanogens to bacteria in terms of gene copy numbers significantly decreased by a factor of 2–6 due to elevated temperature. Composition and diversity of bacteria and methanogens, respectively, were significantly related to soil depth. Temperature and soil depth interacted significantly on the bacterial diversity.	Kim <i>et al.</i> (2012)

Latitude, longitude	Type of peatland	Type of temperature manipulation	Results	Reference
52.94 °N, 122.86 °E; Da Xing'anling Mountains, northeast China.	Continuous permafrost peatland, depth of active layer 45–65 cm. <i>Eriophorum vaginatum</i> , <i>Vaccinium uliginosum</i> , <i>Chamaedaphne calyculata</i> , <i>Ledum palustre</i> , <i>Sphagnum palustre</i> .	Incubated litter of <i>E. vaginatum</i> and <i>Sphagnum</i> for 54 d at 10 °C or 20 °C.	Increase in temperature significantly promoted litter decomposition and CO ₂ emission. Increase in temperature significantly increased the abundances of bacteria in <i>E. vaginatum</i> and <i>Sphagnum</i> litter. Enzyme activity in both types of litter was inhibited by an increase in temperature.	Gao <i>et al.</i> (2022)
52° 56' N, 122° 51' E; northeast China.	Boreal peatland. Glacic Historthel.	Cuboidal OTCs. Mean air temperature increased by 0.41 °C during three growing seasons. Soil temperature increased by 0.77 °C and 0.61 °C at depths of 5 and 15 cm, respectively. Soils sampled from 0–10 and 10–20 cm below the plant litter layer.	<i>mcrA</i> gene abundance in shallow soil and deep soil exhibited insensitivity to warming. Soil archaea 16S rRNA gene abundance in both shallow soil and deep soil increased under warming. Soil <i>pmoA</i> gene abundance of both layers, and bacterial 16S rRNA gene abundance in shallow soil, decreased due to warming. Warming inhibited beta-glucosidase activity in two soil layers and invertase activity in deep soil, stimulated acid phosphatase activity in shallow soil.	Song <i>et al.</i> (2019)
52° 56' N, 122° 51' E; Da Xing'anling Mountain, China.	Permafrost peatland, maximum thaw depth 50–70 cm. Tussocks dominated by <i>E. vaginatum</i> with mosses and small shrubs predominant in microsites between tussocks. <i>Ledum palustre</i> , <i>Betula fruticosa</i> , <i>Vaccinium uliginosum</i> , <i>Chamaedaphne calyculata</i> , <i>Rhododendron parvifolium</i> . Soils are Glacic Historthels.	Cuboidal OTCs for six growing seasons. Mean air temperature increased by 0.47 °C. Soil temperature at 5 cm depth increased by 0.6 °C and at 15 cm depth by 0.53 °C. Warming did not change soil water content. Tussock soils sampled at 0–15 cm and 15–30 cm below the plant litter layer; rhizosphere and non- rhizosphere soils sampled under shrubs at 0–15 cm and 15–30 cm.	6-year warming increased the abundance of bacteria in 0–15 cm soil under tussock and from shrub rhizosphere, and of archaea under tussock and from shrub rhizosphere. 6-year warming increased methanogen abundance in 0–15 cm soil and methanotroph abundance in 15–30 cm soil under tussock. Beta- glucosidase activity increased in 0–15 cm soil under tussock and from shrub rhizosphere but invertase activity in 15–30 cm soil under tussock and from shrub rhizosphere decreased under warming.	Song <i>et al.</i> (2021a)
52° 44' N, 122° 39' N; Great Hing'an Mountains, China.	Glacic Histoturbels, poor fen on continuous permafrost, active layer 0–60 cm. <i>Vaccinium uliginosum</i> , <i>Eriophorum vaginatum</i> , <i>Chamaedaphne calyculata</i> , <i>Sphagnum</i> spp., <i>Ledum palustre</i> .	Incubation at 5 °C or 15 °C under anaerobic conditions. 8 soil depths: 0–20, 20–40, 40–60, 60–80, 80–100, 100–120, 120–140, 140–150 cm, in 4 locations.	Cumulative emissions of CO ₂ at 15 °C across all soil depths was higher than at 5 °C. High bacteria, archaea, methanogen and methanotroph gene abundances were observed in 0–20 cm and 20–40 cm layers and such abundances increased with temperature increase.	Jiang <i>et al.</i> (2020)

Latitude, longitude	Type of peatland	Type of temperature manipulation	Results	Reference
Seven permafrost peatlands, northeastern China.	Continuous permafrost, discontinuous island permafrost, sporadic island permafrost. Soils are Glacic Histoturbels.	Incubation for 90 days at 5 °C or 15 °C for each soil layer (0–15 and 15–30 cm). Q-PCR for fungal ITS.	Increased temperatures significantly reduced the abundance of bacteria in both the topsoil and subsoil of the Huzhong peatland and the topsoil of Tangwanghe peatland. Abundance of soil archaea significantly increased in topsoil of 3 peatlands and in subsoil of 5 peatlands. Abundances of <i>mcrA</i> tended to increase at 15 °C compared with 5 °C across the 7 sampling sites. For 4 sites, abundance of <i>pmoA</i> increased from 84.98 times to 646.69 times.	Song <i>et al.</i> (2021b)
47° 30.4760' N, 93° 27.1620' W; Marcell Experimental Forest, northern Minnesota, USA.	Weakly ombrotrophic peatland with perched water table. <i>Picea marina</i> , <i>Larix laricina</i> , <i>Rhododendron groenlandicum</i> , <i>Chamaedaphne calyculata</i> , <i>Sphagnum angustifolium</i> , <i>S. fallax</i> in hollows, <i>S. magellanicum</i> in hollows.	Decaying mycorrhizal fungal necromass incubated within mesh bags across a 9 °C whole ecosystem temperature enhancement.	Temperature had no significant effect on hummock-associated bacterial trophic groups. Temperature was significantly positively correlated with copiotrophic bacterial abundances and negatively with oligotrophic bacterial abundances in the hollows.	Maillard <i>et al.</i> (2022)
46° 49' 35" N, 6° 10' 20" E; Jura Mountains, Le Forbonnet, France.	Transitional minerotrophic (Fen) to ombrotrophic area (Bog).	OTCs. At 7 cm depth, minimum peat temperature was lower at the Bog OTC (3.3 °C) than at the Bog-Control plot (5.0 °C). Mean peat temperature was higher at the Fen OTC (5.7 °C) than at the Bog OTC plot (4.9 °C). Twelve peat cores 30 cm long collected, cut into five slices.	After three years of experimental warming, in warmed plots, PLFAs from G-positive and G-negative bacteria were significantly higher at the Fen site compared with the Bog site.	Delarue <i>et al.</i> (2015)
33° 56' N, 102° 52' E; Zoige National Wetland Reserve, Tibetan Plateau, southwestern China.	Dominant plants: <i>Eleocharis valleculosa</i> , <i>Polygonum amphibium</i> , <i>Carex muliensis</i> . Peat soils associated with these plants. Alpine wetland.	Anoxic microcosms incubated at 15 °C or 20 °C for 12 weeks.	Positive correlation between temperature and CH ₄ emissions. However, temperature had no effect on the main methanogenic pathway - acetotrophic methanogenesis. Methanogenic community composition was not related to temperature, but was associated with vegetation, which was also involved in CH ₄ emissions.	Cui <i>et al.</i> (2015)

Table A4. Studies of the effects of water-table drawdown and drought on bacterial and archaeal communities in peatlands.

Latitude, longitude	Type of peatland	Type of manipulation	Results	Reference
Alaska Peatland Experiment, southwest of Fairbanks, Alaska.	Rich fen (pH 5.6 – 5.9). <i>Carex atherodes</i> , <i>Calamagrostis</i> sp., <i>Comarum palustre</i> , <i>Equisetum fluviatile</i> .	Lowered, raised and control water table manipulation maintained during growing season 2015 and first half of growing season 2016. Cores subsampled at 1–10 cm, 10–20 cm, 30–40 cm, 60–70 cm. Fine roots of each dominant plant species were collected.	Bacteria and archaeal communities were most sensitive to water-table treatments, particularly at 10–20 cm; this coincides with the rhizosphere. Iron cyclers, particularly <i>Geobacteraceae</i> , were enriched around the roots of sedges, horsetails and grasses. Two methanogen communities were found: a rooting zone community dominated by the archaeal family <i>Methanobacteriaceae</i> and a deep peat community dominated by the family <i>Methanomicrobiaceae</i> .	Rupp <i>et al.</i> (2021)
61° 47' N, 24° 18' E; central Finland.	Natural minerotrophic tall sedge fen; natural ombrotrophic cotton grass pine bog with <i>Sphagnum fuscum</i> hummocks.	Ditch drained in 1961 (51 years before sampling); adjacent natural and drained sides of different fertility along a border ditch. Water table -8.0 cm and -34.9 cm for the natural and drained fens. Water table -12.0 cm and -16.4 cm for the natural and drained bogs.	Drainage increased the fatty acids of Gram-positive and Gram-negative bacteria in the surface and subsurface layers of the fen and decreased them in the bottom layers of the bog side.	Mpamah <i>et al.</i> (2017)
Lakkasuo, central Finland.	Fibric Histosol, ombrotrophic bog. Undrained site: pH 4.1, <i>Sphagnum angustifolium</i> is main species, water table is < 5 cm from surface. Drained site: pH 3.8, <i>Pleurozium</i> sp. is main moss species, high number of pine trees.	Ditches installed in 1961 (70 cm depth, spacing 40–60 m). Four cores drilled with a Russian peat corer in each of drained and undrained sites.	Bacterial-derived membrane fatty acid concentrations peaked in the 0–20 cm drained layers.	Groß-Schmölders <i>et al.</i> (2021)
Fen: UK Grid Reference SH461826; Cors Erddreiniog, mid-Anglesey, north Wales. Bog: UK Grid Reference SH610625; Marchlyn Mawr, outskirts of Snowdonia National Park, northwest Wales, UK.	Alkaline and calcareous fen habitat. <i>Carex echinata</i> , <i>Sphagnum recurvum</i> / <i>auriculatum</i> mire.	Mesocosm cores (20 cm diameter, 35 cm length) in controlled temperature room. Five cores randomly assigned to drought-rewet, five as controls.	Prokaryotic community composition varied with habitat and depth. Community differences between mesocosm cores was stronger than the effect of the drought treatment. “Drought-responsive” OTUs were disproportionately drawn from the phyla Bacteroidetes and Proteobacteria.	Potter <i>et al.</i> (2017)

Latitude, longitude	Type of peatland	Type of manipulation	Results	Reference
Groundwater well site: 49° 13' 25.72" N, 1° 21' 50.70" W; Pristine site: 49 ° 14' 1.97"N, 1° 21' 24.19" W; Parc Naturel Regional des Marais du Cotentin du Bessin, Normandy, France.		Sixteen cores were collected 50 cm below surface. Four experimental treatments where peat core saturation varied: (1) 3 days saturated – 3 days unsaturated, (2) 9 days saturated – 9 days unsaturated, (3) continuously saturated, (4) continuously unsaturated.	Frequent water level drawdown reduced bacterial richness and diversity in the peat soil and water. Short-term drought cycles (3–9 day frequency) resulted in different communities from those in continuously saturated environments. The site that has more frequently experienced water table drawdown during the last two decades presented the most striking shifts in bacterial community structure.	Nunes <i>et al.</i> (2015)
48° 59' N, 13° 28' E; Šumava Mountains, south- western Czech Republic.	Two ombrotrophic bogs, two minerotrophic treeless poor fens, and four spruce swamp forests.	Peatlands were drained with ditches in the 1960s to increase productivity of forests and meadows.	Bacterial diversity decreased and Acidobacteria became the dominant phylum on drained sites, reflecting a convergence in bacterial community composition across peatlands after long-term drainage. The archaeal communities changed very strongly and became similar across drained peatlands. Bog represented a relatively resilient system while fen seemed to be very sensitive to environmental changes.	Urbanová & Bárta (2016)
42° 09' 45.8" N–42° 10' 9.2" N, 126° 43' 49.4" E–42° 10' 9.2" E; Baijinghe Peatland, Changbai Mountains, northeast China.	Natural part: pH 5.8, treeless poor fen, <i>Carex rostrata</i> , compact moss layer of <i>Sphagnum flexuosum</i> , very few shrubs. Drained part: pH 5.4, more shrubs, <i>Dasiphora fructicosa</i> , with <i>Betula ovalifolia</i> , <i>Rhododendron capitatum</i> , <i>Ledum palustre</i> .	Western part of peatland drained in the 1970s. Ditches 0.5 m deep, 10 m spacing. Water table level 0.65 to 10.65 cm in natural peatland, -24.72 to -4.20 cm (i.e. below the soil surface) in drained peatland. Soil samples taken at 0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, 40–50 cm.	Bacterial and actinomycetic PLFAs in the oxic zone were lower in the drained peat than in natural peat. Bacterial PLFAs were higher in the transitional zone of the drained peat than in the natural peat, but remained similar in the anoxic zone of the drained and natural peat. Soil bacterial communities strongly and positively linked with Beta-1,4-glucosidase activities.	Xu <i>et al.</i> (2021)



Latitude, longitude	Type of peatland	Type of manipulation	Results	Reference
Hongyuan County Town, southeastern part of Tibetan plateau.		Mesocosms. Six water levels (0 cm, -10 cm, -20 cm, -30 cm, -40 cm, -50 cm); two temperatures (passive warming with OTCs and ambient temperature); two precipitation levels (20 % reduction in rainfall and ambient rainfall. OTCs increased soil temperature at -10 cm by an average of 1.7 °C across the growing season.	Results after 5 and 15 months. Water-table drawdown and drought exhibited significant effects on archaeal communities. When the water table was at or above 10 cm, the archaeal abundance remained high ($\sim 10^9$ cells per g dry soil) whereas the archaeal abundance below 10 cm was reduced to $\sim 10^8$ cells per g dry soil where the water table was lowered to 20 cm or below. When the water table was kept constant, warming caused a significant reduction in archaeal abundance. Drought only caused a significant reduction in the archaeal abundance when the water level was higher than -20 cm.	Tian <i>et al.</i> (2015)
33° 04' N, 102° 34' E; Zoige Plateau, Qinghai-Tibetan Plateau.	Moderate rich fen, dominated by grasses and sedges.	Long-term (48 years) drainage site used as a grazing pasture in 1970s. Drainage ditch 0.3–0.5 m deep and 1–1.5 m wide. Short term (3 years) drainage site, drainage ditch 0.3–0.5 m deep and 0.5 to 1.0 m wide.	Both duration of drainage and water table drawdown had significant effects on the diversity and composition of bacterial communities; certain bacteria were replaced by fungal decomposers. Water table drawdown led to an increase in the relative abundance of Proteobacteria and a decrease in the abundance of Firmicutes.	Xue <i>et al.</i> (2021)
32° 48' N, 102° 33' E; Zoige Peatland, Sichuan Province, China.	Vegetation consists mostly of sedge species including <i>Scirpus pumilus</i> , <i>Blysmus sinocompressus</i> , <i>Carex muliensis</i> , <i>Kobresia humilus</i> , <i>Kobresia setchwanensis</i> .	In the field deep, shallow and control water tables, were achieved by experimental drainage with ditches 50 cm, 20 cm and 0 cm (intact) deep.	Drainage significantly increased emission rates and total cumulative emissions of CO ₂ and N ₂ O and reduced CH ₄ emissions. Drainage also significantly increased the biomass of aerobic bacteria and methanotrophs.	Cao <i>et al.</i> (2018)
1° 53' 25" S, 113° 32' 09" E; Central Kalimantan, Indonesia.	Dominant vegetation: <i>Combretocarpus rotundatas</i> , <i>Cratoxylum glaucum</i> at Sites (1) and (2); <i>Palaquium leiocarpus</i> , <i>Syzygium creaghii</i> at Site (3). At Sites (1) and (2), peat at 0–5 cm depth almost completely decomposed with indistinct plant structure; at Site (3), weakly decomposed peat with distinct plant structure.	Site (1) ditched, with at least 6-yr drainage history; Site (2) in margin of a pristine area with intermediate water regime; Site (3) undisturbed, near the centre of a pristine peatland. Incubation in darkness of 10 g peat collected from depth 0–5 cm, for 28 days at 26 °C “drought treatment”.	Bacterial community structure of the centre site was distinct from the other sites, and this distinction was maintained until the end of the 28-day incubation. Archaeal community structure was also initially distinguished from the other sites, but after 28 days the archaeal community structures of the three water table regimes were indistinguishable.	Kwon <i>et al.</i> (2013)