Methanogenic Archaea In Peatlands

By: Suzanna L. Brauer, Nathan Basiliko, Henri M.P. Siljanen, & Stephen H. Zinder

Abstract

Methane emission feedbacks in wetlands are predicted to influence global climate under climate change and other anthropogenic stressors. Herein, we review the taxonomy and physiological ecology of the microorganisms responsible for methane production in peatlands. Common in peat soils are five of the eight described orders of methanogens spanning three phyla (Euryarchaeota, Halobacterota and Thermoplasmatota). The phylogenetic affiliation of sequences found in peat suggest that members of the thus-far-uncultivated group Candidatus Bathyarchaeota (representing a fourth phylum) may be involved in methane cycling, either anaerobic oxidation of methane and/or methanogenesis, as at least a few organisms within this group contain the essential gene, mcrA, according to metagenomic data. Methanogens in peatlands are notoriously challenging to enrich and isolate; thus, much remains unknown about their physiology and how methanogen communities will respond to environmental changes. Consistent patterns of changes in methanogen communities have been reported across studies in permafrost peatland thaw where the resulting degraded feature is thermokarst. However much remains to be understood regarding methanogen community feedbacks to altered hydrology and warming in other contexts, enhanced atmospheric pollution (N, S and metals) loading and direct anthropogenic disturbances to peatlands like drainage, horticultural peat extraction, forestry and agriculture, as well as post-disturbance reclamation.

MINIREVIEW – Environmental Microbiology

Methanogenic archaea in peatlands

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ABSTRACT

Methane emission feedbacks in wetlands are predicted to influence global climate under climate change and other anthropogenic stressors. Herein, we review the taxonomy and physiological ecology of the microorganisms responsible for methane production in peatlands. Common in peat soils are five of the eight described orders of methanogens spanning three phyla (Euryarchaeota, Halobacterota and Thermoplasmatota). The phylogenetic affiliation of sequences found in peat suggest that members of the thus-far-uncultivated group Candidatus Bathyarchaeota (representing a fourth phylum) may be involved in methane cycling, either anaerobic oxidation of methane and/or methanogenesis, as at least a few organisms within this group contain the essential gene, mcrA, according to metagenomic data. Methanogens in peatlands are notoriously challenging to enrich and isolate; thus, much remains unknown about their physiology and how methanogen communities will respond to environmental changes. Consistent patterns of changes in methanogen communities have been reported across studies in permafrost peatland thaw where the resulting degraded feature is thermokarst. However much remains to be understood regarding methanogen community feedbacks to altered hydrology and warming in other contexts, enhanced atmospheric pollution (N, S and metals) loading and direct anthropogenic disturbances to peatlands like drainage, horticultural peat extraction, forestry and agriculture, as well as post-disturbance reclamation.

Keywords: methane; fen; bog; climate; sedge; permafrost

INTRODUCTION

Peatlands (a.k.a. bogs and fens, mires and muskeg) are climate change feedback hotspots in the terrestrial biosphere. These wetland ecosystems cover less than 3% of global land area yet hold an estimated 40% of all terrestrial organic carbon (C) as soil organic matter called peat (Gorham 1991; Lehner and Döll 2004; Yu et al. 2010; Scharlemann et al. 2014). Peatlands are able to store tremendous amounts of carbon owing to their often low pH, saturated conditions, low redox potentials, recalcitrant and inhibitory organic compounds in soil and thus extremely low rates of microbial decomposition relative to organic matter inputs from primary production (Moore and Basiliko 2006). Despite overall net uptake of atmospheric C, these saturated, anoxic, organic-rich conditions are also conducive to methane (CH4) production, the terminal step in anaerobic decomposition (Conrad 2009; Zinder 1993). Methane is a much more potent...
greenhouse gas than carbon dioxide ($CO_2$), and methane emissions feedbacks to climate and other environmental changes in peatlands are challenging to predict. Although methanogens represent prototypical members of the domain Archaea (Woese, Kandler and Wheelis 1990), methanogens in peatlands are notoriously challenging to enrich for and isolate; thus, much remains unknown about their physiology and how methanogen communities will respond to environmental changes. Here we review and synthesize the taxonomy and physiological ecology of methanogens in peatlands, including highlighting relatively recent discoveries of putative methanogens in the phylum Crenarchaeota. We briefly cover what is known about methanogen community responses to critical contemporary environmental changes (e.g. permafrost thaw) and end by recommending strategies that may contribute to improving our understanding of the known-unknown (i.e. detected, but not isolated) methanogens in peatlands.

**Methanogen taxonomy and physiological ecology**

Anaerobic methanogenesis is carried out exclusively by members of the archaeal domain. Thus far, methanogens include eight orders, each of which contains at least one cultured representative: the Methanococcales (marine and not found in peat), Methanopyrales (hyperthermophiles not found in peat), Methanobacteriales, Methanomicrobiales, Methanococcales, Methanoanaerarchaeales, Methanospirillales, Methanocellales, Methanonatronarchaeales, Methanomassiliicoccales and Methanomassiliicoccales. Additionally, metagenomic data have facilitated identification of several other groups of putative methanogens including one in the Euryarchaeota, Candidatus Methanofastidiosales, also known as WSA2 (Nobu et al. 2016; one in the Halobacterota, Candidatus Methanofastidiosae, also known as RC-II (Mondav et al. 2014), as well as two in the Crenarchaeota: Candidatus Methanomethylicum, also known as Verstraetearchaeota (Vanwambeke et al. 2016), and candidate phylum Bathychaeota also known as MCG (Zhou et al. 2018a; Evans et al. 2015; Baker et al. 2020). A total of five of these orders and two of the candidate taxa are common in peat: Methanomicrobiales, Methanococcales and Methanosarcinales in the phylum Halobacterota; Methanobacteriales in the phylum Euryarchaeota; Methanomassiliicoccales (RC-III) in the phylum Thermoplasmata, as well as candidate family Methanoflorentaceae (in the Methanococcales) and candidate phylum Bathychaeota (Table 1 and Figs 1–3). Isolates for a number of rentsaceae (in the Methanomicrobiales) and candidate phylum Euryarchaeota; Methanomassiliicoccales (RC-III) in the phylum Halobacterota; Methanobacteriales in the phylum orders and two of the candidate taxa are common in peat: the intestinal isolate that can only grow using methanol and H2 (Fricke et al. 2006), the cultured members of the remaining two orders, Methanobacteriales, Methanonatronarchaeales and Methanomassiliicoccales appear to be obligate methylotrophs that reduce methanol or trimethylamine, using either H2 or formate as the electron donor (Kroninger, Gottschling and Deppenmeier 2017; Sorokin et al. 2018).

Acetate is the dominant CH4 precursor in most freshwater anaerobic soils, although this is not always the case in acidic peatlands and/or permafrost affected peatlands. Aceticlastic methanogenesis often accounts for 2/3 or more of total methanogenesis in some peatlands (Schulz and Conrad 1996; Conrad, Klose and Claus 2002; Metje and Frenzel 2007). Correspondingly, aceticlastic methanogens can predominate among methanogenic populations in peat (Kotsyurbenko et al. 2004; Zhang et al. 2008b). However, in acidic peatlands where the decomposition of organic matter is incomplete and/or turnover rates are much lower compared to other freshwater systems (Conrad 2020), hydrogenotrophic methanogenesis can play a much more important role (Lansdown, Quay and King 1992; Popp et al. 1999; Chasar et al. 2000; Metje and Frenzel 2005). This trend has been observed in collapsing peat underlain by thawing permafrost described below (McCalley et al. 2014). Methylocrophic methanogenesis is generally considered to represent only a small proportion of total methanogenesis in most freshwater systems, including peatlands (Conrad 2020).

Although methanogenic activity is readily detected in acidic peat soils that have pH values as low as 3.5 (Goodwin and Zeikus 1987; Bergman, Svensson and Nilsson 1998; Høj, Olsen and Torvsik 2008; van Winden et al. 2012), very few novel genera or species of methanogenic archaea have been isolated from peat. These include two novel genera, Methanovergul boonei (Bräuer et al. 2006, 2011) and Methanospirillum palustris (Cadillo-Quiroz et al. 2008; Cadillo-Quiroz, Yavitt and Zinder 2009), within what has been called the R10 cluster (Hales et al. 1996) or fen cluster (Juottonen, Galand and Yrjäli 2006) of the Methanococcales, several species of Methanobacterium (König 1984; Krivushin et al. 2010; Schcherbakova et al. 2011; Cadillo-Quiroz et al. 2014) and one species each of Methanobrevibacter (Zhang et al. 2008a) and Methanoculleus (Tian, Wang and Dong 2010). Note that
Table 1. Archaeal orders containing methanogens or potential methanogens found in peat.

<table>
<thead>
<tr>
<th>Order</th>
<th>Phylum</th>
<th>Representative genera</th>
<th>Metabolismɑ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Methanosarcinales</td>
<td>Halobacterota</td>
<td>Methanosarcina, Methanoseta/therix</td>
<td>H, M, RM, A</td>
</tr>
<tr>
<td>Methanocellales (Rice cluster I)</td>
<td>Halobacterota</td>
<td>Methanocella</td>
<td>H</td>
</tr>
<tr>
<td>Methanomicrobiales</td>
<td>Halobacterota</td>
<td>Methanoregula</td>
<td>H</td>
</tr>
<tr>
<td>Methanomassili-coccales (Rice cluster III)</td>
<td>Thermoplasmota</td>
<td>Methanomassiliicoccus</td>
<td>RM</td>
</tr>
<tr>
<td>'Bathyarchaeota' (Miscellaneous)</td>
<td>Euryarchaeota</td>
<td>Methanobacterium</td>
<td>H (RM in Methanosphaera)</td>
</tr>
<tr>
<td>Crenarchaeotal Group; Rice cluster IV</td>
<td></td>
<td>'Bathyarchaeota' clones</td>
<td>M?, AMO?</td>
</tr>
</tbody>
</table>

ɑMetabolisms: H, hydrogenotrophic; M, methylotrophic (disproportionating); RM, reductive methylotrophic; AMO, anaerobic methane oxidation.

Figure 1. Neighbor-joining tree inferring the phylogenetic relationship between the SSU rRNA sequences retrieved from known cultured methanogens and the related sequences from peat. Bootstrap values ≥ 65 shown for nodes that were also supported by maximum likelihood. Supported nodes are marked with filled circles. Scale bar indicates fractional differences in nucleotide sequences.

no novel species of aceticlastic methanogens have been isolated from acidic peat. In past studies, researchers have made additions of acetate to peat microcosms that were either inhibitory or non-stimulatory (Williams and Crawford 1984; Goodwin and Zeikus 1987; Bridgham and Richardson 1992; Watson and Nedwell 1998; Blodau, Roehm and Moore 2002). Because of the toxicity of even low concentrations (3–5 mM) of acetate at low pH, some strategies for enriching aceticlastic methanogens in low pH environments have included co-culturing with syntrophic partners (Schmidt et al. 2016) or successive additions of low concentrations (≤ 1 mM) of acetate (Bräuer, Yavitt and Zinder 2004). However, eventual isolation of these strains has thus far proven unsuccessful (Horn et al. 2003; Sizova et al. 2003; Bräuer, Yavitt and Zinder 2004).
Figure 2. Phylogenetic relationship between short metagenomic methyl-coenzyme M reductase alpha subunit (mcrA) sequences found in bogs and known methanogen and Batharchaeotal mcrA sequences inferred using the iTOL-tree (Letunic and Bork 2019) with RaxML (Stamatakis 2014). Metagenomic mcrA genes were obtained by searching with an mcrA gene hmmer-profile (Wheeler and Eddy 2013) against an NCBI-SRA database of all bog ecosystems. The databases of peatland related ecosystems were collected with the SRAdb (Zhu et al. 2013) package in R (R Core Team 2019). In total, 203 bog SRA files were screened for mcrA genes.

Methanogens living in ombrotrophic bogs must adapt to high concentrations of protons (low pH) and to extremely low concentrations of ions like sodium and potassium; thus, methanogen diversity is generally reduced in bogs and increases with increasing pH and nutrient contents along a bog to poor fen, to intermediate and rich fen gradient. Bräuer et al. (2015) examined the genome sequence of M. boonei, and described some aspects of its genome that were congruent with adaptation to these conditions. The deduced amino acid sequence of the ion-pumping ATPCK subunit of the $A_1A_0$ ATPase/synthase in M. boonei belonged to an ATPCK group able to pump either protons or Na$^+$, whereas the other ATPCK group can only pump Na$^+$. The membrane-bound Mtr methyltransferase complex plays a key role in methanogen energy conservation, and the MtrE subunit has been found to pump Na$^+$ in methanogens. The MtrE in M. boonei lacks the amino acid motif considered essential to pumping Na$^+$, and may be a proton pump. Finally, most methanooarchaea only have genes encoding the low- and medium-affinity K$^+$ transporters, Trk and Kup, respectively. M. boonei is one of the few methanooarchaea possessing genes encoding the high-affinity ATP-driven Kdp transporter. Other methanooarchaea with predicted Kdp transporter genes include Methanobacterium strains SWAN-1 and AL-21, both isolated from acidic bogs, and Methanosphaera palustris isolated from a fen where the porewater K$^+$ concentration was only 3–8 $\mu$M. Interestingly, these genes are all related to a family from Geobacter, suggesting horizontal gene transfer that allowed these methanooarchaea to adapt to hypokalemic environments. Other genome studies of Methanomicobiales (Brown et al. 2017) have similarly revealed that unique transporters for additional scarce nutrients (besides K$^+$) such as Co, Ni, Mg, Fe, NO$_3^-$, HCO$_3^-$ and sulfonate were present in the peat-dwelling strains M. palustris and M. boonei but not strains from other habitats such as sewage sludge, marine sediments, oilfields, saline swamp mud or a tar pit. Comparison genomes included those for Methanoregula formicica, Methanolinea tarda, Methanoculleus marisnigri, Methanocorpusculum labreanum.

One, thus-far-uncultivated, elusive phylum is the Batharchaeota. Sequences clustering in this phylum have been detected in a wide variety of peatlands throughout the globe including those in Finland (Galand et al. 2002; Putikinen et al. 2009), Norway (Hej, Olsen and Torsvik 2008), China (Tian et al. 2012; Gu et al. 2013; Cao et al. 2014; Wei et al. 2014; Xiang et al. 2017), Slovenia (Stopnišek et al. 2010), Japan (Akiyama et al. 2011; Narihiro et al. 2011), Germany (Hunger et al. 2011; Steger et al. 2011).
Figure 3. Phylogenetic relationship between short metagenomic methyl-coenzyme M reductase alpha subunit (mcrA) sequences found in fens and known methanogen and Barhyarchaeota mcrA sequences inferred using the iTOL-tree (Letunic and Bork 2019) with RaxML (Stamatakis 2014). Metagenomic mcrA genes were obtained by searching with an mcrA gene hmmer-profile (Wheeler and Eddy 2013) against an NCBI-SRA database of all fen ecosystems. The databases of peatland related ecosystems were collected with the SRAdb (Zhu et al. 2013) package in R (R Core Team 2019). In total, 272 fen SRA files were screened for mcrA genes.

In addition to being implicated in methylotrophic methanogenesis (Evans et al. 2015), members of the Bathymarchaeota have been proposed to carry out the anaerobic oxidation of methane (Harris et al. 2018), acetogenesis (He et al. 2016), photosynthesis (Meng et al. 2009), or to utilize carbohydrates, aromatics, proteins, acetate or other organics (Biddle et al. 2006; Lloyd et al. 2013; Meng et al. 2014; Na et al. 2015; Lazar et al. 2016). However, in the absence of isolated representatives, it is difficult to infer the physiology of Bathymarchaeota in enrichment cultures, or by genomic data alone. For example, in an earlier case, before a representative of the Methanomassiliicoccales (RCIII group) was isolated, it was proposed that members were broader-spectrum soil heterotrophs rather than methanogenic based on the substrates that favored enrichment (Kemnitz, Kolb and Conrad 2005). In hindsight, responses to organic substrate amendments were likely due to indirect effects including stimulation of syntrophic bacteria. Additionally, members of the Bathymarchaeota are not only phylogenetically diverse, but also show a high level of genomic diversity based on metagenomic analyses; thus, there may be high metabolic diversity among species (Meng et al. 2014) or among subgroups (Xiang et al. 2017; Zho et al. 2018b). About half of the rRNA gene sequences collected in this review (using the NCBI Nucleotide Blast tool) appear to share the highest identity (95–97% ID) with both fosmid clone 37F10 (shown in Figure S1, Supporting Information) and metagenome BE326-BA-RLH, an organism predicted to be involved in anaerobic methane oxidation (Harris et al. 2018). These sequences (in the top 2 clusters in Figure S1, Supporting Information) share

2011), Denmark (Göres, Conrad and Petersen 2013), Brazil (Etto et al. 2012), as well as several US peatlands including those in Alaska (Rooney-Varga et al. 2007), Minnesota (Lin et al. 2012), North Carolina, (Hawkins, Johnson and Bräuer 2014), New York (Cadillo-Quiroz et al. 2006, 2008, 2010) and West Virginia (Yavitt et al. 2012). Members of this class have been previously known as RC-IV (Großkopf, Stubner and Liesack 1998), group 1.3 crenarchaeota (He), Olsen and Torsvik 2008), the deep peat group (Putikinen et al. 2009) or more commonly, the MCG or miscellaneous crenarchaeotal group (Kubo et al. 2012). Sequences from this group can represent a large portion (≥ 50%) of the archaeal population in some peatlands, for example in China (Xiang et al. 2017), Brazil (Etto et al. 2012) the southeastern continental US (Hawkins, Johnson and Bräuer 2014) and Alaska (Rooney-Varga et al. 2007). Yet in other studies, the bathyarchaeotal sequences are considerably rarer. This large variation in the proportions and abundance of Bathyarchaeota detected may depend on environmental conditions (Xiang et al. 2017; Yu et al. 2017; Zhou et al. 2018a, b; Fan et al. 2019), primers used (Cadillo-Quiroz et al. 2010), or other unknown factors (Biddle et al. 2006).
91–94% ID with sequences affiliated with MCG cluster 6 in the literature (Kubo et al. 2012). The other half (shown in the bottom half of the tree in Figure S1 (Supporting Information), approximately 4 clusters) appear to be most closely (85–90% ID) affiliated with sequences in MCG cluster 8, including Candidatus Bathyararchaeota archaeon BA2, an organism predicted to carry out methylothrophic methanogenic production (Evans et al. 2015; Berghuis et al. 2019; Evans et al. 2019). Thus, there is a potential for these Bathyararchaeota may be involved with methane cycling in global peatland ecosystems.

To assess the relative abundance of various methanogenic groups in bogs and fens using a method independent of PCR bias, an extensive search was carried out using a hmmer-profile (Wheeler and Eddy 2013) of the methyl-coenzyme M reductase alpha subunit (mcrA) gene to query the NCBI-SRA database of all peatland ecosystems, either categorized as fens or bogs. Short metagenomic mcrA sequences were aligned to the mcrA reference database with the mafft-aligner-algorithm (Katoh et al. 2019). These fragments were carefully selected, evaluated as mcrA with nblast (nt-database) searches and after the global alignment (as nucleic acid and amino acid sequences) with maft these fragments were closely related to the reference mcrA sequences after analysis with the evolutionary model finder, iq-tree and UF-boot (Trifinopoulos et al. 2016, Kalyaanamoorthy et al. 2017, Nguyen et al. 2015, Hoang et al. 2018). Finally, the sequences were phylogenetically placed in the iTOL-tree (Letunic and Bork 2019) with RaxML (Stamatakis 2014). Results indicate that bogs had a few clusters of Methanomicrobales, Methanocellales and Methanomassiliicocccales, as well as a limited number of Methanobacteriales related mcrA gene sequences (Fig. 2). Fen datasets revealed a dramatic increase in diversity across those four main orders, and notably a significant increase in Methanobacteriales-type mcrA gene sequences (Fig. 3). Additionally, a small number of mcrA sequences related to Methanothermococcus and Methanocaldococcus were found. Finally, results of the RaxML analyses showed Bathyararchaeota distantly related mcrA sequences. These distantly related sequences were also analyzed after mafft-alignment with iq-tree, which also tests the best evolutionary model for the data. Results indicate that these groups may be performing methanogenesis, anaerobic methane oxidation or another function especially in fens (Figure S2A, Supporting Information). If additional Bathyararchaeotal mcrA gene sequences are present, they may be too divergent (compared to the two sequences currently known) to be detected; thus, targeted/capture metagenomics should be used to detect Bathyararchaota in future studies (Kushwaha et al. 2015; Manoharan et al. 2015).

**Methanogen community responses to environmental change**

Methane feedbacks to environmental changes in wetlands represent an important knowledge gap in the role those wetlands will play in the future global climate system, particularly through 2100 (Dean et al. 2018). Because methanogenesis is a strictly anaerobic process with most known methanogens lacking metabolic strategies for protection from reactive oxygen species, CH4 emissions from peatlands are governed by soil moisture as an overarching control (Blodau 2002). Anaerobic oxidation of some CH4 produced is common in peatlands (Gupta et al. 2013, and see Smemo and Yavitt 2011 for perspectives on AOM in peatlands), yet rates are generally slow, and therefore the position of CH4 production in peat soil profiles (i.e. in fresher surface organic substrate v recalcitrant deeper substrates) and oxidation by aerobic CH4-oxidizing bacteria above the water table control net emissions (Blodau 2002). Indeed, average summer water-table position is a strong universal predictor of relative rates of emissions within sites, however emissions can vary by more than two orders of between even botanically-similar sites at the same water-table position (e.g. see Fig. 1B in Moore et al. 2011). Vegetation controls on CH4 emissions are multi-faceted, with both stimulation and suppression of methanogenesis beneath the water table from substrate or O2 supply respectively, and stimulation and suppression of aerobic oxidation through the supply of O2 or by aerenchyma serving as chimney allowing CH4 to evade CH4-oxidizing bacteria above the water table, respectively (Lai 2009).

Responses of peatland methanogen communities to environmental changes are influenced by site characteristics. Peatland classification systems vary to some extent, but in general, bogs are regarded as being primarily rain-fed, while fens are hydrologically connected to groundwater (e.g. National Wetlands Working Group 1997). Although in part dependent on the local climate, fens are typically wetter with more stable water-table positions, have higher soil and pore water pH due to higher base cation concentrations transported in from surrounding mineral soils, and are more likely to be dominated by graminoid (e.g. sedge) vegetation. Bogs are acidic with pH values often ca. 4.0 due to atmospheric inputs of inorganic acids, internal acidity generation from vegetation and low buffering capacity from groundwater-supplied base cations, and are often dominated by Sphagnum (a genus) mosses, with evergreen and deciduous woody shrubs and stunted spruce (Picea sp.) and tamarack/larch (Larix sp.) trees. The chemistry and plant communities across fens can vary, with for example low pH and bog-like vegetation in sites situated in catchments with shallow, coarse-textured soils low in calcium and other base cation elements (i.e. where the groundwater is more like rainwater chemically), to well-buffered pH circumneutral systems with very high calcium concentrations (e.g. see Godin et al. 2012 for descriptions of poor fens that resemble bogs to calcareous rich fens). As peat soil profiles grow over time (i.e. because primary productivity by plants exceeds mineralization losses by microbes), conditions often become more bog like, with hydraulic conductivity slowing over time as peat becomes more decomposed and amorphic. This soil profile growth also leads to peatland surfaces and local water table becoming perched higher than the surrounding groundwater and cutting off the supply of base cation elements from nearby mineral soils (Table 2 footnote). Peatlands can display varying degrees of microtopography, often consisting of raised hummocks, low hollows and flat ‘lawn’ areas that are relatively drier and wetter and have vegetation that is adapted to microsite physicochemical characteristics; and typically bogs display more pronounced undulating hummock-hollow topography (varying every few m) than fens. Permafrost-affected peatlands are often characterized by having raised palsas (e.g. as in Yavitt et al. 2006) or larger more continuous peat plateaus that are elevated and isolated from surrounding mineral-influenced groundwater by the permafrost (i.e. perennially frozen soil water within the surface 1m).

Key anthropogenic disturbances facing peatlands include direct and indirect effects of climate change such as higher temperatures (and associated permafrost thaw in permafrost-affected sites), altered precipitation and hydrologic dynamics, as well as altered disturbance regimes such as fire, invasive species, atmospheric pollution (notably enhanced reactive N, S and...
Table 2. Methanogen community characteristics in peatlands across natural gradients (A) and under key anthropogenic stressors (B).

<table>
<thead>
<tr>
<th>A. Natural gradient studies</th>
<th>Location</th>
<th>Notes on study and study sites</th>
<th>Methanogen community profiling method</th>
<th>Key findings (influence/changes/controls on methanogen community structure)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fen-boga or other natural trophic gradients</td>
<td>USA</td>
<td>Bog v temperate marsh peatland</td>
<td>Archaeal 16S rRNA gene profiling</td>
<td>High phylogenetic diversity at both sites, including aceticlastic methanogens in the bog (pH 4.1)</td>
<td>Basilko et al. (2003)</td>
</tr>
<tr>
<td>Canada</td>
<td>Rich to poor fen gradient</td>
<td>Archaeal 16S rRNA gene profiling</td>
<td>Methanosarcinaceae were dominant in most sites; Interestingly Methanomicrobiales was absent and Methanosaetaceae abundant in a poor fen (pH 4.7), contrasting a rich fen (pH 6.3) without Sphagnum moss</td>
<td>Godin et al. (2012)</td>
<td></td>
</tr>
<tr>
<td>Finland</td>
<td>Reciprocal soil transplant between bog and fen in microbe-excluding membrane</td>
<td>mcrA gene and transcript profiling</td>
<td>Fen peat placed in an acidic bog led to lower rates of CH₄ production, but acetate utilization (by members of Methanosaetaceae) persisted</td>
<td>Juottonen et al. (2020)</td>
<td></td>
</tr>
<tr>
<td>Finland</td>
<td>Bog fen comparison</td>
<td>mcrA gene profiling</td>
<td>Aceticlastic Methanosaetaceae dominated meso- and oligotrophic fen communities (and community structures were similar, while members of CO₂-reducing Methanomicrobiales dominated a bog)</td>
<td>Juottonen et al. (2005)</td>
<td></td>
</tr>
<tr>
<td>China</td>
<td>Adjacent riverine fen (marsh) sites with different Carex species</td>
<td>13C-DNA probing of mcrA genes to ID active methanogens</td>
<td>Both sites (pH 5.0 and 5.5) supported CO₂ reducing methanogens; Carex angustifolia also supported active aceticlastic Methanosaetaceae (but interestingly not Methanosaeta sp), while the Carex lasiocarpa site did not support aceticlastic methanogenesis</td>
<td>Lin et al. (2015)</td>
<td></td>
</tr>
<tr>
<td>USA</td>
<td>Sub-arctic and temperate sites with pH and vegetation differences</td>
<td>Archaeal 16S rRNA gene profiling</td>
<td>Methanomicrobiae and Methanobacteriaceae predominated colder sites; Methanosaetaceae only found in sites dominated by Carex sp. sedges and with little to no Sphagnum moss</td>
<td>Rooney-Varga et al. (2007)</td>
<td></td>
</tr>
<tr>
<td>Vegetation and/or topographic microforms within sites</td>
<td>Czech Republic</td>
<td>Three plant functional type microforms (Sphagnum, Eriophorum and Vaccinium) sampled each in three acidic (pH peatlands</td>
<td>Prokaryote 16S rRNA gene profiling</td>
<td>Few differences between plant species and sites (only one taxon of Methanoregula was more abundant under sedge); Methanomicrobia, Methanobacteria and Thermoplasmatales predominated while Methanosarcinaceae and Methanosaetaceae were detected, but were very rare</td>
<td>Chronakova et al. (2019)</td>
</tr>
</tbody>
</table>
### Table 2. Continued

<table>
<thead>
<tr>
<th>A. Natural gradient studies</th>
<th>Location</th>
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<tbody>
<tr>
<td>Finland</td>
<td>Hummock-lawn microforms in an oligotrophic (pH &gt; 4.4) fen</td>
<td>Archaeal 16S rRNA gene profiling</td>
<td>In surface soils, Methanomicrobiales (CO₂ reducers) dominated hummocks, while more versatile <em>Methanosarcina</em> sp. dominated lawns; no difference in deeper soils</td>
<td>Galand et al. (2003)</td>
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<tr>
<td>Finland</td>
<td>Hummock-hollow-lawn microforms in four bogs</td>
<td>mcrA gene profiling</td>
<td>Between site differences in methanogen community structure were greater than between forms within sites; CO₂-reducing Methanoregulaceae and RCII/Methanoflorentaceae predominated in all sites; Methanosaetaceae were not detected</td>
<td>Juottonen et al. (2015)</td>
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<td>Sweden and Denmark</td>
<td>Hummock to lawn gradients in three bogs (also see below for between-site comparison)</td>
<td>mcrA gene and transcript profiling</td>
<td>CO₂-reducing Methanoregulaceae predominated in all bog (pH &lt; 4.0) sites and microforms, followed by <em>Methanosarcinaceae</em> in two sites Methanocellales in one site; Methanosaetaceae were not detected</td>
<td>Marti et al. (2015)</td>
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<td>Soil profile (depth) gradients</td>
<td>Canada</td>
<td>Depth profile in a <em>Sphagnum</em> (pH 3.8) bog</td>
<td>¹³C signatures to predict methanogenic pathways</td>
<td>Acetate utilization predominated in surface soils, while CO₂ reduction predominated at lower depths</td>
<td>Hornibrook et al. (1997)</td>
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</table>

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<thead>
<tr>
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<th>Location</th>
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</thead>
<tbody>
<tr>
<td>Drought and warming</td>
<td>USA</td>
<td>Controlled microcosm experiment exploring warming (0–40 °C) in a <em>Sphagnum</em> bog peat</td>
<td>Archaeal 16S rRNA gene profiling</td>
<td>Distinct psychrophilic and mesophilic methanogen communities and associated bacterial syntrophs peak at 4 and 20 °C; both methanogen communities are predominantly <em>Methanobacteriaceae</em> taxa, however putative fermentative bacteria shift with <em>Clostridia</em> sp. more important at warmer temperatures</td>
<td>Kolton et al. (2019)</td>
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<td>Russia</td>
<td>pH (known to decrease with drought) and temperature were controlled in a microcosm study with bog peat (4, 15 and 25°C and pH 3.8, 4.8 and 6)</td>
<td>tracers to partition CO₂ reduction vs. aceticlastic activity; Archaeal 16S rRNA gene profiling</td>
<td>At low temperature and pH, only CO₂ reduction occurs driven by Methanobacteriaceae taxa; while at high temperatures, regardless of pH, aceticlastic activity predominated (60-70%)</td>
<td>(Kotsyurbenko et al. 2007)</td>
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<td>Japan</td>
<td>Aridified and sasa-invaded former Sphagnum bog (pH 4.2) peatland</td>
<td>mcrA and archaeal 16S rRNA gene profiling</td>
<td>Methanomicrobiales taxa predominated in Sphagnum sites (90%), but invasion with the broad-leaf bamboo after drought led to no detectable mcrA sequences and appearance of other distinct Euryarchaeota taxa</td>
<td>Narihiro et al. (2011)</td>
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<td>Finland</td>
<td>Two fen sites at different latitudes with experimental water-table lowering and passive soil warming</td>
<td>mcrA gene and transcript profiling</td>
<td>Warming generally did not enhance drying effects (that were large); aceticlastic Methanosetaeaceae taxa and CO₂-reducing Methanobacteriaceae were prominent in the drying regime in both sites (one more oligotrophic); interestingly this corresponded to reduced sedge and increased shrub biomass</td>
<td>Peltoniemi et al. (2016)</td>
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<td>China</td>
<td>Mesocosm experiment with temperature and water table</td>
<td>Archaeal 16S rRNA gene profiling</td>
<td>Warming effects were negligible in the 1–2 year experiment; CO$_2$ reducing Methanobacteriales and Methanomicrobiales taxa were more important in the drier experimental regimes, while RCII (CO$_2$-reducing, can. 'Methanoflorentaceae') taxa predominated under wetter conditions</td>
<td>Tian et al. (2015)</td>
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<td>Finland</td>
<td>Water-table drawdown experiment across a sedge fen</td>
<td>mcrA gene profiling</td>
<td>Methanocellales taxa dominated the reference wet areas; the community shifted to the ‘Fen cluster’ (Methanomicrobiales) with drying</td>
<td>Yrjala et al. (2011)</td>
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<td>Sweden</td>
<td>Palsa degradation to thermokarst gradient</td>
<td>$^{13}$C signatures to predict methanogenic pathways; Archaeal 16S rRNA gene profiling</td>
<td>Enhanced C lability following thermokarst formation associated with sedges led to enhanced acetoclastic methanogenesis; a single CO$_2$ reducing taxon (formerly RCII, here isolated as can. 'Methanoflorens stordaleniensis') also became dominant and is an important predictor of disturbance and CH$_4$ cycling feedbacks to thaw</td>
<td>Hodgkins et al. (2014); McCalley et al. (2014); Mondav et al. (2014)</td>
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<td>Canada</td>
<td>Compared palsa, recently collapsed palsa, and surrounding bog that had not been permafrost-affected for longer</td>
<td>Archaeal 16S rRNA gene profiling</td>
<td>Methanogen DNA was not detected in permafrost sites; recently degraded permafrost soils were characterized by Methanosarcinaceae (authors suggested were acetoclastic) and Methanobacteriales (CO$_2$-reducing) taxa, while the bog was characterized by Methanobacteriales and Methanocellales (RCI)</td>
<td>Yavitt et al. (2006)</td>
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<td>Norway</td>
<td>Compared degrading palsa to thermokarst to stabilized depression of a former collapsed palsa</td>
<td>mcrA gene profiling</td>
<td>Thermokarst formation led to a mixed CO$_2$-reducing (Methanobacterium and Methanocellales) and potentially acetoclastic (Methanosarcina) community. Longer-term bog succession had a similar-structured, but much less active community</td>
<td>Liebner et al. (2015)</td>
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### Table 2. Continued

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</tr>
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<tr>
<td>Atmospheric N pollution deposition</td>
<td>Sweden and Denmark</td>
<td>Three bogs of similar pH (3.9) receiving 1.5, 7 and 25 kg N per ha per year also represented different climatic environments</td>
<td>mcrA gene and transcript profiling</td>
<td>Substantially higher methanogen numbers in the high N deposition (but also warmer) site; there were subtle community changes, but Methanoregulaceae predominated in all sites and microforms, followed by Methanosarcinaceae in two sites and Methanocellales in one site; Methanosaetaceae were not detected</td>
<td>Marti et al. (2015)</td>
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<tr>
<td>Drainage for forestry and wood ash fertilization</td>
<td>Finland</td>
<td>Compared ash-fertilized and non-fertilized within a drained peatland</td>
<td>mcrA gene profiling</td>
<td>A drained bog supported only CO(_2) - reducing methanogens; RCI (now Methanocellales) predominated in both sites; though ash addition selected for Fen Cluster taxa (Methanomicrobiales) that were not in the control site</td>
<td>Galand et al. (2005)</td>
</tr>
<tr>
<td>Horticultural peat extraction and reclamation</td>
<td>Canada</td>
<td>Eight sites representing pristine, mined and reclaimed acidic bogs</td>
<td>Archaeal 16S rRNA and mcrA gene profiling</td>
<td>Methanogens were not detectable in some actively mined (drained sites), but CO(_2) - reducing methanogens (RCII, now Candidatus Methanoflorentaceae) and Methanomicrobiaceae predominated, and in one trial the methanogen community of the restored site resembled the nearby pristine site</td>
<td>Basiliko et al. (2013)</td>
</tr>
<tr>
<td>Impacts of agriculture and reclamation</td>
<td>Finland and Germany</td>
<td>Rewetted bog sites with dung applied to simulate post-animal grazing reclamation contexts</td>
<td>mcrA gene profiling</td>
<td>Dung impacted sites facing rewetting (i.e. again becoming methanogenic) were dominated by enteric Methanobrevibacter sp. and had high rates of CH(_4) production in stark contrast to reference sites</td>
<td>Hahn et al. (2018)</td>
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*Fens are connected to groundwater sources and although they range in nutrient concentration and pH (rich, intermediate and poor), are higher in base cations and alkalinity than bogs, which are isolated from groundwater sources. A prototypical peatland succession model proceeds from shallow aquatic ecosystem, to rich fen, to poor fen, to bog as the peat soil profile aggrades and hydraulic conductivity decreases—eventually isolating the majority of the system from all water inputs except precipitation. Bogs tend to have a continuous Sphagnum moss cover and few sedges, while mesotrophic (intermediate) and eutrophic (rich) fens tend to be dominated by graminoid vascular species (e.g. sedges in the genera Carex and Eriophorum).*
metal loading), and direct drainage exploitation for mining, silviculture and agriculture (e.g. IUCN 2017; Grzybowski and Glińska-Lewczuk 2020). A growing body of literature has explored how these anthropogenic changes affect methane cycling rates, but there are still numerous gaps in understanding how changes influence methanogen communities. Many anthropogenic disturbances lead to shifts in broader ecosystem properties like plant functional types (e.g. with loss of keystone sphagnum mosses from bogs and acidic fens and the encroachment of vascular plants, or sedge and aquatic Sphagnum proliferation in thermokarst formation through permafrost degradation), and this means that studies exploring methanogen communities across natural gradients (e.g. fen to bog, different vegetation and hydrological micro-features within sites, etc.) can be useful to make predictions of the effects of anthropogenic disturbances.

A search of peer-reviewed literature on the Web of Science Core Collection database (Clarivate Analytics, Boston, MA) at the time of writing yielded 112 works associated with topic words ‘methanogen’ and ‘peatland or fen or bog or mire’. Of these, ca. 16 focused explicitly on how methanogen community structure changed with anthropogenic-type disturbances described above, while ca. 15 contrasted methanogen community structure across sites or microforms (e.g. see descriptions of microtopographic features above) without an explicit link to anthropogenic disturbance; most of these studies are summarized in Table 2. Many anthropogenic disturbances led to changes that are somewhat analogous to changes seen in the prototypical fen to bog succession, only in reverse (Table 2 footnote) with regards to vegetation and hydrological changes. In two studies, one for warming by (Dieleman et al. 2015) and one for atmospheric nitrogen pollution deposition by Larmola et al. (2013), results demonstrated that Sphagnum-dominated poor fen and bog plant communities shifted rather quickly towards those seen in richer, sedge-dominated peatlands. Shifting plant communities commonly mediate microbial feedbacks to environmental changes. Regarding specific impacts on methanogen communities, there are general trends that fens with sedges and higher pH support acetoclastic along with CO2 reduction pathways (Table 2A), however underlying controlling factors are complex. For example (Kotsyurbenko et al. 2007) showed that acetoclastic pathways are absent below pH 4 in bog soils at low temperatures, but can be substantial at low pH when soil temperatures are high. Also, Rooney-Varga et al. (2007) demonstrated a clear link between sedges (and little to no Sphagnum) and the acetoclastic pathway across extensive study sites (further corroborated by isotope-based methanogenesis pathway analyses by Hines et al. 2008), yet Basiliko et al. (2003) and Godin et al. (2012) illustrated that Methanosetaeaceae taxa might be important even in acidic bog and poor fen sites with 100% Sphagnum cover. Though it should be noted that the latter two studies were carried out with surface peat soils in relatively lower latitude locations in sub-boreal Canada and the northern continental US, and Kotsyurbenko et al. (2007) reported that acetoclastic methanogenesis can occur in low-pH peat soils if the temperatures are high.

A number of climate change impact studies have examined in situ warming and drought on methanogen communities in bogs and fens in Europe and Asia (Table 2). Community structure changes appear to be context specific, with cases of shifts from one CO2-reducing group to another (e.g. Tian et al. 2015), increasing importance of acetoclastic methanogens (e.g. Peltoniemi et al. 2016), or in one case when drought was coupled with a major plant invasion, loss of all known methanogen taxa (Narihiro et al. 2011). Reported impacts in studies of climate change degrading permafrost peatland landforms have been more consistent, at least when the degradation results in thermokarst and sedge expansion after thaw (Table 2). For example, where initial arcausal populations are often dominated by hydrogenotrophic methanogens, as the degree of thaw and rates of decomposition increased, the proportion of acetoclastic methanogens increased (e.g. McCalley et al. 2014). It is important to note that there are still relatively few studies, and permafrost degradation can lead to outcomes other than thermokarst formation (and associated shifts in vegetation, methane communities and increased CH4 emissions) outside of lowlands. For example, the effects of slow active-layer deepening or rapid drainage as gullies form from loss of ice wedges on methanogen communities could be quite different from what has been observed for thermokarst formation following thaw.

A number of case studies have explored direct impacts associated with horticultural peat extraction and reclamation, drainage and forestry and post-agricultural reclamation of peatlands on methanogen communities (Table 2), but given the extent and diversity of context-specific land uses, more work is needed. There are also critical gaps in the literature regarding atmospheric deposition impacts on methanogen communities. Important studies have shown that chronic S loading can suppress methane emissions at large scales (e.g. Gauci et al. 2004), while chronic N loading has been shown to enhance emissions from a bog (Juutinen et al. 2018), but little is known about the impacts and feedback roles of methanogen communities. Similarly, despite the known role of certain trace metals in CH4 cycling metalloenzymes (Glass and Orphan 2012), that continental gradients of metals might limit methanogenesis in peatlands (Basiliko and Yavitt 2001), and that metal pollution disrupts vegetation and bacterial and fungal communities in peatlands (Luke et al. 2015), work is still needed on methanogen community-metal loading interactions in terms of trace nutrients and potential toxicant effects.

We have attempted to summarize and synthesize what we believe are most of the peer-reviewed studies on methanogen community responses to environmental changes (Table 2). However, given the global extent (ca. 4 × 106 km2; Parish et al. 2008) and variability within and between peatlands, and the types and variability of environmental change pressures, much more work is needed before strong conclusions about feedbacks can be drawn. These studies will ideally go hand in hand with work enriching for, isolating and exploring the physiological ecology of the vast numbers of ‘known unknown’ peatland methanogens to provide a comprehensive picture of both how and why methanogen communities respond to increasing environmental change pressures.

CONCLUSIONS AND OUTLOOK

Recent progress has contributed substantially to our understanding of the taxonomy and physiological ecology of methanogens in peatlands, yet substantial gaps remain. Environmental omics approaches continue to be refined and play a key role in identifying the ‘known-unknown’ methane cycling archaeal taxa that are most important in peatland feedbacks to anthropogenic change, but alone they still fail to elucidate fundamentals of metabolism and ecology. The isolation of Methanoflorens stordalenmirensis in the context of palsa degradation was an excellent example of a paired community biomarker and isolation approach (Mondav et al. 2014), and similar work should continue across permafrost peatland thaw, and other environmental change contexts. For example, to date no novel species of acetoclastic methanogens have been
isolated from acidic peat, the role of the mcrA-containing Bath-
yarchaeota within the phylum Crenarchaeota is not known, and
the potential role of archaean in the omnipresent process
of anaerobic CH4-oxidation in peatlands (Gupta et al. 2013) is
not clear. Future efforts should clearly focus on novel methods
of isolation to acquire a greater diversity of representative
organisms in pure culture that are guided by in situ studies of
methanogen community responses to environmental stressors.
In cases where isolation is elusive, long-term enrichment
processes (e.g. with a dominant methanogen and syntrophic
colonies) coupled with physiological measurements and
physiological and metabolic attributes can yield important information on the
physiological ecology and taxonomy of novel methanogens
(Carson et al. 2019). To guide enrichment and isolation so that
efforts are placed on the most interesting and important taxa,
meaningful climate change simulation, pollutant (N, S and
metals) adsorption, and land-use change studies on methanogen
communities are still needed.

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SUPPLEMENTARY DATA

Supplementary data are available at FEMSLE online.

Conflicts of interest. None declared.

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