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Peatland Microbial Community Composition Is Driven by a Natural Climate Gradient

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Abstract

Peatlands are important players in climate change–biosphere feedbacks via long-term net carbon (C) accumulation in soil organic matter and as potential net C sources including the potent greenhouse gas methane (CH_4). Interactions of climate, site-hydrology, plant community, and groundwater chemical factors influence peatland development and functioning, including C dioxide (CO_2) and CH_4 fluxes, but the role of microbial community composition is not well understood. To assess microbial functional and taxonomic dissimilarities, we used high throughput sequencing of the small subunit ribosomal DNA (SSU rDNA) to determine bacterial and archaeal community composition in soils from twenty North American peatlands. Targeted DNA metabarcoding showed that although Proteobacteria, Acidobacteria, and Actinobacteria were the dominant phyla on average, intermediate and rich fens hosted greater diversity and taxonomic richness, as well as an array of candidate phyla when compared with acidic and nutrient-poor poor fens and bogs. Moreover, pH was revealed to be the strongest predictor of microbial community structure across sites. Predictive metagenome content (PICRUSt) showed increases in specific genes, such as purine/pyrimidine and amino-acid metabolism in mid-latitude peatlands from 38 to 45° N, suggesting a shift toward utilization of microbial biomass over utilization of initial plant biomass in these microbial communities. Overall, there appears to be noticeable differences in community structure between peatland classes, as well as differences in microbial metabolic activity between latitudes. These findings are in line with a predicted increase in the decomposition and accelerated C turnover, and suggest that peatlands north of 37° latitude may be particularly vulnerable to climate change.

Keywords Peatlands · Microbiology · Carbon cycling · Climate change

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Introduction

Despite covering only 3–4% of the Earth's land surface area, peatlands in mid to high northern latitudes have a large influence on global C cycling [1, 2], holding as much as one-third of the planet's soil C [2]. In addition to storing C, peatlands also emit CO_2 and CH_4, depending on the hydrologic conditions [3]. Water-saturation in deep peat soil (the catotelm layer) is advantageous for microbial CH_4 production [4], for which a molecule of CH_4 has a global warming potential 23 times greater than a molecule of CO_2 under the IPCC's 100 year timeframe [5]. These emissions make peatlands a crucial player in future global climate change and the global C budget [4], as average global temperatures over land and sea are predicted to rise 3 to 7 °C by the end of the century due to anthropogenic manipulation of the atmosphere [6]. A significant consideration in the face of climate change is whether northern peatlands will continue to store more C than they release.

One area that may hold clues as to the fate of northern peatlands as temperatures rise is peatlands at the southernmost regions currently permissible to peat formation. When compared with the northern peatlands, annual organic matter decomposition and net production are higher in the southern peatlands, and they also experience a greater rate of decomposition relative to the biological production [7]. The Appalachian Mountains in eastern North America contain a diversity of peatland sites that may provide insight into climate–microbial relationships. These peatlands formed during the last Glacial Maximum, approximately 13,000–18,000 years ago [8–11]. Sites at the southern end of the gradient are older. Although Gajewski et al. (2001) reported *Sphagnum* in the Southern Appalachians during the Glacial Maximum, not all *Sphagnum* species are peat forming, and Halsey et al. (2000) concluded no *Sphagnum*-dominated bogs occurred during glacial times, consistent with present-day fens in the region. However, these conclusions are based on few sites, and thus, the history of sites is uncertain. Toward the northern end of the gradient, peatlands formed during the Holocene and range from rich fens to bogs [8]. How peatlands along this long latitude gradient respond to present-day and future climate is uncertain. It is also unclear whether sites along the gradient harbor the same taxa of microorganisms that are responsible for C cycling processes. This uncertainty critically limits our ability to put peatlands into a broad context of the global dynamics of atmospheric CO_2 and CH_4.

Here we sampled peat soil from 20 eastern North American peatlands across a natural climate gradient from the James and Hudson Bay Lowlands of Ontario, Canada to North Carolina, USA. We assessed differences in microbial (bacterial and archaeal) community assemblages and predicted functional gene types (using PICRUSt [12]). We expected that community composition would differ among peatland types in regard to communities associated with higher rates of C turnover, with the largest difference between bogs and rich fens. Since fens occurred along the entire gradient, we also examined the null hypothesis that fens had the same community composition regardless of location along the gradient. We were especially interested in knowing if assemblages toward the southern end of the gradient were unique or subsets of those in more northern counterparts. Thus, we aim to provide insight into the possible future of the extensive northern peatlands in regard to accelerated C turnover.

Methods

Study Sites and Sample Collection

Twenty eastern North American peatlands across 9 geographic locations, ranging from 36.16° to 53.69° latitudes, were chosen for this comparison study (Table 1). Peatlands were classified into 4 wetland classes (bog, poor fen, intermediate fen, and rich fen) based on the relationship between pH and calcium content [13] (Fig. S1), hydrological input, and PI reporting. Samples from each peatland were collected in triplicate cores at three depths: 10–20 cm, 30–40 cm, and 60–70 cm below the peat surface using a 10-cm PVC corer. Daisy Lake, Sugar Hill, and Tater fen lacked collection at the 60–70 cm depth, due to shallow peat profiles. Understory data was primarily measured in 1 m^2 plots, while canopy cover was taken above core location. Following sampling, peat was frozen (− 20 °C) and shipped to the USFS lab in Houghton, MI for DNA analysis as described by Harbison et al. [14].

Chemistry and Environmental Data

Environmental parameters for each site and sample included *Sphagnum* and vegetation cover, depth to water-table, peat and water pH, and core temperature. Average global air temperatures of peatlands from the USA were acquired from the National Oceanic and Atmospheric Administration (NOAA), while average air temperatures for the Canadian peatlands were obtained from the Government of Canada's Environment and Natural Resources website database. Peat soil samples were analyzed for Ca, Co, K, Mg, Na, and Ni concentrations. For each element, peat was combusted to 550 °C, and the ash was dissolved in acid and analyzed on a Varian 810 ICP_MS [15].

Microbial Sequencing Analysis

For community sequencing, DNA was extracted from peat samples with MoBio (now QIAGEN) Laboratories PowerSoil® DNA Isolation Kit and cleaned using the

Table 1 Peatland habitat description and geographic detail and coordinates

Location	Peatland	Average annual temperature (°C)	Latitude (decimal degrees)	Longitude (decimal degrees)	Elevation (m)	Average pH	Habitat classification	Vegetation analysis
Western North Carolina	Pineola	10.1	36.02	− 81.9	1066	5.6	Intermediate fen	100% canopy cover, primarily Red Maple and Eastern Hemlock; understory includes Impatiens, Carex, and Angelica; 20–25% Sphagnum cover
Western North Carolina	Sugar	10.1	36.08	− 81.89	1229	5.12	Intermediate fen	75–100% canopy cover, primarily Red Spruce; understory includes Carex, Ilex, Mnium, Osmundastrum; 40–55% Sphagnum cover
Tennessee, USA	Ripshin	13.4	36.17	−82.15	1085	5.66	Intermediate fen	No canopy cover; understory includes Carex, Ribes, Polygonaceae, Forb, Rush, Typha, Grass, and Willow species; 20–90% Sphagnum cover
Western North Carolina	Tater Hill	10.1	36.28	− 81.72	1258	5.96	Rich fen	No canopy cover; understory includes Carex, Drosera, Houstonia, Juncus, Osmundastrum, Schoenoplectus, and Scirpus; 20–30% Sphagnum cover
West Virgina, USA	Cranberry Glades	10.2	38.2	− 80.27	1026	4.07	Bog	10% canopy, primarily Red Spruce; understory included Salix, Eriophorum, and Vaccinium; 60–70% Sphagnum cover
West Virgina, USA	Big Run	10	39.12	− 79.58	981	4.67	Poor fen	No canopy cover; understory includes Eriophorum and Rubus; 10% Sphagnum cover
Ohio, USA	Cedar	10.5	40.06	− 83.79	295	7.75	Rich fen	No canopy cover; understory includes sedge species and cedar; 0% Sphagnum cover
New York, USA	Purvis Road/Dryden Bog	8.1	42.45	− 76.26	372	4.33	Poor fen	No canopy cover; understory includes Chamaedaphne; 10–40% Sphagnum cover
New York, USA	McLean	8.1	42.55	− 76.27	341	4.09	Bog	No canopy cover; understory includes Chamaedaphne, Oxycoccus, and Eriophorum; 10–85% Sphagnum cover
Ontario, Canada	Mer Bleue	6.6	45.41	− 75.48	69	4.04	Bog	No canopy cover; understory includes Chamaedaphne, Ledum, Kalmia, Vaccinium, and Polytrichum; 35–61% Sphagnum cover
Sudbury gradient, Ontario, Canada	Whitson lake	3.5	46.35	− 80.59	299	5.8	Intermediate fen	No canopy cover; understory includes Polygonaceae and Forb; 10% Sphagnum cover
Sudbury gradient, Ontario, Canada	Long lake	3.5	46.37	− 81.07	286	5.3	Intermediate fen	0–25% canopy coverage; understory includes Polygonaceae and Forb; 30–40% Sphagnum cover
Sudbury gradient, Ontario, Canada	Cartier	4	46.4	− 81.31	423	4.01	Bog	0–10% canopy coverage; understory includes Forb species (up to 90%), presence of Rumex, Salix, Eriophorum, and Vaccinium; 5–40% Sphagnum cover
Sudbury gradient, Ontario, Canada	Daisy lake	3.5	46.45	− 80.88	249	4.8	Intermediate fen	No canopy cover; understory includes Rumex; low Sphagnum cover
Ontario, Canada	White river intermediate fen	1.7	48.35	− 85.36	485	5.37	Intermediate fen	No canopy cover; understory includes Sweet gale and mostly sedge with some shrub species; no report on Sphagnum cover
Ontario, Canada	White river poor fen	1.7	48.35	− 85.34	467	4.04	Poor fen	Some trees are within a 5-m radius; understory includes Ericaceous and

Table 1 (continued)

Location	Peatland	Average annual temperature (°C)	Latitude (decimal degrees)	Longitude (decimal degrees)	Elevation (m)	Average pH	Habitat classification	Vegetation analysis
								larch/spruce; no report on Sphagnum cover
Hudson Bay Lowlands Ontario, Canada	Victor Mine (MOE Fen)	− 0.6	52.69	− 83.94	88	6.54	Rich fen	50–75% canopy cover; primarily Tamarack; understory includes Rhytiadelphus, Tomentypnum, Scorpidum, Chamaedaphne, Andromeda, Vaccinium, Rubus, Menyanthes, Equisetum, and Carex; 3–13% Sphagnum cover
Hudson Bay Lowlands Ontario, Canada	Victor Mine (VICM 101/102)	− 0.6	52.72	− 83.94	88	3.98	Poor fen	No canopy cover; the dominate shrubs were Ericaceous Birch; habitat primarily consisted of sedges, moss, lichen, and shrub species
Hudson Bay Lowlands Ontario, Canada	Victor Mine (MOE Bog)	− 0.6	53.69	− 83.94	91	4.07	Bog	10–25% canopy cover; primarily Black Spruce; presence of Polytrichum, Cladina, Chamaedaphne, Rhododendron, Kalmia, Vaccinium, Rubus, Picea, and Carex; 31–51% Sphagnum cover

PowerClean® kit, following the manufacturers protocol with a heating step (65 °C for 30 min) added during the DNA extraction following bead beating. DNA extracts for each sample were sequenced and collected on the Next-Generation Sequencing (NGS) Illumina MiSeq platform by the Department of Energy's (DOE) Joint Genome Institute (JGI) for bacteria and archaea using the V4 region of SSU rRNA (515/806) primer pairing. Sequences are retained on the JGI database and fall under the project: "Fungal, bacterial, and archaeal communities mediating C cycling and trace gas flux in peatland ecosystems subject to climate change," with the project ID: 1445. These raw sequence data (in addition to other Global Peatland Microbiome Project target sites) were housed on the server based JGI database, and data for the peatlands of interest were downloaded from the JGI server in 2016. Sequences were first quality filtered using BBMap package [16]. PANDAseq [17] was used to align forward and reverse reads, and aligned sequences were then processed with QIIME [18], and the USEARCH version 8 [19] software using a 97% confidence value for OTU assignment [14, 20]. Contigs were generated from complementary forward and reverse sequences while discarding sequence reads shorter than 240 base pairs (bp) or longer than 350 bp. The Greengenes 2013 database [21] was used for taxonomic assignment of bacterial and archaeal assemblages. It is important to note that the Greengenes database has not been updated since 2013. However, since this study peered into phylum level identification, it was considered a sufficient database. Taxonomic identification data was visualized using QIIME 1 scripts [18], while environmental biplots and non-metric multidimensional scaling (NMDS) utilizing Bray-Curtis dissimilarity was generated with ggplot2 RStudio packages [22]. The indicator phyla analysis was utilized with the CRAN indicspecies package. Predictive microbial metabolic activity was generated and visualized with PICRUSt [12].

Results and Discussion

Bacterial and Archaeal Community Composition

Members of the Proteobacteria were the dominant identified phylum on average across all sites (31%) followed by Acidobacteria (20%) and Actinobacteria (6.9%; Fig. 1). Relative abundance of sequences related to Acidobacteria was higher in bogs and poor fens, likely reflecting the acidic pH values, greater accumulation of peat, and slower turnover rates common in bogs and poor fens, and thus highlighting the slow metabolic rates of these organisms [23]. Acidobacteria were less common in intermediate and rich fens as demonstrated by the rise of microbial taxonomic richness and diversity in these higher pH and more nutrient-rich peatlands (Fig. 1; Table 2). Comparatively, nutrient rich and more neutral sites (intermediate and rich fens) hosted a greater relative abundance of Bacteroidetes. Members of the Bacteroidetes phylum have high decomposition potential and have been observed to act as primary mediators for cellulose degradation in acidic *Sphagnum* peat [24]. Multiple studies have suggested that

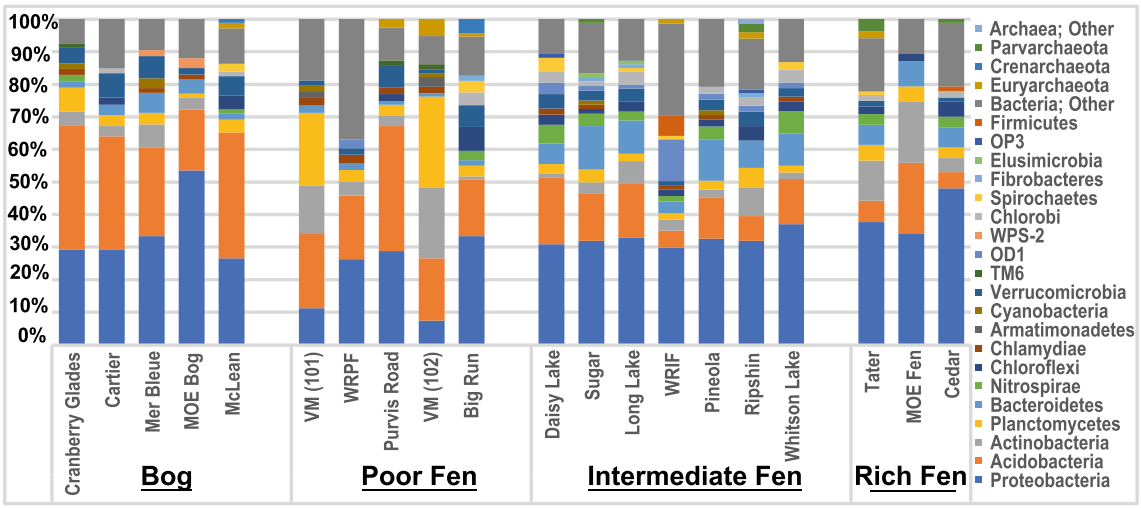

Fig. 1 Taxonomic bar plot with total percentages (all depths averaged) of bacterial and archaeal relative abundance at phylum classification

plant biomass degradation and nutrient cycling are primarily mediated by Proteobacteria and Acidobacteria, accompanied by Firmicutes, Bacteroidetes, Chlamydiae/Verrucomicrobia, and Actinobacteria [25–28]. We speculate that among our sites faster C turnover rates in intermediate and rich fens is influenced, at least in part, by the increased abundance of Bacteroidetes.

In line with previous findings [29–31], beta-diversity, assessed via an NMDS Bray-Curtis-dissimilarity ordination, showed that pH was the strongest predictor in bacterial and archaeal community clustering (Fig. 2). This is supported by an NMDS biplot demonstrating that pH and Ca explained a large degree of the variance in microbial communities across a gradient from bogs to rich fens (Fig. S2). This ordination analysis (Fig. 2) also showed overlap in microbial community assemblages within bogs and poor fens and a large separation between the microbial communities in poor versus intermediate and rich fens. This finding is most likely due to nutrient and pH constraints on microbial communities in bogs and poor fens [29, 32]. Bacterial diversity (Shannon Diversity Index) was highest in rich fens (Table 2) with the Cedar peatland in Ohio having the highest number of detected OTUs (4019 OTUs) and diversity, and also the highest pH measurement. Generally, evenness increased from bog to rich fen (Table 2), Pineola fen had the highest evenness value, indicating a reduction in the number of dominant bacterial or archaeal OTUs in this southern Appalachian Mountain peatland. Results corroborate previous findings demonstrating that microbial diversity in wetlands increases from bog to fen and/or to riparian environments [33, 34], most likely due to increases in pH, nutrient content, and local surface and/or groundwater input(s) in fens and riparian wetlands.

Table 2 Diversity analysis of peatlands of interest depicting total microbial species count, alpha diversity (Shannon index), and evenness

Peatland	Species count	Shannon index	Evenness
Cranberry	1675	5.0721	0.684
Cartier	1093	4.6257	0.663
Mer Bleue	1699	5.1828	0.6994
MOE Bog	198	3.3972	0.6451
McLean	1395	4.9061	0.6791
Victor Mine (101)	172	3.342	0.6833
WRPF	193	4.2334	0.8119
Purvis Road	1545	4.8471	0.661
Victor Mine (102)	351	3.6686	0.6448
Big Run	2046	5.4929	0.7209
Daisy Lake	1026	5.7118	0.824
Sugar	716	5.9592	0.9073
Long Lake	1804	5.9564	0.7967
WRIF	211	4.5808	0.8591
Pineola	718	5.9867	0.9128
Ripshin	856	5.8029	0.8826
Whitson Lake	1449	6.1148	0.8405
Tater	1593	5.9943	0.8188
MOE Fen	1406	5.5566	0.7672
Cedar	4020	6.6025	0.8267

An indicator phyla analysis was performed utilizing taxonomic tables on all comparative peatlands by depth, demonstrating that rare and uncultivated bacterial phyla were unique to certain peatland classes (Table 3). Overwhelmingly, rich fens hosted the highest number of indicator phyla (14 phyla) between the three sample depths. Of these, candidate groups PAUC34f and GOUTA4 were most significant at lower peat depth. PAUC34f has been recently described in marine "Dead Zones" where they showed metabolic potential for complex carbohydrate compound degradation under anaerobic conditions [35]. GOUTA4 has been observed in various environments and expresses potential for bioremediation, but its

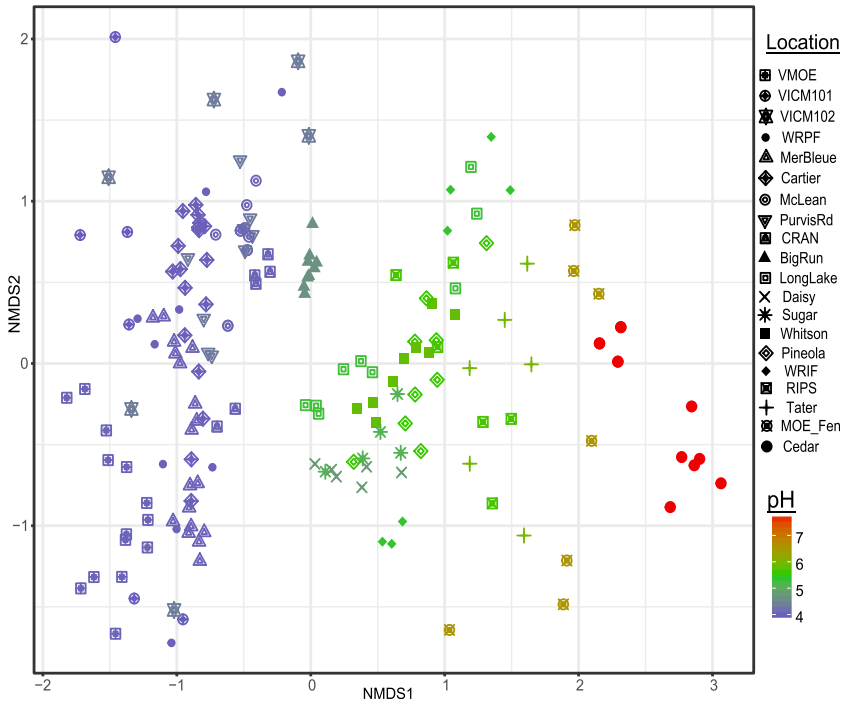

Fig. 2 Non-metric multidimensional scaling (NMDS) plots of bacterial/archaeal communities. Ordination is based on Bray-Curtis dissimilarity values

metabolic/ecological roles have yet to be fully understood [36, 37]. Compared with bogs and poor fens, intermediate and rich fens (when grouped together) had a large array of distinguishing indicator phyla, most of which belong to candidate divisions. The three phyla common to intermediate and rich fens at all three depths were candidate phyla GN02, WS3, and OP11. GNO2 has been detected, accompanied by other candidate phyla, in a sulfur-rich sands oil deposits [38], and found in significant abundances in microbial mats in Shark Bay, Australia [38]. Members of OP11are predicted to consume starch, lignin, and cellulose, as genes encoding amylopullulanase, laccase, and endoglucanase enzymes have been found in an anoxic spring [39]. These compounds are common in plants and peat, thus explaining the presence of OP11 in these nutrient-rich peatlands. WS3, now named Latescibacteria, has been classified as a member of the Fibrobacteres-Chlorobi-Bacteroidetes (FCM) superphylum [40]. Members of the Latescibacteria have been suggested to have anaerobic fermentative capabilities, with the capacity to degrade various forms of polysaccharides and glycoproteins [40].

Although poor fens revealed no unique indicator phyla at the 10 cm depth, bogs had one indicator phylum, candidate division FBP, a group believed to share a close relationship with the recently named *Armatimonadetes* phylum (previously OP10) [41]. At 60 cm, bogs hosted candidate division WPS-2. This candidate group, while still understudied, is phylogenetically related to cyanobacteria, and has been shown to tolerate polluted soils, as evidenced by the name "Wittenberg polluted soil" [42]. Overall, the large number of candidate divisions found in this study highlights the fact that peatland microbial ecology is still fairly understudied and the fact that many peatland microbes remain uncultivated. Moreover, these candidate phyla may potentially be contributing to the increased microbial decomposition rates seen in these more nutrient rich peatlands.

In line with previous studies [14], relative abundance of Archaea increased with depth from 10 to 60 cm for nearly all sites (Fig. S3). This can be explained by previous findings that many Archaea groups thrive under anoxic conditions and are major agents in anaerobic respiration [43, 44]. A more in-depth analysis (phylum classification) revealed that the archaeal phylum Parvachaeota, member of the DPANN superphylum, considerably increased in relative abundance in the intermediate and rich fens compared with poor fens and bogs. Dominance of the Parvachaeota was most notable in an intermediate fen, (Sugar Mountain, 60% of total archaeal phyla) and a rich fen (Cedar, 53% of total archaeal phyla) (Fig. 3). This phylum has been described in acid mine drainage, hot springs, and marine environments [45, 46]. Genomic data suggest that members of the Parvachaeota could be involved in nitrogen, and C cycling via saccharide and protein degradation, in producing ATP through fermentation and aerobic respiration, and are likely heterotrophic since the six known C fixation pathways were absent from Parvarchaeota genomes [46]. Sequences within the phylum-level archaeal classification of "Other" also increased on average relative abundance in the intermediate and rich fens, compared with poor fens and bogs (Fig. 3). The presence of unassigned sequences ("Other") shows the need for further investigations into microbial community profiling in these environments. Euryachaeota, however, did not show a consistent trend, but demonstrated varied relative abundance values across all four peatland types. The methanogens of this phylum are of special

Table 3 Indicator phyla analysis across all four wetland types at three depths of peat. Phyla are all bacteria unless designated with a caret (^) for Archaea; a minus symbol (−) indicates absence. Percentage denotes the total proportion per peatland class. Significance codes (*p* value): 0 "***" 0.001 "**" 0.01 "*" 0.05

Indicator Phylum	Bog	Poor Fen	Intermediate Fen	Rich Fen
Depth = 10 cm				
FBP	0.01%*	-	-	-
WS5	-	-	0.18%**	-
PAUC34f	-	-	-	0.03%**
GOUTA4	-	-	-	1.16%**
GN04	-	-	-	0.94%*
OC31	-	-	-	0.05%*
GN02	-	-	0.04%***	
WS3	-	-	0.16%**	
OP11	-	-	0.30%*	
SR1	-	-	0.02%*	
Tenericutes	-	-	0.09%*	
AD3	-	-	0.07%**	
Depth = 30 cm				
WS5	-	-	0.02%**	-
PAUC34f	-	-	-	0.01%***
GOUTA4	-	-	-	0.40%***
LCP.89	-	-	-	0.02%*
TA06	-	-	-	0.01%*
Fusobacteria	-	-	-	0.01%*
Caldiserica	-	-	-	0.01%*
OC31	-	-	-	0.04%*
Gemmatimonadetes	-	-	0.18%**	
OP11	-	-	0.63%***	
GN04	-	-	0.21%**	
WS3	-	-	0.24%***	
OP8	-	-	0.28%*	
Tenericutes	-	-	0.03%*	
SR1	-	-	0.02%*	
GN02	-	-	0.03%*	
WPS.2	-	-	0.04%***	
AD3	-	-	0.77%**	
Depth = 60 cm				
WPS.2	0.07% *	-	-	-
GOUTA4	-	-	-	0.42%*
TM7	-	-	-	0.02%*
MVS.104	-	-	-	0.02%*
GN04	-	-	1.16%***	
Gemmatimonadetes	-	-	0.15%***	
OP11	-	-	0.76%*	
^Parvarchaeota	-	-	1.95%*	
WS3	-	-	0.27%**	
GN02	-	-	0.05%**	
SR1	-	-	0.01%*	

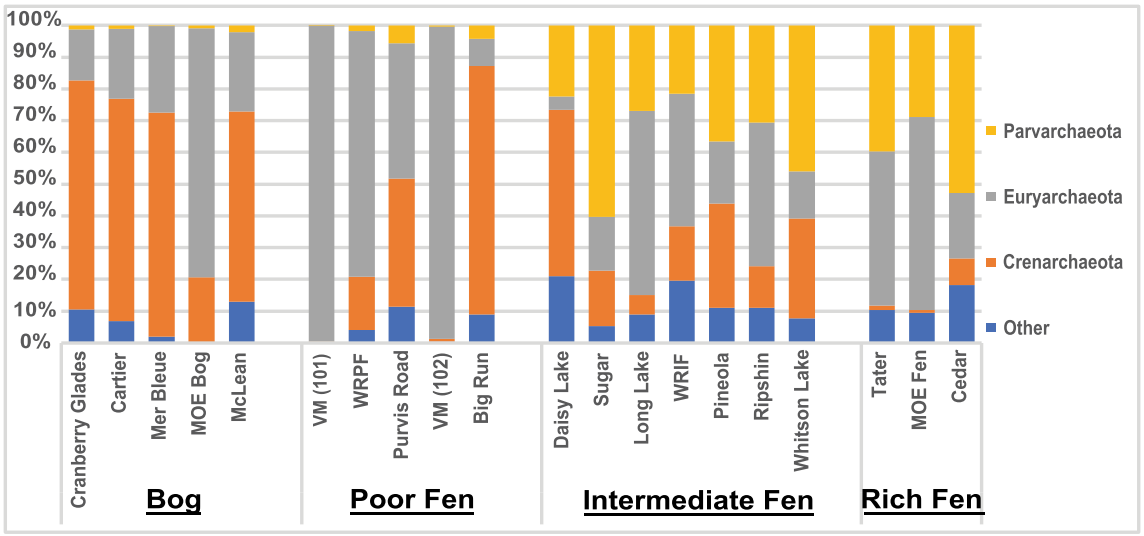

Fig. 3 Phylum classification of Archaea per site (all depths averaged)

interest in terms of C cycling, as they are largely responsible for CH_4 emissions observed in various wetlands [47]. It is important to note that there has been new discoveries in regards of taxonomy of Euryachaeota, showing this phylum to be more diverse than previously thought [48]. Literature data indicate that these methanogens should be more active in higher pH sites, since CH_4 production increased nearly 7-fold in peat with a 2 unit increase in pH [49]. This is perhaps due to increased bacterial activity as methanogens often require bacterial end products for methanogenic substrates [47]. With the exception of Daisy Lake, Crenarchaeota displayed the lowest relative abundance in intermediate and rich fens. A 2006 study found that Crenarchaeota carry out ammonia-based chemolithoautotrophic energy metabolism in marine ecosystems [50], yet their roles in peatland nutrient cycling are still understudied.

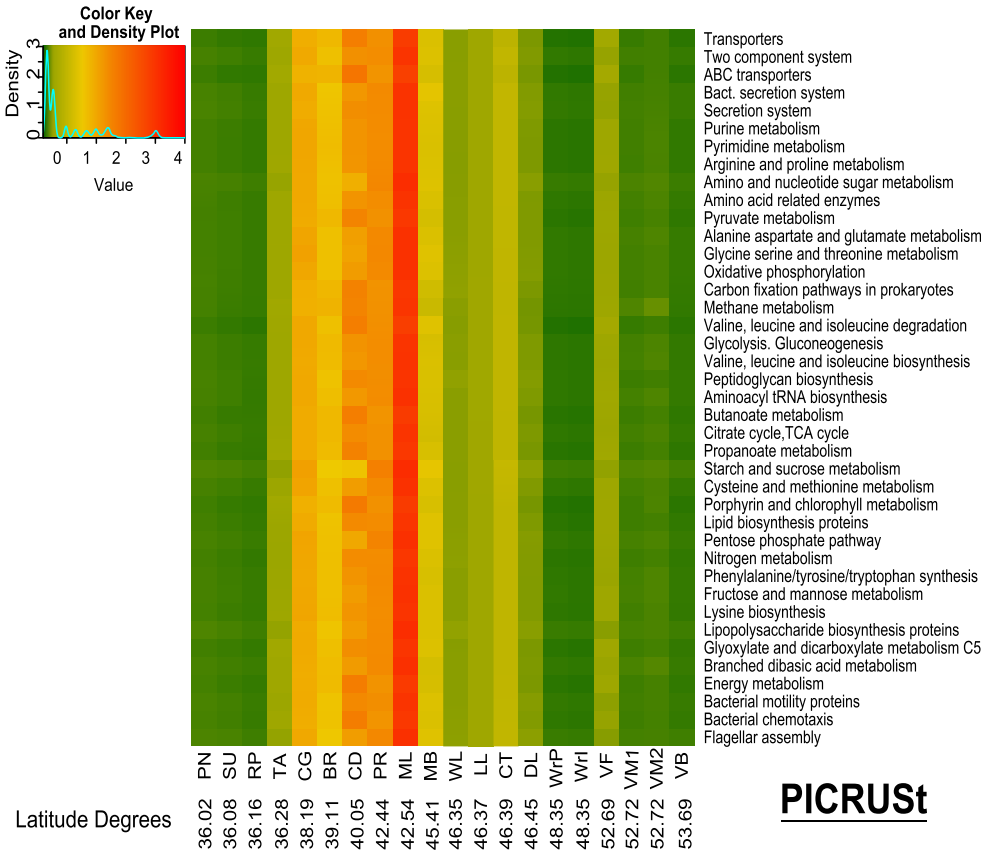

Fig. 4 Heat map of KEGG level three classifications for peatlands of interest (generated via the PICRUSt predictive genomic software. Peatlands along the x-axis are ordered from the most northern latitude to the most southern latitude. Pineola, PN; Sugar, SU; Tater Hill, TA; Ripshin, RA; Cranberry Glades, CG; Big Run, BR; Cedar, CD; Purvis Road, PR; McLean, ML; Mer Bleue, MB; Whitson Lake, WL; Long Lake, LL; Cartier, CT; Daisy Lake, DL; White River Poor Fen, WrP; White River Intermediate Fen, WrI; Victor Fen, VF; Victor Mine 101, VM1; Victor Mine 102, VM2; Victor Bog, VB

Microbial Metabolic Potential

PICRUSt [12] generation of Kyoto Encyclopedia of Genes and Genomes (KEGG) level 3 classification assigned predicted functional content (predicted metagenome content) based on the Illumina sequencing reads of the SSU rRNA gene. Forty KEGG pathways were selected (Fig. 4), where significant differences in predicted abundance were seen between sites including genes involved in environmental information processing, metabolism, genetic information processing, and cellular processing. Peatlands were organized along the x-axis in decreasing latitude, revealing that peatlands between the latitudes of 38.19° and 45.4° were predicted to have the highest number of genes associated with specific KEGG classification pathways including, but not limited to the metabolism of methane, nitrogen, lipid, amino-acids, purine, and pyrimidine. It was noted that a significant number of the genes enhanced in 38–45° N latitude peatlands was related to degradation of microbial breakdown products such as amino acids, lipids, and DNA. It is speculated that these peatlands may be in a state of transition (from bogs to fens to marshes) due to global warming. In a supporting warming experiment, Tveit et al. [51] found that microbes in peat exposed to higher temperatures in vitro shifted their metabolism from the breakdown of plant polymers toward the breakdown of bacterial cell products [33]. Moreover, increased peat temperature leads to an increase in anoxic peat CH_4 emissions, likely due to enhanced metabolic degradation of soil organic C (SOC) [47]. Additionally, microbial heterotrophic activity, measured by CO_2 and CH_4 production, in wetland soils of the everglades, was highest in surface soils [52], where temperature change can more readily impact the soil processes.

The data presented herein (Fig. 4), in addition to findings in the literature, predict that as temperature changes, such as increased averages in global air temperatures, certain microbial communities react and change swiftly, and in consequence can directly influence soil C cycling dynamics and greenhouse gas emissions. This alteration in microbial community structure, as well as a shift in metabolic activity, could induce functional shifts in peatlands, especially concerning those located above 37° N latitude. Supported by community structure analysis and beta-diversity dissimilarity ordination (Figs. 1 and 2), these data show that the older, southern Appalachian Mountain peatlands resemble the fens of the northern latitudes. It is possible that the colder temperatures during glaciation may have supported bogs in the southern Appalachian Mountains. Such as with these older inland southern peatlands, long-term warming may lead to unique community composition and in turn, potentially initiate shifts from C sequestration to more rapid release.

Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflicts of interest.

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