

Biogeography of microbial communities in high-latitude ecosystems: Contrasting drivers for methanogens, methanotrophs and global prokaryotes

Christophe V. W. Seppey^{1,2} | Léa Cabrol^{3,4}  | Frederic Thalasso⁵ |
 Laure Gandois⁶ | Céline Lavergne^{7,8} | Karla Martinez-Cruz^{9,10} |
 Armando Sepulveda-Jauregui¹¹ | Polette Aguilar-Muñoz^{7,8} |
 María Soledad Astorga-España⁹ | Rolando Chamy⁸ |
 Bruna Martins Dellagnezze¹² | Claudia Etchebehere¹² |
 Gilberto J. Fochesatto¹³ | Oscar Gerardo-Nieto⁵ | Andrés Mansilla⁹ |
 Alison Murray¹⁴ | Maxime Sweetlove¹⁵ | Nikita Tananaev^{16,17}  |
 Roman Teisserenc⁶ | Alexander T. Tveit¹ | Anton Van de Putte¹⁵ |
 Mette M. Svenning¹ | Maialen Barret⁶

¹Department of Arctic and Marine Biology, UiT The Arctic University of Norway, Tromsø, Norway

²Institute of Environmental Science and Geography, University of Potsdam, Potsdam-Golm, Germany

³Aix-Marseille University, CNRS, IRD, Mediterranean Institute of Oceanography (MIO) UM 110, Marseille, France

⁴Millennium Institute Biodiversity of Antarctic and Subantarctic Ecosystems (BASE), Santiago, Chile

⁵Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional (Cinvestav-IPN), Departamento de Biotecnología y Bioingeniería, México, Mexico

⁶Laboratoire Écologie Fonctionnelle et Environnement, Université de Toulouse, CNRS, Toulouse, France

⁷HUB AMBIENTAL UPLA, Laboratory of Aquatic Environmental Research, Universidad de Playa Ancha, Valparaíso, Chile

⁸Escuela de Ingeniería Bioquímica, Pontificia Universidad Católica de Valparaíso, Valparaíso, Chile

⁹Departamento de Ciencias y Recursos Naturales, Universidad de Magallanes, Punta Arenas, Chile

¹⁰Environmental Physics Group, Limnological Institute, University of Konstanz, Konstanz, Germany

¹¹GAIA Antarctic Research Centre, Universidad de Magallanes, Punta Arenas, Chile

¹²Microbial Ecology Laboratory, Department of Microbial Biochemistry and Genomic, Biological Research Institute "Clemente Estable", Montevideo, Uruguay

¹³Department of Atmospheric Sciences, University of Alaska Fairbanks, Fairbanks, Alaska, USA

¹⁴Division of Earth and Ecosystem Sciences, Desert Research Institute, Reno, Nevada, USA

¹⁵Royal Belgian Institute for Natural Sciences, OD-Nature, Brussels, Belgium

¹⁶Melnikov Permafrost Institute, Russian Academy of Sciences, Yakutsk, Russia

¹⁷Institute of Natural Sciences, North-Eastern Federal University, Yakutsk, Russia

Correspondence

Léa Cabrol, Aix-Marseille University, Univ
Toulon, CNRS, IRD, M.I.O. UM
110, Mediterranean Institute of
Oceanography, Marseille, France.
Email: lea.cabrol@mio.osupytheas.fr

Abstract

Methane-cycling is becoming more important in high-latitude ecosystems as global warming makes permafrost organic carbon increasingly available. We explored 387 samples from three high-latitude regions (Siberia, Alaska and Patagonia) focusing on mineral/organic soils (wetlands, peatlands,

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2023 The Authors. *Environmental Microbiology* published by Applied Microbiology International and John Wiley & Sons Ltd.

Funding information

ECOS sud CONICYT, Grant/Award Numbers: Project MATCH C16B03, grant no. 256132/H30; ERANet-LAC program, Grant/Award Number: project METHANOBASE (ELAC2014_DCC-0092); French Ministries of Foreign Affairs and International Development (MAEDI); German Federal Ministry of Education and Research, WISNA program; Mexican National Council for Science and Technology (CONACYT), Grant/Award Number: grant no. 277238; National Education, Superior Education and Research (MENESR); Chilean National Agency of Research and Development (ANID), Grant/Award Number: MillenniumScienceInitiativeProgram-ICN2021_002

forest), lake/pond sediment and water. Physicochemical, climatic and geographic variables were integrated with 16S rDNA amplicon sequences to determine the structure of the overall microbial communities and of specific methanogenic and methanotrophic guilds. Physicochemistry (especially pH) explained the largest proportion of variation in guild composition, confirming species sorting (i.e., environmental filtering) as a key mechanism in microbial assembly. Geographic distance impacted more strongly beta diversity for (i) methanogens and methanotrophs than the overall prokaryotes and, (ii) the sediment habitat, suggesting that dispersal limitation contributed to shape the communities of methane-cycling microorganisms. Bioindicator taxa characterising different ecological niches (i.e., specific combinations of geographic, climatic and physicochemical variables) were identified, highlighting the importance of *Methanoregula* as generalist methanogens. *Methylocystis* and *Methylocapsa* were key methanotrophs in low pH niches while *Methylobacter* and *Methylomonadaceae* in neutral environments. This work gives insight into the present and projected distribution of methane-cycling microbes at high latitudes under climate change predictions, which is crucial for constraining their impact on greenhouse gas budgets.

INTRODUCTION

High-latitude ecosystems, and the microbial communities inhabiting them, are important in the context of climate change (Cavicchioli et al., 2019). Polar amplification enhances permafrost thaw (Biskaborn et al., 2019), thus causing drastic habitat changes that can turn mineral and organic soils into wetlands and lakes (Olefeldt et al., 2016). The estimated 1700 Pg of carbon stored in permafrost, which represent more than twice of today's atmospheric carbon stock (Brouillette, 2021), are therefore more accessible to microbial mineralisation under anaerobic conditions and converted to greenhouse gases such as methane (CH₄; Schuur et al., 2015). The role of microbial communities in CH₄ cycling depends on the intrinsic traits of the involved microorganisms, as well as on the ecological characteristics of their dynamic habitats. Despite their importance, sub-Antarctic ecosystems have been less studied than their northern counterparts and deserve more attention since they might be controlled by different drivers.

Half of atmospheric CH₄ arises from natural sources, among which wetlands and lakes contribute to up to 70% of natural biogenic emissions (Saunio et al., 2020). Most of this CH₄ is produced by methanogenic archaea under anoxic conditions in wetlands or lake sediments. Nonetheless, a substantial fraction of this CH₄ can be oxidised by methanotrophic prokaryotes under aerobic conditions before it reaches the atmosphere (Bastviken et al., 2008; Oh et al., 2020; Smith et al., 2018; Thottathil et al., 2018). Methane oxidation is also possible under anoxic conditions in lakes (Cabrol et al., 2020; Thalasso et al., 2020), wetlands (Gupta et al., 2013; Segarra et al., 2015) and peatlands (Miller et al., 2019). Net CH₄ emissions result from an

interplay between CH₄ producing and consuming microorganisms. Deciphering the physicochemical, geographical and climatic factors driving the abundance and composition of methanogens and CH₄ oxidisers is therefore important for understanding their contribution to the CH₄ cycle (Singh et al., 2010).

For almost a century, the main hypothesis explaining the distribution of microbial communities was associated to local physicochemical parameters selecting microbial assemblies through species sorting, also known as environmental filtering (Baas Becking, 1934; Martiny et al., 2006). It was assumed that microbial features such as microscopic size, high reproduction rate or cyst stages allow many of these organisms to disperse over long distances through wind, animals or anthropogenic dispersal (Kleinteich et al., 2017), leading to weaker biogeographic patterns than those observed for plant and animal taxa (Meyer et al., 2018).

Nevertheless, an increasing amount of evidence show that microbes also display biogeographic patterns (Hanson et al., 2012, 2019). These studies show that historical processes, such as the dispersal barriers and geographic distance, drift, past ecological and evolutionary events, might all substantially contribute to the biogeography of microbes (Schwob et al., 2021). The relative contribution of dispersal limitation and species sorting on microbial assembly is highly dependent on the considered spatial scale, on habitat heterogeneity level, and on the selective strength of the environmental conditions (Langenheder & Lindstrom, 2019), as well as on the considered fraction (guild) of the community and its functional, ecological and physiological traits (Lindstrom & Langenheder, 2012). Especially, the dispersal capacity of microorganisms, which explains their wide geographic distribution, can be increased by a large niche width, high phenotypic plasticity and fast

growth rates (Litchman, 2010), as well as the ability to survive unfavourable conditions during the dispersal process (e.g., tolerance to oxygen, pigmentation to survive UV, encystment; Choudoir et al., 2018). Despite major advances the last decade, our understanding of the interaction between microbial life strategy, habitat and dispersal dynamics remains incomplete (Langenheder & Lindstrom, 2019).

Besides their ecological relevance as key players of climate regimes regulation, methanogens and methanotrophs have specific life traits and habitat requirements which make them good models to provide insight into the relationship between habitat specialisation, biogeographic patterns and dispersal. For instance, it can be expected that methanogenic communities would be strongly impacted by dispersal limitation as their sensitivity to oxygen and desiccation impede their aerial dispersion (Ochsenreiter et al., 2003). Methanogens are restricted to low-redox habitats with limiting amounts of thermodynamically favourable electron acceptors other than CO₂, where they are therefore not out-competed (Valentine, 2007). In addition, methanogens are dependent on very specific and restricted substrates, among a limited range of possibilities (CO₂/H₂, formate, methanol and methylated-groups, acetate, some alkanes), usually provided by a complex network of bacterial fermentative partners, which further limits their dispersal success (Conrad, 2007; Zhou et al., 2022). Because of their aerobic nature, methanotrophic bacteria would better tolerate air dispersal but many strains would be restrained to CH₄-rich habitats, and therefore be more constrained by species sorting than the overall bacterial community. There has been repeated (ecosystem-dependent) evidence linking methane-cycling microbial community shifts (due to climate and environmental changes) and CH₄ emissions (Aronson et al., 2013; Winder et al., 2023). However, there are contrasting results about how climate warming is expected to affect the methanogenesis/methanotrophy balance and CH₄ emissions at high latitudes (Oh et al., 2020; Zhu et al., 2020; Jansen et al., 2022; Rößger et al., 2022).

In this work, we explored an extensive dataset composed of 16S rRNA sequences of 387 microbial communities collected from Arctic/sub-Arctic (Alaska, Siberia) and sub-Antarctic (Patagonia) ecosystems, spanning from soils to wetlands and lakes. The sampled habitats, namely mineral and organic soils as well as pond and lake sediment and water, were selected as likely to host methanogenic or methanotrophic organisms. The distribution of these habitats in the landscape, and their transition, is impacted by climate change. This large dataset is accompanied by a comprehensive physicochemical characterisation of the habitats, carried out according to systematic and standardised methodologies for sampling and analysis in all three regions, thus ensuring direct inter-comparability

of the results (Barret et al., 2022). This study aims at investigating and hierarchising how geographic distance as well as physicochemical and climatic parameters explain the diversity of methanogenic, methanotrophic and overall prokaryotic communities in Arctic, sub-Arctic and sub-Antarctic terrestrial ecosystems. Moreover, we aim to identify key microorganisms that are indicators for specific ecological niches in these regions and how climate change might modify their distribution. Beyond their important role in CH₄ cycling and global warming, these functional guilds provide a relevant study case to test if the geographic, physicochemical and climatic effects observed on the overall prokaryotic community apply to more specialised microbial guilds. Finally, we assessed the implications of climate change on high-latitude niches and their microbiome shifts, and the putative associated feedback of ecosystem transitions in terms of methane cycling.

EXPERIMENTAL PROCEDURES

Sampling

A total of 387 samples (Table 1; Table S1) were collected during summer in three regions including Patagonia (12 January to 13 February 2016), Alaska (9 June to 25 June 2016) and Siberia (27 July to 10 August 2016). The sampling zones were geographically distributed from 54.94927° to 52.07250° S and 72.0384° to 67.33174° E for Patagonia and subantarctic Magellanic ecoregion (Rozzi et al., 2008), 63.21332° to 68.62497° N and 150.7974° to 145.9737° E for Alaska, and 67.44435° to 67.53515° N and 86.59196° to 86.70704° W for Siberia (Figure 1). The sampling area covered 7.05*10⁶, 2.15*10⁶ and 1410 hectares for Alaska, Patagonia and Siberia, respectively. Elevation above sea level, annual average air temperature and precipitation sum, as well as measured pH and dry weight for each combination of region and habitat can be found in the Figure S1A–E.

The samples covered four habitat types expected to host methanogens and methanotrophs in high latitudes (Saunois et al., 2020), namely mineral soil, organic soils (as found in peatlands), water and sediment from lakes and ponds (Table 1; Table S1). The mineral and

TABLE 1 Number of samples per habitat type and region.

	Alaska	Patagonia	Siberia	Overall
Mineral	38	14	14	66
Organic	52	76	50	178
Sediment	19	27	15	61
Water	22	25	35	82
Overall	131	142	114	387

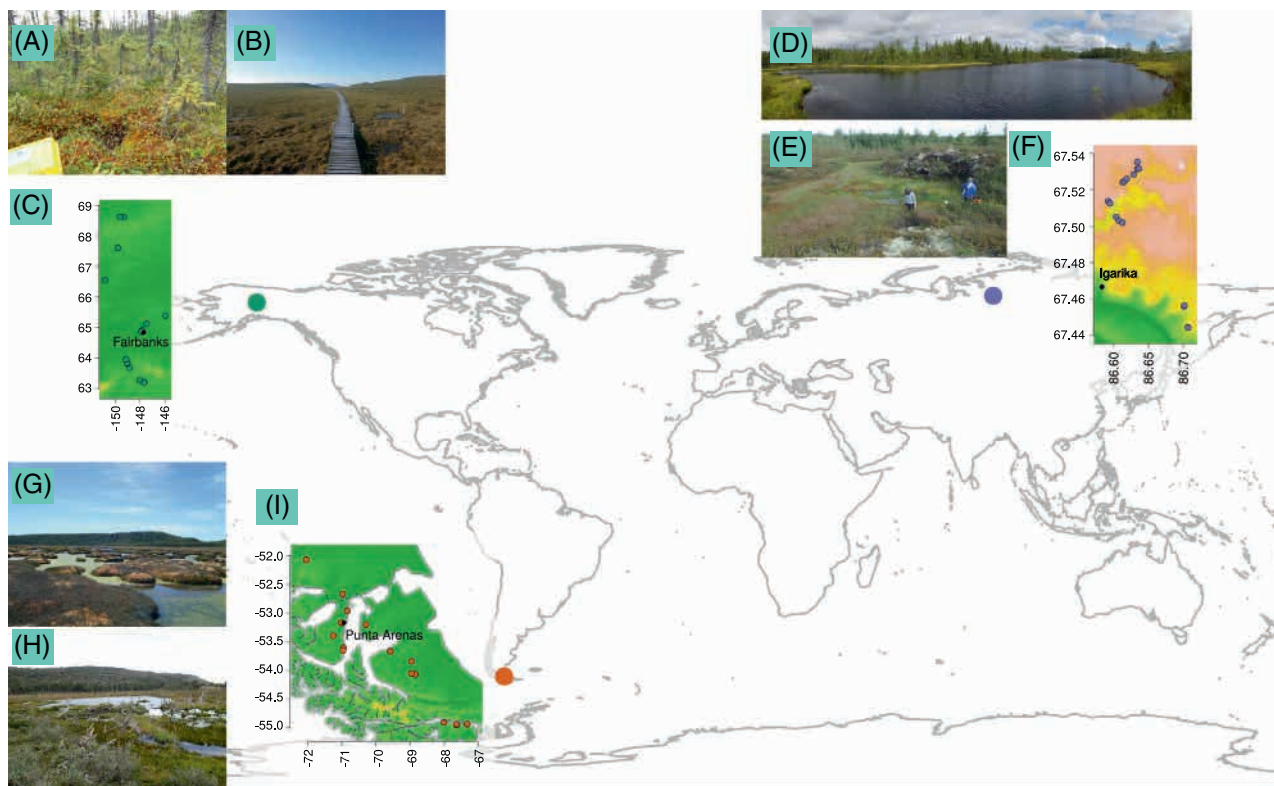


FIGURE 1 Global map showing the location of the sampling regions and pictures of some characteristic studied ecosystems (Alaska: A, B, C; Siberia: D, E, F; Patagonia: G, H, I). The three sub-maps (C, F, I) show the sampling sites locations. The colour scales of the sub-maps (from green to light pink) indicate the altitudinal gradient, relative to each sampling region (Alaska 66–6188 m, Siberia 1–71 m, Patagonia 1–2652 m).

organic soils were taken at depths ranging from the soil surface down to 30 cm deep, with a sterilised shovel or knife, and transported to the laboratory in a sterile plastic bag. The water was sampled from depths going from 10 cm to 14 m in Van Dorn bottle while the superficial sediments (10 cm from sediment surface) were taken with a grab sampler. A detailed description of sampling strategy is available in Barret et al. (2022). All samples were transported and kept at 4°C until further processing. Sampling strategy and protocols, as well as subsequent analytic methodologies, were identical between all field campaigns, to ensure the reliability of intra- and inter-regional comparisons.

Physicochemical variables

The temperature (temp) of the soils, water and sediment samples were measured in situ. In the water column, the conductivity (conduc), the redox potential (redox), the dissolved oxygen (diss_O2), temperature and the pH were measured with a multiparametric probe (HI9828, Hanna Instrument, Woonsocket, US). Dissolved CH₄ concentrations (diss_CH4) and CH₄ emission rates were measured using membrane-integrated cavity output spectrometry (UGGA, LosGatos Research, San Jose, USA) as described in

Gonzalez-Valencia et al. (2014). For soil and sediment samples, pH and conductivity were measured after resuspension in deionised water (1:5, w/w) and 1 h equilibration under agitation. Dry weight (dry_wgh) and organic matter content (OM) were measured in the laboratory after drying overnight at 105°C and ignition at 550°C, respectively. To determine if a soil was mineral or organic, we used a threshold of 40% of OM according to (Schoor et al., 2015). The complete description of analytical methods for the determination of physicochemical variables is available in Barret et al. (2022).

Geographic variables

The spatial structure was represented by the five principal coordinates of a neighbourhood matrix (Borcard & Legendre, 2002) with a truncation distance threshold equal to the maximum geographical distance (PCNM1-5, function *pcnm*, package ‘vegan’ 2.5–2: Oksanen et al., 2018; Figure S2). The principal coordinate analysis was calculated on the basis of geographic distances between sampling sites, determined on an ellipsoid map (function *distGeo*, package ‘geosphere’ 1.5–7: Hijmans, 2017). The principal coordinates (PCNM variables) derived from these eigenvalues were used as explanatory geographic

variables for further analysis. The PCNM analysis allows to detect and quantify spatial patterns over a wide range of scales, from coarse (PCNM1) to precise (PCNM5) geographic patterns. Here, PCNM1 mostly discriminates the north/south hemisphere, PCNM2 differentiates the three regions, PCNM3 correlates with the latitude within a region, PCNM4 varies according to the longitude within a region, and PCNM5 is also associated to the longitude within a region but at a finer scale resolution.

Climatic variables

The climatic dataset was represented by 19 WorldClim variables (Fick & Hijmans, 2017) calculated on the monthly temperature and rainfall values from 1970 to 2000. For each sample, the bioclim values were retrieved from the 30 s resolution rasters according to the geographic coordinates of each sampling site. Spearman correlation coefficients were calculated between each pair of WorldClim variables in order to remove collinear variables ($\rho > |0.7|$; Dormann et al., 2013). The five selected independent climatic variables were the annual mean temperature (bio_1), maximum temperature of the warmest month (bio_5), mean temperature of the wettest quarter (bio_8), annual precipitation (bio_12) and precipitation of the wettest month (bio_13) (Figure S3). The ‘wettest quarter’ corresponds here to the period of 3 months (1/4 of the year) with highest precipitations.

DNA extraction, qPCR, PCR amplification and sequencing

Water samples were pre-filtered with 80 μm mesh size (nylon net filters, Merck Millipore, Cork Ireland) and filtered at 0.22 μm (nitrocellulose GSWP membrane filters, Merck Millipore, Cork Ireland) until filter clogging. The 0.22- μm filter was frozen at -20°C until DNA extraction.

DNA was extracted from the 0.22- μm filters, soil and sediment samples with the PowerWater and PowerSoil DNA isolation kits, respectively (MoBIO Laboratories, Inc Carlsbad, CA, USA). The DNA extracts were stored at -20°C . The V4-V5 region of bacterial and archaeal 16S rRNA gene was then amplified using the universal primers 515F (GTGYCAGCMGCCGCGGTA) and 928R (CCCGYCAATTCMTTTRAGT; Wang and Qian, 2009). The PCR reactions were run with 400 nM of each primer, 50 μM of each dNTP, 0.05 U/ μL of MTP Taq DNA polymerase (Sigma, France) and the volume was adjusted to 50 μL with ultra-pure water. The amplification consisted of a denaturation step at 94°C for 2 min followed by 30 cycles at 94°C for 60 s, 65°C for 40 s and 72°C for 30 s with a final extension at 72°C

for 10 min. Amplicons were sequenced (2×250 pb) using a MiSeq Illumina sequencer at the GenoToul platform (Toulouse, France). DNA sequences are available on the European Nucleotide Archive projects: PRJEB36731 (Siberia), PRJEB36732 (Alaska) and PRJEB36733 (Patagonia).

The abundances of four genes were measured by quantitative PCR (qPCR): bacterial 16S rRNA gene, archaeal 16S rRNA gene, *pmoA* gene (marker gene for aerobic methane oxidising bacteria through the particulate methane monooxygenase) and *mcrA* gene (marker gene for methanogens and ANMEs through the methyl coenzyme M reductase), according to the methodology detailed in Cabrol et al. (2020). Relationships between functional gene abundances and environmental parameters were investigated through Spearman correlation tests.

Sequence analysis

The sequences were analysed using the FROGS pipeline version 3.2.3 (Escudie et al., 2018) on Galaxy platform. The pre-processing consisted in selecting sequences from 350 to 550 nucleotides length, trimming the primers and removing sequences containing ambiguous nucleotides (two nucleotides distant of less than 10 nucleotides with a Phred score below 10). The sequences were then clustered with Swarm v1 (Mahé et al., 2014) in two steps with $d = 1$ and $d = 3$. Swarm is an unsupervised agglomerative, single-linkage method of amplicon sequences clustering into fine-scale OTUs, developed to avoid the effects of fixed clustering threshold and amplicon order input. It uses pairwise distance and abundance structure of the amplicons to build the OTUs, which allows the OTUs to grow iteratively and reach their natural limits, certain taxa covering a larger genetic range than others. The chimaeras were then sorted out using Vsearch de novo method (Rognes et al., 2016). OTUs were filtered by only keeping the ones occurring in at least 2 samples. OTUs were finally assigned to the Silva database (Release 138, Quast et al., 2013) using Blastn+ (Camacho et al., 2009).

Definition of microbial guilds

Community analyses were carried out on three microbial guilds built on the basis of 16S taxonomic affiliation: ‘all prokaryotes’, containing all bacterial and archaeal OTUs; ‘methanogens’, containing OTUs assigned to Methanobacteriales, Methanococcales, Methanopyrales, Methanofastidiosales, unknown Halobacterota (see note further down), Methanocellales, Methanomicrobiales, Methanonatronarchaeia, *Methanosaetaceae*, *Methanicrococcus*, *Methanococcoides*, *Methanohalobium*,

Methanohalophilus, *Methanobolus*, *Methanomethylivorans*, *Methanosalsum*, *Methanosarcina*, *Methermicrococcaeae*, *Methanomethyliales*, *Methanomassiliococcales*, *Thermogymnomonas*; and ‘methanotrophs’, containing OTUs assigned to *Methylobacterium-Methylorubrum*, *Methylocapsa*, *Methylocella*, *Methylocystis*, *Methyloferula*, *Methylosinus*, *Methylovirgula*, *Methyloceanibacter*, *Methylococcaceae*, *Methylohalobius*, *Methylomarinovum*, *Methylothermus*, *Methylomonadaceae*, *Methylacidiphilaceae*, ANME-1, *Archaeoglobus*, ANME-2a-2b, ANME-2c, ANME3, *Methanoperedenaceae*, *Methylomirabilaceae*. The OTUs affiliated to Halobacterota at the phylum level without more precision were aligned against the NCBI database to verify their identity: their affiliations were then corrected to *Methanoregula* or *Methanospirillum* for further analysis. The OTUs affiliated to *Methylovirgula* were checked by aligning their sequences against the NCBI database, and were more similar to the methane oxidiser *Methylovirgula thiovorans* (Gwak et al., 2022) than to the obligate methylophilic *Methylovirgula ligni* (Vorob'ev et al., 2009): we consider them as methanotrophs. To avoid samples with too low sequencing depth, we only kept samples with at least 10,000 reads for the prokaryotic group, resulting in a final set of 387 samples. After subsetting OTUs identified as methanogens and methanotrophs, only samples with a minimum number of 30 reads were kept for further analyses, leading to 125 and 261 samples for methanogenic and methanotrophic guilds, respectively (Table S1). Subsequent analyses were conducted on relative abundance of OTUs in each sample in order to avoid bias of sequencing depth. Bray–Curtis distance was computed on the square root of relative abundances (Hellinger transformation). Fifteen guild-habitat combinations were defined according to the different combinations of guilds (i.e., prokaryotes, methanogens, methanotrophs) and habitats (i.e., all habitats, mineral soil, organic soil, sediment, water) and tested in the subsequent analysis. The percentage of sequences assigned to methanogens or methanotrophs in each region*habitat combination is presented in Table S2.

In our approach, the assignment to a functional guild is inferred from taxonomic affiliations, which is supported by the global congruency between 16S rRNA gene-based and functional (*pmoA*, *mcrA*) genes-based phylogenies (Conrad, 2007; Borrel et al., 2013; Knief, 2015) and low horizontal gene transfer (HGT) events in methanogens (Baptiste et al., 2005). However, some uncultivated or uncharacterised by metagenome-assembled genomes (MAGs) approaches—methanogenic and methanotrophic taxa may be omitted. This would be the case if their 16S rRNA gene sequence is phylogenetically too distant from that of the known taxa compiled in our list, if their taxonomic affiliation is not available at a sufficiently resolutive rank, and/or if the targeted functional trait is not conserved at high taxonomic ranks, as it can be the case for some methane-oxidisers. For

instance, *mcrA*-carriers have been found in as-yet uncultivated MAGs outside of the traditionally recognised methane-metabolising groups which can be interpreted as HGT and depends on the considered methanogenic metabolic pathway (Borrel et al., 2019; Evans et al., 2019). Nevertheless, the present approach offers a better comparability between total prokaryotes and the two methane-related guilds. For example, OTU clustering method is identical and beta diversity is therefore fully comparable between the three groups.

Distance decay relationship

To assess the relationship between community similarity and geographic distance (both expressed as logarithm), a distance decay relationship (DDR) was calculated for each guild. The similarity between two communities was calculated as 1—the Bray–Curtis distance between the Hellinger-transformed relative abundances. Some community distances were equal to 0 and had been changed to the minimum distance non equal to 0 before the log transformation (Wu et al., 2019). For each guild, the relation between the log of the community similarity and the log of the geographic distance was assessed through a linear model tested by ANOVA, considering all habitats together. To test the difference in DDR slope steepness between the different guilds, 25 DDR bootstraps (each containing a subset of 80% of the original samples) were performed and their linear model slope were compared by Nemenyi test using the Tukey distribution (function *kwAllPairsNemenyiTest*, package ‘PMCMRplus’ 1.9.6: Pohlert, 2022). To be representative of the original sampling design, the samples selected for each bootstrap were stratified according to regions and habitats in the same ratio as in the whole dataset.

In addition, to assess the effect of the habitat on the relation between community similarity and geographic distance, a second series of DDR was calculated for each habitat independently, considering all guilds together. The difference of DDR slopes between the habitats was statistically tested as explained above.

Variation partitioning

To measure the proportion of variation in community composition accounted for by each of the three types of explanatory variables, namely nine physicochemical variables (water depth, temp, conduc, redox, diss_O2, diss_CH4, dry_wgh, pH, OM), five geographic variables (PCNM 1 to 5) and five climatic variables (bio_1, 5, 8, 12, 13), a variation partitioning (function *varpart*, package ‘vegan’ 2.5–2: Oksanen et al., 2018) was calculated for each combination of guild (prokaryotes, methanogens, methanotrophs) and habitat (mineral

soils, organic soils, sediments, waters). The three matrices of explanatory variables were first normalised by scaling to an average of 0 and a standard deviation of 1. The variation partitioning was performed as the partial canonical analysis of the Bray–Curtis distance matrix of the communities with respect to each explanatory matrix (physicochemical, geographic, and climatic), using the other matrices as random variables. As certain physicochemical values were missing in some samples, only variables available in at least 75% of the samples for a given guild-habitat combination were considered in the analysis. For the remaining variables, the samples with missing physicochemical values were discarded. For each of the 15-variation partitioning, the explanatory power of a type of variables was statistically tested by permutation test (10,000 permutations, function *anova.cca*, package ‘vegan’ 2.5–2: Oksanen et al., 2018). As the numbers of physicochemical, geographic and climatic variables were different, the adjusted R^2 was used to assess the variation explained by each type of variables. Two combinations of guild and habitat were discarded (methanogens*mineral soils and methanogens*water) because of a number of samples below the degree of freedom +1. In the results we will only consider the unique (i.e., not shared) contribution of each group of variables individually.

Recursive partitioning

To assess the hierarchy of individual variable’s influence on the community structures, three recursive partitioning trees (one for prokaryotes, one for methanogens and one for methanotrophs) were computed on the Bray–Curtis distance matrices with respect to the nine physicochemical, five geographic and five climatic variables altogether (De’Ath, 2002) (function *rpart*, package ‘mvpart’ 1.6–2: Therneau & Atkinson, 2014). Multivariate regression tree (MRT) analysis forms clusters of increasingly homogeneous microbial sub-communities by repeated splitting of the overall community, with each split defined by a simple rule (inferior or superior to a quantitative threshold) based on environmental values (either physicochemical, geographic or climatic value). The successive splits define increasingly specific niches (i.e., cluster of samples characterised by a specific combination of geographic, climatic and physicochemical variables) minimising the Bray–Curtis dissimilarity of sub-communities within each niche. Equivalently, this maximises the distance between different sub-communities. The sub-communities and their associated environmental splitting criteria (thresholds) are represented graphically by a binary tree pruned at a maximum depth of three levels to keep a reasonable number of variables to interpret.

To determine which taxa were the most specific to the niches, bioindicator OTUs (*indval*) were identified

for each niche of the recursive trees (function *indval*, package ‘labdsv’ 1.8–0: Roberts, 2013). Only OTUs with a relative abundance average (among all samples) of at least 0.01% were considered in the *indval* analysis. An OTU was defined as a bioindicator if it had a high indicator value for a given niche (Dufrene & Legendre, 1997), meaning high fidelity (high relative abundance in the samples of the niche) and high specificity (low relative abundance in the samples not belonging to the niche: see Formula S1). An OTU was considered as a niche bioindicator if the probability of obtaining a higher indicator value for the non-niche samples was below 0.001 (tested on 10,000 permutations). As Archaea only represented a small fraction of the prokaryotes, bacterial and archaeal bioindicators were represented in separated trees.

RESULTS AND DISCUSSION

Abundances of methanogens and methanotrophs

The functional qPCR results show that the sediments contained significantly more *mcrA* gene copies than the three other habitats, while the mineral soils harboured more *pmoA* genes than the other habitats (Nemenyi tests $p < 0.001$, Figure S4C,D). Nevertheless, the large number of *mcrA* gene copies can potentially be biased by the fresh weight underestimation because of water loss during sampling. The functional qPCR-based and 16S amplicon-based quantifications (Table S2) were positively correlated for both methanogens (Spearman $\rho = 0.66$, $p < 0.01$) and, to a lesser extent, methanotrophs ($\rho = 0.31$, $p < 0.01$), suggesting that the 16S-based approach provides a reliable representation of both functional guilds (Figure S5A,B).

The abundance of the two marker genes positively correlated with dissolved CH_4 concentration (Spearman correlation, *pmoA*: $\rho = 0.65$, $p < 0.001$; *mcrA*: $\rho = 0.64$, $p < 0.001$, Figure S6). Methanotroph abundances were slightly negatively correlated to atmospheric CH_4 emission rates ($\rho = -0.22$, $p < 0.05$) which is consistent with their role as CH_4 regulators. Methanogen abundances were not significantly correlated to CH_4 emission rates, which can be explained by the fact that emission rates are net values integrating different processes such as CH_4 production and consumption, in sediment and along the water column. Relationships were also found with physicochemical variables: methanotroph abundance positively correlated more strongly (than methanogens) with a high dry weight ($\rho = 0.63$, $p < 0.001$), while methanogen abundance positively correlated more strongly (than methanotrophs) with high suspended organic matter ($\rho = 0.71$, $p < 0.01$, Figure S6).

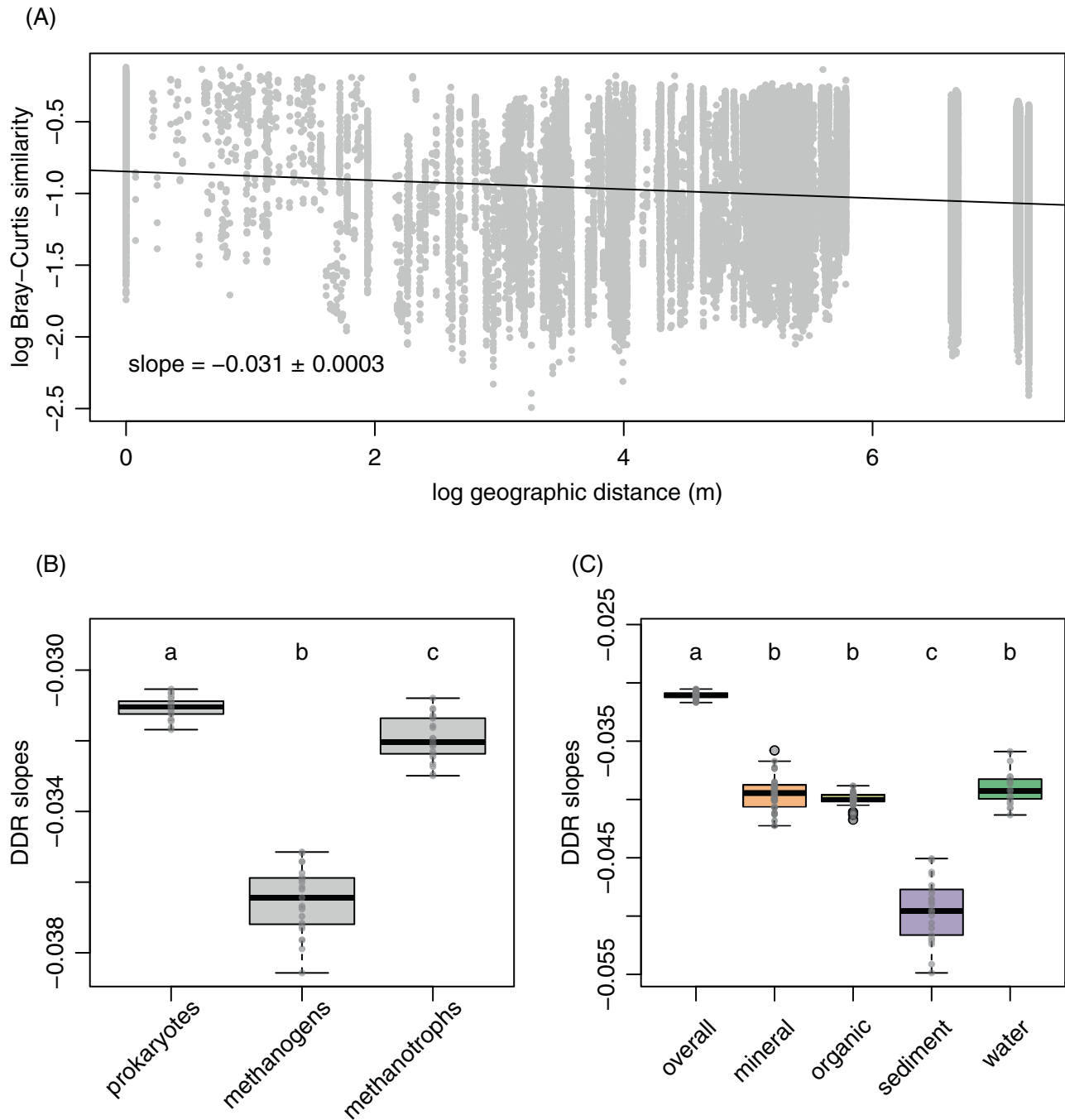


FIGURE 2 (A) Distance decay relationship (DDR) of 387 prokaryotic communities retrieved from four habitats (mineral soils, organic soils, sediments and waters) in Northern Siberia, North-central Alaska and Southern Patagonia. (B) Distribution of DDR slopes for the prokaryotic, methanogenic and methanotrophic communities taken from all habitats, obtained from 25 bootstraps. (C) Distribution of DDR slopes for the prokaryotic community, separated according to the habitat type, obtained from 25 bootstraps. The letters above the boxplots represent significantly different distributions according to a Nemenyi test ($p < 0.001$).

Effect of geographic distance on the similarity between communities

For the three guilds (prokaryotes, methanotrophs, methanogens), the distance decay relationship (DDR) showed that community similarity decreased with geographic distance as reported in other studies

(Figure 2A; Astorga et al., 2012; Martiny et al., 2011), with absolute DDR slope values in the same range as usually reported for prokaryotes (e.g., Liu et al., 2021; Zinger et al., 2014). The relationship appeared to be significantly stronger (Nemenyi test; $p < 0.001$) for methanogens and methanotrophs (DDR slopes of -0.0367 ± 0.0009 and -0.0320 ± 0.0006 , respectively)

than for the whole prokaryotic community (-0.0309 ± 0.0003 ; Figure 2B). This indicates that the impact of dispersal limitation is higher for methanogens and methanotrophs than for the general prokaryotic communities. Moreover, methanotrophic communities were less impacted by geographical distance than methanogens (Nemenyi test: $p < 0.01$), suggesting a higher dispersal capacity. The different impact of spatial distance on community dissimilarity among the three groups is not due to their different richness, diversity, nor sample number, as shown by the statistical analysis presented in Figure S7A–C, but rather to habitat or community properties. Communities in heterogeneous habitats, spatially isolated ecosystems, or with low dispersal rates, have usually higher compositional turnover rate (i.e., steeper DDR slopes) (Lenoir et al., 2012; Zinger et al., 2014). It is recognised that the importance of dispersal limitation in community assembly processes depends on several organism properties including abundance, dispersal capacity, phenotypic plasticity, niche width and growth rate (Astorga et al., 2012; Gao et al., 2020; Langenheder & Lindstrom, 2019; Lindstrom & Langenheder, 2012). Although the capacity of some methanogens to survive oxygen was demonstrated (Lyu & Lu, 2018), most methanogens are obligate anaerobes, which would drastically hinder the efficiency of wind, aquatic or animal dispersal (Yavitt et al., 2012). Both methanogens and methanotrophs are dependent on a reduced variety of substrates, whose availability mostly depends on other microbial partners, thus reducing their adaptation capacity compared to generalists. In addition, the stronger relationship between geography and community distance could be explained by the slow growth rate of methanogens making them less competitive after dispersal in a new area, and therefore less likely to colonise new ecosystems (Litchman, 2010). Methanotrophs are expected to better disperse than methanogens since most of them are well adapted to oxic conditions (except ANME), and some can live on low CH_4 concentrations as found in the atmosphere (Conrad, 2009; Tveit et al., 2019), or on other substrates (Dedysh & Dunfield, 2011).

Habitat type also impacted the relationship between community similarity and geographic distance (Figure 2C). Our results show that homogeneous subsets of habitats (with similar environmental properties), were more impacted by geographic differentiation (i.e., steeper DDR slope) than the overall set of samples mixing habitats with different characteristics. The DDR slope was the steepest in sediments which strongly suggests that sediment microbes are less prone to dispersion than microbes from habitats in contact with air, such as surface water and superficial soil. The strong geographic effect on sediment communities could be related to a higher proportion of strict anaerobes that would difficultly survive long distance

dispersion like wind or migratory animals (Shi, Xiang, et al., 2015a) or to the sediment being physically isolated from air. Difference of dispersal limitation magnitude as a function of the habitat was also observed in alpine meadows and marsh meadows of the Qinghai-Tibetan Plateau (Zhang et al., 2019).

Contribution of environmental, spatial and climatic constraints/determinants to microbial variability

The sum of physicochemical, climatic and geographic variables explained 25%, 38% and 30% of the total variation for prokaryotic, methanogenic and methanotrophic communities, respectively (Figure 3, exclusive contributions only; all 'shared' contributions (interactions) can be found in Figure S8). For all three guilds, regardless of habitat, physicochemical variables alone (exclusive contribution) had the strongest contribution to the variation, explaining 15% of the variance for prokaryotes, 8% for methanogens and 15% for methanotrophs (Figure 3; Figure S7). A stronger impact of physicochemical variables than geographical distance or climate on microbial community assembly was observed in several other studies (e.g., Chu et al., 2010; Lindstrom & Langenheder, 2012; Liu et al., 2019; Looby & Martin, 2020), while others reported a stronger effect of geography (e.g., Shi, Grogan et al., 2015b; Wang et al., 2016; Wu et al., 2018; Yang et al., 2016). Here, the amplitude of the physicochemistry contribution on community structure variation differed according to the guild-habitat combinations, ranging from 6% (methanotrophs in mineral soils) to 26% of the explained variance (methanotrophs in sediments). Our results demonstrate that, despite its global importance, the relative magnitude of environmental filtering (through physicochemical characteristics) on microbial communities depends on the targeted guild and the considered habitat. This agrees with the unification of community assembly processes in one conceptual model as proposed by Langenheder and Lindstrom (2019).

Climate variables explained 13% and 22% of the variance accounted for by a single group of variables in prokaryotic and methanotrophic mineral soil communities, respectively. This could be related to a higher dry weight ($64\% \text{ w/w} \pm 20\% \text{ SD}$) than in other habitats (organic soils: $14\% \pm 12\% \text{ SD}$, sediments: $17\% \pm 18\% \text{ SD}$, water: $1 \cdot 10^{-4} \pm 3 \cdot 10^{-4}$, Nemenyi test: $p < 0.001$). Due to the buffering capacity of water, lower moisture content could make mineral soil communities more susceptible to changing conditions, but this hypothesis contrasts with earlier observations (Conant et al., 2011). Methanogenic communities in organic soils were also impacted mainly by climate (20% of the explained variance, permutation test: $p < 0.001$). The organic

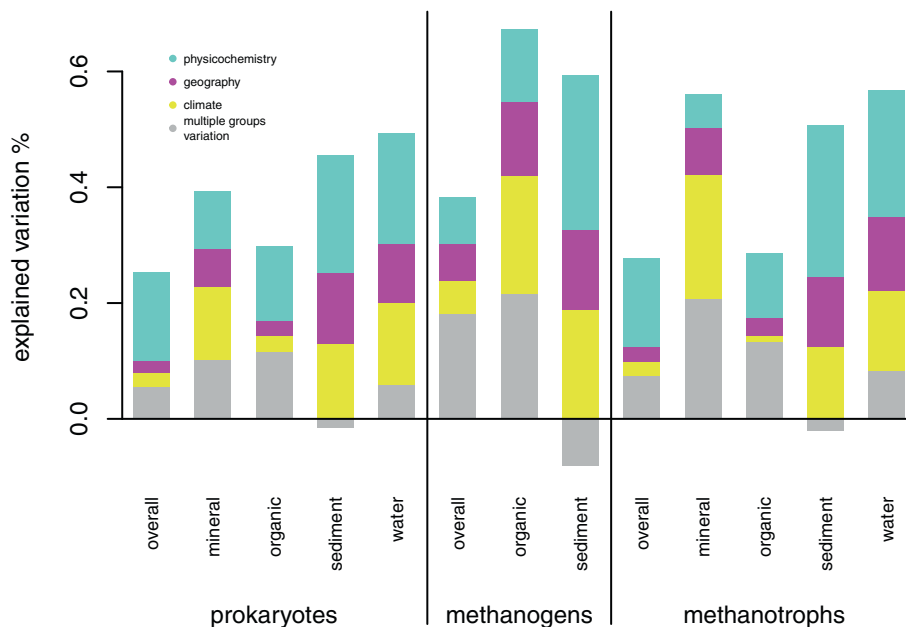


FIGURE 3 Variation partitioning analysis showing the variation explained exclusively by physicochemistry, geography and climatic variables for prokaryotic, methanogenic and methanotrophic communities retrieved in four habitat types (mineral soils, organic soils, sediments and waters) from Northern Siberia, North-central Alaska and Southern Patagonia. Two habitats were not considered for the methanogenic community due to insufficient number of samples. The variation explained by more than one group of variables is shown in grey. All the variation partitioning had been tested according to a Monte Carlo permutations test and revealed significant impacts of the three groups of explicative variables on the microbial communities ($p < 0.001$). Exceptions to that were the impact of physicochemistry on methanotrophs in mineral soils ($p < 0.05$), the impact of geography on methanotrophs in mineral soil ($p < 0.1$) and the impact of climate on methanotrophs in organic soils ($p \geq 0.1$). More details are shown in the Figure S8, including the shared contributions of several groups of variables, the p -values and number of samples for each scenario, and the individual variables included in each explicative group.

soils studied here are mostly from *Sphagnum*-peatlands and palsa, and many studies had shown that methanogenic communities found in such habitats are impacted by climatic variables such as in situ temperature (Fu et al., 2015) and moisture regime (Tian et al., 2015). Climate can also have an impact on peatland vegetation cover (e.g., *Sphagnum* domination vs. terrestrial vegetation, Jassej et al., 2018), which in turns modifies the soil organic matter composition, thus resulting in a direct impact on associated microbial communities (Cervantes et al., 2000; Ye et al., 2012).

In most guild-habitat combinations, geography was the weakest contributor to explained variation. In sediment, however, geography alone explained 12% of the variation for prokaryotes, 14% for methanogens and 12% for methanotrophs. The high geographic structure and differentiation of sediment communities could be explained by (i) a lack of contact with the atmosphere, preventing aerial dispersal and (ii) a selective pressure favouring anaerobic organisms which might not survive air dispersal. The magnitude of the geographic effect also depended on the guild. Spatial variables explained two to three times more variation for methanogens (6%) than for the two other guilds (prokaryotes: 2%, methanotrophs: 3%), which is in line with the outcomes from DDR analyses where the methanogens were more affected by geographic distance than the

methanotrophs. This stronger impact of geography on methanogenic communities is particularly clear in organic soils where the influence of the PCNM variables reached the same explanatory level as the physicochemical variable (13% of variation explained by each group of variables).

Identification of individual drivers of community structure in high latitude terrestrial ecosystems

We applied MRT independently to each of the three microbial guilds. The aim of the MRT analysis was to iteratively divide a group of communities into two subgroups, maximising their dissimilarity according to the threshold value of one explanatory variable. For all guilds, the first most discriminating variable was pH, with a threshold value around 5.0 (Figure 4A–C), in line with the strong impact of physicochemical variables shown in the variation partitioning. pH is known to impact prokaryotic community structures in a wide range of habitats including high latitude regions (Chu et al., 2010; Crevecoeur et al., 2019; Fierer et al., 2006) and peatlands (Wen et al., 2017; Yang et al., 2017). A discriminating threshold for bacterial communities around pH 5.0 has previously been demonstrated for a

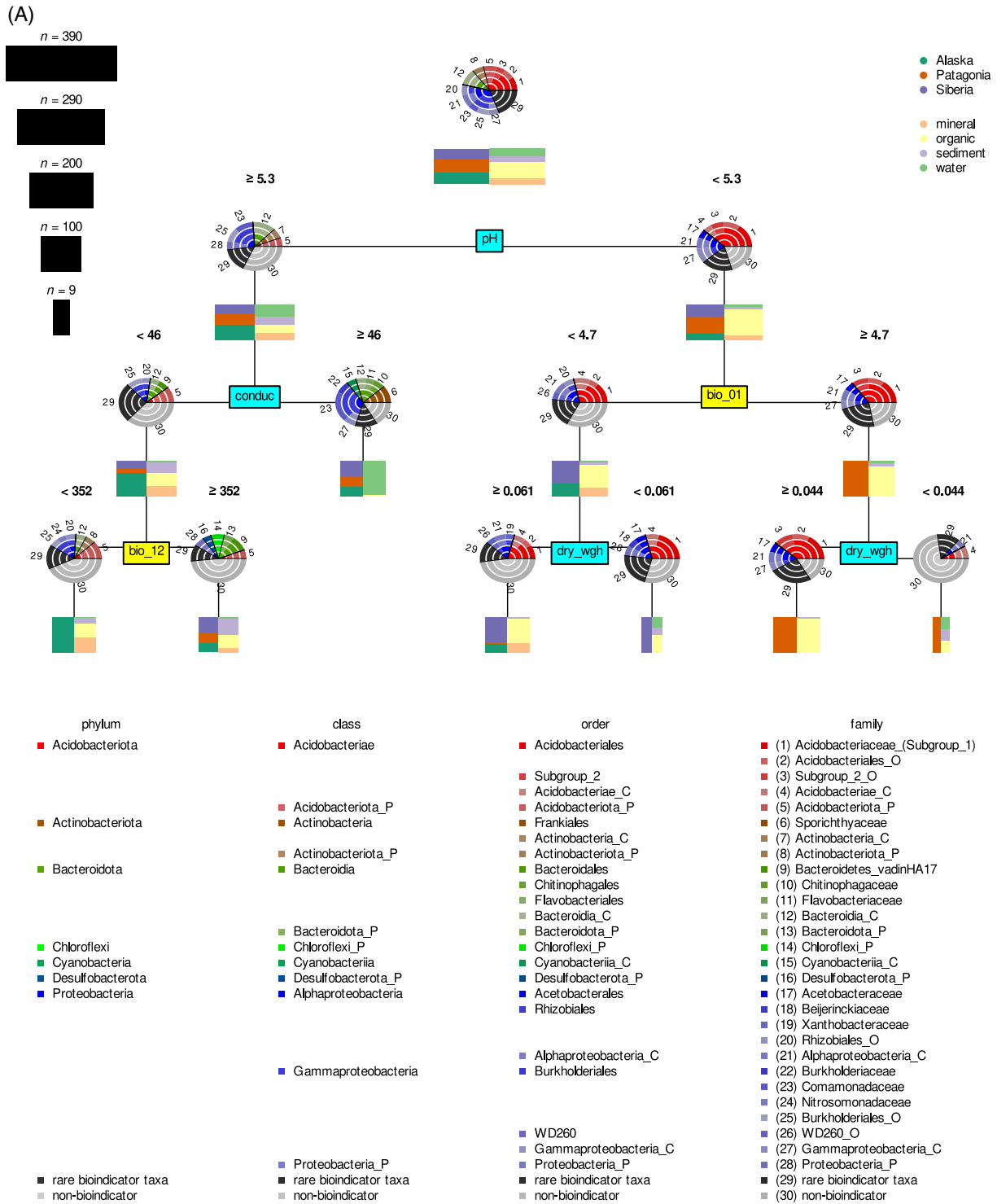


FIGURE 4 Multivariate recursive partitioning tree (MRT) from 387 prokaryotic communities (A, only Bacteria shown here), 125 methanogenic communities (B) and 261 methanotrophic communities (C) from all habitats (mineral soils, organic soils, sediments and water) and all regions (Northern Siberia, North-central Alaska, Southern Patagonia). The communities were discriminated according to a quantitative threshold (indicated in bold) of physicochemical (cyan), geographic (magenta) and climatic (yellow) variables. Each node represents an ecological niche, that is, a combination of physicochemical, geographic and climatic variables. At each node, the width of the barplot represents the number of samples (n) composing the node, while the colours of the barplot correspond to the frequency of the different regions and habitat types represented in the samples composing the node. The community composition of each niche is shown by a pie chart. In the pie charts, the abundance of each taxa is represented as relative abundance among all the members of the guild, namely prokaryotes (A), methanogens (B) or methanotrophs (C), in the given niche. The bioindicator OTUs (specific of the niche) are coloured according to their taxonomic affiliation, while the grey fraction represents the non-bioindicator OTUs. The pie charts are organised in increasing taxonomic resolution going from higher (centre) to lower (periphery) taxonomic level. Only taxa cumulating at least 5% of the node community were represented. If a taxon did not reach this threshold, it was pooled in its higher taxonomic level. If, at the highest taxonomic level, the threshold was still not reached, the taxon was pooled in the ‘rare bioindicator taxa’ category.

(B)

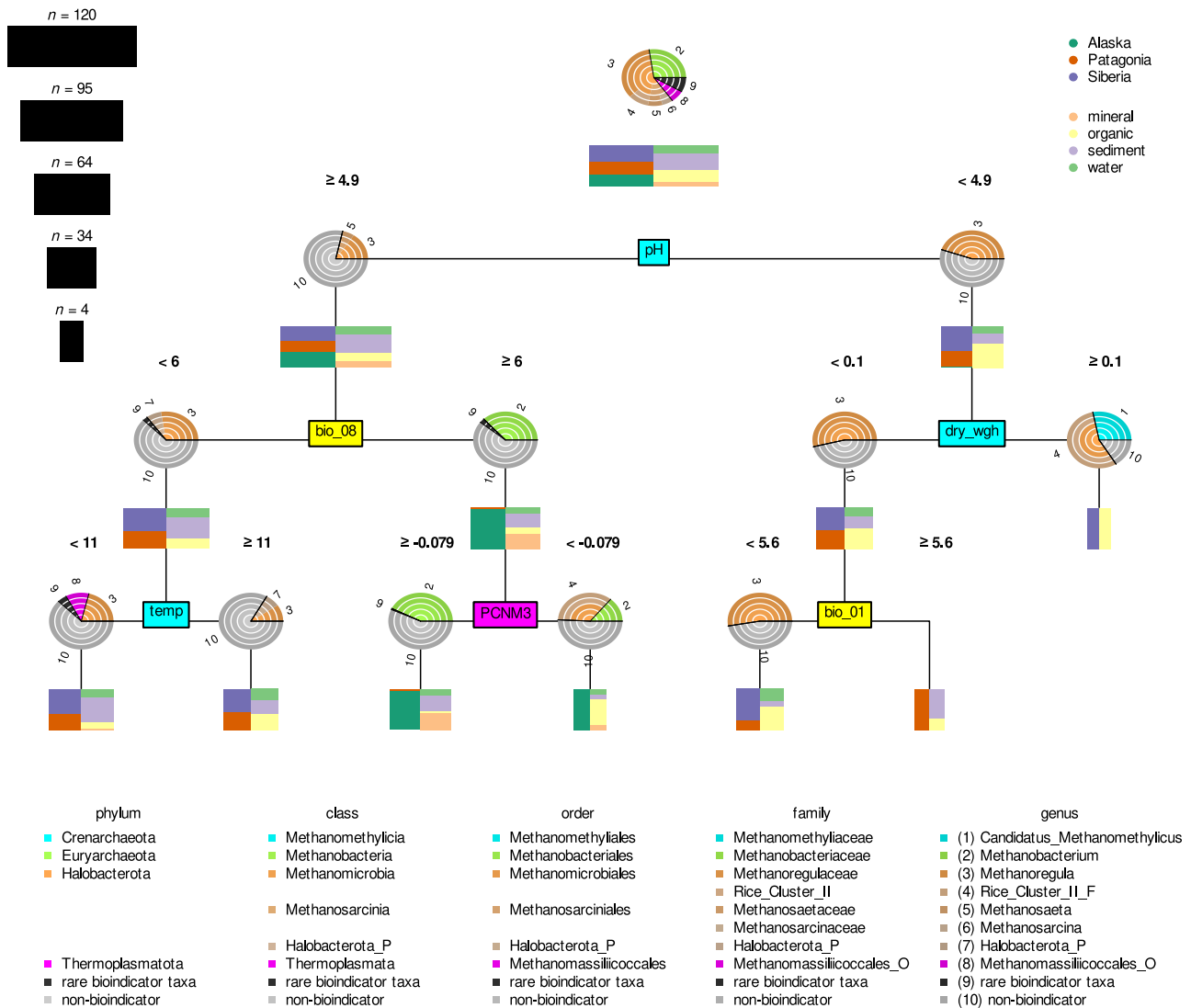


FIGURE 4 (Continued)

wide range of soil types (Malard et al., 2019; Rousk et al., 2010). However, pH is not always identified as the most influential environmental parameter on microbial variability, even in similar ecosystems investigated through similar approaches (e.g., Nazaries et al., 2018; Xiang et al., 2017; Zu et al., 2016). Here, by including many habitats, three different microbial guilds and by integrating environmental, geographic and climatic drivers, we have demonstrated that pH is not only a major driver but the strongest one, at least for high latitude regions. It should be noted that pH can be regarded as a cumulative and integrative parameter that can potentially mask and/or reflect unmeasured environmental drivers and their interactions, such as vegetation, hydrography or chemical concentrations.

Low pH samples comprised mainly organic-rich samples from peatlands in our study. For methanogenic

and methanotrophic guilds, these low-pH samples were further split according to their dry weight (Figure 4B,C). Taken as a whole, dry weight was the second-most important factor discriminating the communities, around a threshold of 7% dry_wgh. The composition of wetland soil microbial communities is known to be sensitive to changes in moisture (Zhang et al., 2019). This is especially true for methanotrophs and the soil CH₄ oxidation rate which are affected by the changes in soil gas diffusion resulting from altered moisture content (Tate, 2015).

Within prokaryote and methanotrophic guilds characterised by pH >5, the communities were further discriminated by conductivity, with a threshold around 50 mS/cm, which mostly discriminated water samples from solid samples (Figure 4A,C).

(C)

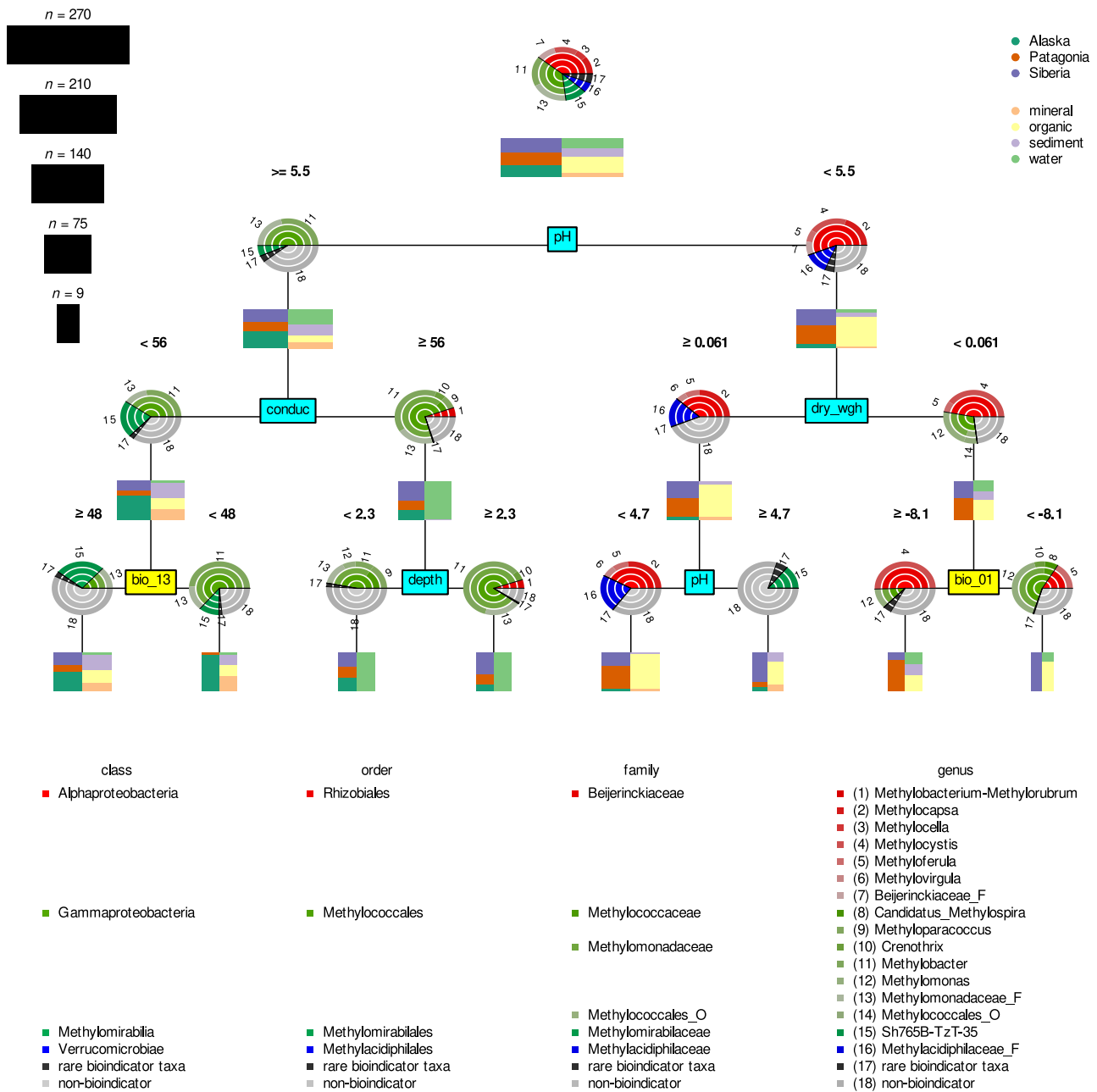


FIGURE 4 (Continued)

In situ temperature only occurred as a determinant at a lower level (third rank) in the methanogenic guild. It mainly separated lake sediments ($<11^{\circ}\text{C}$) from wetland soils ($>11^{\circ}\text{C}$), in a sub-community previously defined by bioclimatic and pH criteria (Figure 4B). A similar threshold around 10°C has been proved to increase and change the pathways of CH_4 production in arctic peat (Tveit et al., 2015) and subantarctic lake sediments (Lavergne et al., 2021). Therefore, our results suggest that community shifts could be associated to increased CH_4 production rates at higher temperatures.

Nevertheless, the in situ temperature (at the time of sampling) is fluctuating within short time periods and does not fully reflect the local climate variability and exposure. This could explain why, here, the bioclimatic variables better explained the microbial assemblies than the in situ temperature within all guild communities, especially considering DNA-based analyses, which show microorganisms present on a wider timescale than just the sampling moment.

Climatic variables were determinant drivers for some sub-communities in the three guilds. In the lower pH

niches, annual mean temperature (bio_01) was an important discriminant factor for the three guilds, albeit at different levels in the trees (second rank for prokaryotes, third rank for methanogens and methanotrophs). The annual mean temperature might indirectly impact the communities through interaction with other environmental variables like the vegetation cover or water table depth, similar to what had been shown for CH₄ emissions (Abdalla et al., 2016). The mean temperature of the wettest quarter of the year (bio_08) was a determinant driver for sub-communities of methanogens, in higher pH samples (Figure 4B), with a threshold value of 6°C. This climatic variable directly impacts the moisture content of the ecosystems. Total annual precipitation (bio_12) and precipitation of the wettest month (bio_13) were determinant drivers for sub-communities of prokaryotes and methanotrophs, in higher pH solid samples (Figure 4A,C). Overall, it seems that climate impacted the three guilds, but in different ways according to pH. The communities retrieved from low pH samples, mostly composed of peat soils, were more constrained by temperature, while the higher pH communities, mostly composed of lake waters and sediments, were more constrained by the precipitation regime combined or not with temperature (e.g., annual precipitation and temperature of the wettest quarter of the year).

Geographic variables were the least involved in discriminating guilds through recursive partitioning analysis, in accordance with the variation partitioning results. PCNM3 was the only geographic variable (representative of the latitude within a region) identified as a determinant driver (third rank of the MRT) for methanogenic sub-communities previously constrained by bioclimatic and pH criteria. In that case, PCNM3 separated southern and northern Alaskan samples. Beside the direct influence of individual PCNM variables revealed by recursive partitioning, clear geographic patterns did appear when considering subgroups of samples more homogeneous according to physicochemical and/or climatic criteria (i.e., ecological niches at lower ranks in the trees). Geographic clustering sometimes resulted from partitioning according to climatic variables. For example, for prokaryotes, average temperature threshold (bio_01) was related to the discrimination between Patagonian communities and the two other regions. For methanogens, temperature of the wettest season (bio_08) discriminated Alaskan samples from the other regions. Geographic and climatic effects on microbial communities are tightly linked and disentangling these effects is certainly one of the most challenging issues in biogeography.

Identification of methane-cycling bioindicators for ecological niches

This section highlights the bioindicators related to CH₄ cycling found in the different high-latitude niches

(a niche being defined based on the MRT analysis as a specific combination of geographic, climatic and physicochemical variables). In the next sub-sections, the percentages given represent the average relative abundance of a taxon in the niche community. When referring to the MRT analysis carried out on prokaryotic, methanogenic or methanotrophic community, the relative abundance refers to the respective community. For a summary of the taxa discussed in the section 3.5 of the main manuscript, see Table S3, and for more details about the organisms identified in the different high-latitude niches see supplementary material *Supplement to: Identification of bioindicators for ecological niches*.

On average, the OTUs identified as bioindicators represented over half the community in their specific niche (61 ± 23% on average, see Tables S4–S7 for niche per niche details for all guilds), suggesting that each niche is characterised by a high proportion of taxa specific to this niche. This high proportion of bioindicators per niche ensures that, for a given niche, our conclusions regarding the niche ecology and functioning, drawn from the knowledge of the niche bioindicators, are representative of the entire niche. Moreover, this high proportion indicates that MRT analysis is relevant for this dataset, enabling to identify highly contrasted ecological niches (together with their specific bioindicators) in high latitude communities.

Methanogenic bioindicators

The main methanogenic taxa were the hydrogenotrophic Methanomicrobiales representing 48% of the overall methanogenic communities. Methanoregulae are found in a large range of pH (Juottonen, 2020). Among them, *Methanoregula* dominated as bioindicator of acidic niches (only represented by the unique OTU C_666, 45%; pH <4.9), which is in line with the previously reported prevalence of *Methanoregula* in other acidic ecosystems (Wen et al., 2017). The OTU C_666 shared 98.6% of homology with *Methanoregula boonei* 6A8 which has genes for adapting to low pH (Bräuer et al., 2015). The OTU C_666 is identical to a sequence found from polar to temperate habitats (Horn et al., 2003; Schmidt et al., 2016; Sizova et al., 2003), suggesting that this taxon can tolerate a wide range of temperature, explaining its presence in our dataset. In contrast, the non-acidic niches were characterised by different OTUs assigned to *Methanoregula* (OTUs C_344, C_1825 and C_2028 [16%: pH ≥ 4.9]) suggesting a pH-based specialisation within this genus (Figure 4B).

The methylotrophic methanogens Methanomassiliicoccales were important bioindicators of only one niche, namely the niche with a pH ≥4.9, average temperature of the wettest season (bio_08) <6°C and in

situ temperature $<11^{\circ}\text{C}$ (12%; Figure 4B). This result expands the known environmental distribution range of free-living (i.e., non-host-associated) Methanomassiliicoccales, which is usually considered as limited (Cozannet et al., 2021), although this order has been reported as dominant in high elevation permafrost-affected wetlands (Yang et al., 2017) and temperate peatlands (Zalman et al., 2018). The methylotrophic *Candidatus Methanomethylicus* was also specific of a very restricted (only four samples from Siberia) acidic niche with high solids content (28%; pH <4.9 and dry_wgh $>10\%$).

Several methanogenic taxa were found evenly and ubiquitously in all niches, explaining why they were not identified as specific bioindicators despite their high relative abundance. For instance, *Methanosarcina* represented 5% of the overall methanogenic community but were not identified as bioindicators of any ecological niche in our study. This ubiquity in high-latitude niches could be explained by *Methanosarcina*'s metabolic versatility, being able to produce CH_4 through different pathways (Kurth et al., 2020). Some acetoclastic *Methanosaeta* OTUs were bioindicators of non-acidic samples only, at low relative abundance (6%; pH ≥ 4.9). *Methanosaeta* (from the same OTUs as our in-situ bioindicators) and *Methanosarcina* dominated acetate-amended incubations carried out with some of the samples included in the present study (samples belonging to the non-acidic niches where *Methanosaeta* was bioindicator; Dellagnezze et al., 2023; Lavergne et al., 2021), thereby showing congruency between the current analysis and experimental approaches.

Methanobacterium was the most abundant methanogenic genus, making up 27% of the overall methanogenic community). Yet, only a few OTUs from *Methanobacterium* were found to be bioindicators, meaning that this genus has adapted to many high latitude niches indiscriminately, which is in line with its reported prevalence in cold ecosystems (Wen et al., 2017). *Methanobacterium* was bioindicator of non-acidic niches with a high temperature in the wettest season (37%; pH >4.9 and bio_08 >6), with distinct OTUs according to the geography (OTU C_2343 for PCNM3 <-0.08 , and OTUs C_103 and C_4657 for PCNM3 ≥ -0.08). Juottonen (2020) retrieved a *Methanobacterium* sequence similar to C_2343 in an acidic boreal mire. Members of *Methanobacterium* are known to be hydrogenotrophs, with some strains using formate, alcohols and CO (Boone, 2015). One of the *Methanobacterium* bioindicators (OTU C_103) was enriched in H_2/CO_2 -amended and some endogenic (unamended) incubations of samples from Patagonian lake sediments included in the present study (Lavergne et al., 2021). *Methanobacteriaceae* were also dominant in incubations of West Siberian bog samples (Kotsyurbenko et al., 2007).

Methanotrophic bioindicators

The methanotrophic bioindicators of acidic niches (pH <5.5) showed a large palette of metabolic pathways for C incorporation (Figure 4C). The water-saturated acidic niches were mostly represented by *Methylocystis* and *Methylomonas* (40% and 23% respectively; pH <5.5 and dry_wgh <0.061), both taxa being previously reported in acidic wetlands (Danilova et al., 2013; Esson et al., 2016; Putkinen et al., 2014; Zhang et al., 2019). These two genera, from Alpha and Gammaproteobacteria respectively, mainly differ in the way they assimilate carbon through the ribulose monophosphate and the serine pathway respectively (Knief, 2015). Moreover, *Methylocystis* is equipped with two isozymes of pMMO with different CH_4 oxidation kinetics (Baani & Liesack, 2008), and some isolates have the capacity to use acetate as a survival strategy in absence of methane (Belova et al., 2011). *Methylocystis* has diverse transport systems ensuring pH homeostasis for acidity adaptation (Nguyen et al., 2018). Acidophilic methanotrophs are less common among the Gammaproteobacteria than Alphaproteobacteria, but some Gammaproteobacteria methane oxidising bacteria are acid-tolerant, such as *Methylomonas paludis* NR_108887 who is the closest relative of our prominent bioindicator OTU C_2309 in acidic Siberia peatland samples (Danilova et al., 2013). The predominance of *Methylomonas* in the coldest niche (bio_01 $<-8.1^{\circ}\text{C}$) is consistent with the report of psychrotolerant/psychrophilic representatives such as *M. scandinavica* (Kalyuzhnaya et al., 1999).

The dryer acidic niches (pH <5.5 and dry_wgh $>6.1\%$), and particularly the very acidic niche (pH <4.7), were mostly represented by *Methylocapsa* and *Methylacidiphilaceae* (27% and 18% respectively; dry_wgh $>6.1\%$ and pH <4.7). *Methylocapsa* were dominated by the OTU C_362, closely related to *M. palarum* (NR 137418.1, Dedysh et al., 2015), an obligate methanotroph isolated from subarctic discontinuous permafrost (Miroshnikov et al., 2017). The presence of *Methylacidiphilaceae* in very acid samples (pH <4.7) is also in line with the extremely acidophilic nature of their unique representant, *Methylacidiphilum*, with optimal growth below pH 3.5 (Op den Camp et al., 2009). It is also noteworthy that this family is adapted to CH_4 and O_2 limitation (Carere et al., 2017; Smith and Wrighton, 2019) and shows a large temperature tolerance, being found from thermophilic environments (Dunfield et al., 2007; van Teeseling et al., 2014) to high latitudes (Bashenkhaeva et al., 2020; Dedysh et al., 2021; Zakharova et al., 2021).

Methyloferula (OTU C_1921) and *Methylovirgula* were also bioindicators of acidic niches, but at lower relative abundances. OTU C_1921 is affiliated to *Methyloferula stellata*, an acidophilic methanotroph isolated from *Sphagnum* peat bogs in Russia (Vorobev et al., 2011), while *Methylovirgula* OTUs were affiliated

to *M. thiovorans*, able to oxidise both methane and reduced sulphur compounds for growth (Gwak et al., 2022).

In contrast, *Methylobacter* dominated most of the non-acidic niche bioindicators (pH >5.5, 28%–59%, including the predominant and widespread *Methylobacter* OTU C_112). This indicates the homogeneity of methanotrophic communities in high latitude non-acidic niches. *Methylobacter* was previously identified as a keystone connector in marshes and alpine meadows, probably stabilising the community (Guggenheim et al., 2020; Zhang et al., 2019) and as a potential major contributor to aerobic and anaerobic CH₄ oxidation in boreal freshwater ecosystems (Cabrol et al., 2020; Rissanen et al., 2018; Graef et al., 2011), as confirmed by functional approaches (He et al., 2022). Our results thus confirm that *Methylobacter* likely encompasses important, cosmopolitan methanotrophs, present and active across many freshwater, soil and wetland ecosystems worldwide (Lv et al., 2014; Smith et al., 2018). Some exceptions to *Methylobacter* dominance in non-acidic samples were found in shallow waters (depth <2.3 m, with *Methyloparacoccus* and *Methylomonas* as bioindicators) and solid samples from the wettest ecosystems (bio_13 > 48, with anaerobic CH₄-oxidiser *Methylomirabilaceae* as bioindicators).

Prokaryotic bioindicators

Several prokaryotic bioindicators identified in the Bacteria MRT can act as partners of CH₄-cycling organisms and have been previously reported in association with methanogens and/or methanotrophs. For example, *Acidobacteriaceae*, representing a significant part of the bioindicators in all acidic niches here, had been previously reported in soil methanotrophic enrichments (Dedysh et al., 2012; Nguyen et al., 2018). Among them, the most abundant *Granulicella* and *Occallatibacter* were also previously identified as part of the active methanotrophic interactome in ombrotrophic peatlands (Kaupper et al., 2020). In our study, Bacteroidetes group vadinHA17 was mostly an indicator of non-acidic (pH ≥ 5.3) solid (conduc <46 mS/cm) samples receiving more than 352 mm of precipitation per year (Figure 4A). The abundance of Bacteroidetes group vadinHA17 had been previously shown to correlate with methanogen abundance in a sulfidogenic bioreactor (Baldwin et al., 2015). OTUs assigned to Chloroflexi (from which over 58% belonged to Dehalococcoidia) and Methanomicrobiales co-existed in the same niche (conduc <46 mS/cm and bio_12 ≥ 352 mm/year), both representing over 5% of the sub-community (Figure 4A; Figure S9). This association is in line with Chloroflexi correlating with Methanomicrobiales and Methanosarcinales in Sakinaw lake (Gies et al., 2014) and Dehalococcoidia being found in CH₄ rich sediments (Biderre-Petit et al., 2016). Knowing that Chloroflexi can provide ethanol and hydrogen to methanogens (Wrighton et al., 2014), it

is probable that a syntrophy exists between these two taxa in high latitude niches. Desulfobacterota was also predominant in solid and wet climate samples (5%: pH ≥ 5.3; conduc <46; bio_12 > 352), represented by some Syntrophobacterales, a taxon which is known to live in syntrophic relationship with methanogens (Stams & Plugge, 2009). Bathyarchaeota also made up over 52% of the Archaea community in non-acidic solid samples (conductivity <46 μS/cm, Figure S9) and are likely involved in the CH₄ cycle either as acetate producer (He et al., 2016; Lazar et al., 2016), or more directly as a potential methanogen or anaerobic CH₄ oxidiser (ANME), as indicated by a Mcr-encoding gene in some representative genomes (Evans et al., 2015). A last example of taxa potentially interacting with methanogens and/or methanotrophs was the *Acetobacteraceae* that were found in acidic niches (Figure 4A). This family is known to metabolise formate in fen soils, thus competing with methanogens (Hunger et al., 2011).

Implications regarding the interactions between microbial communities and climate change

One consequence of global warming in high latitudes will be permafrost thaw which can turn mineral and organic soils into wetlands and lakes (Schoor et al., 2022). The high abundance of methanogens found in lake sediments in this study (Table S2) is in line with the observation of lakes acting as major contributors to positive feedback through CH₄ emissions (Schoor et al., 2022). Our correlation analysis between functional markers' abundance and environmental parameters suggests that the increased water table level and organic matter release induced by permafrost thaw will offer more suitable habitats for methanogens to thrive than for methanotrophs. Nevertheless, the results derived from our DDR analysis showed a higher dispersal capacity (i.e., lower DDR slope) for methanotrophs than for methanogens. Our study thus suggests that the migration of methanotrophs into newly formed lakes might be more efficient than that of methanogens. Therefore, the CH₄ filtering role of methanotrophs may not be delayed for long after methanogens have been re-activated or have colonised the new ecosystems and started to produce CH₄.

The ecological niches defined by the MRT analysis based on current climatic data will be modified by global changes. Based on the IPCC predictions for regional changes in temperature and precipitation (<https://interactive-atlas.ipcc.ch/>), the increase in annual average temperature (bio_01), average temperature of the wettest season (bio_08) and precipitation of the wettest month (bio_13) were estimated according to SSP2-4.5 scenario for each region (Table S5). In several cases, these changes could reach tipping points that would infer shifts from one ecological niche

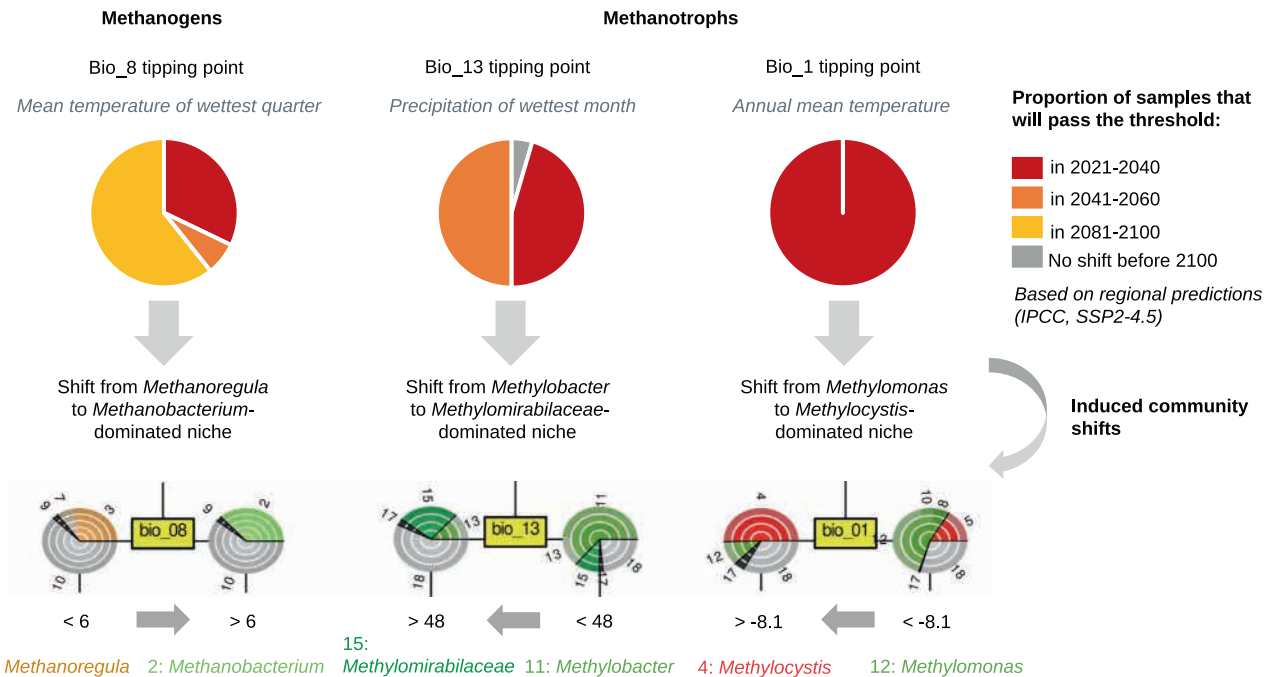


FIGURE 5 Predictions of community shifts with climate change. The top pie charts show the percentage of samples currently below the tipping point for bioclimatic variables 1, 8 and 13 in methanogenic and methanotrophic MRT trees (Figure 4B,C) that are expected to pass the corresponding climatic threshold at different time scales, according to the IPCC predictions (SSP2-4.5) for temperature and precipitations in the Russian Arctic, North-Western North America or Southern South America (details per region are given in Table S5). The mean temperature and precipitation values out of the 34 predictive models selected by the IPCC were considered. The bio_08 threshold is defined in the methanogens MRT tree (Figure 4B), the bio_13 and bio_01 thresholds are defined in the methanotrophs MRT tree (Figure 4C). According to our MRT analysis, crossing the tipping point induces a community change (from the niche below the threshold to the niche above the threshold) characterised by different bioindicators, as indicated by the below pie charts. The taxonomy of the dominant bioindicators is indicated for each niche. MRT, multivariate recursive partitioning tree.

to another. These niche shifts may not modify methanogen or methanotroph abundances (Kruskal Wallis tests based on qPCR data, p values >0.05), but they could result in a modification of the bioindicator composition. For methanogens, the bio_08 threshold defined in our MRT (6°C ; Figure 4B) could be exceeded in 32% of non-acidic pH samples by 2021–2040 and in 100% of them by 2081–2100, therefore implying a community shift from a *Methanoregula* to a *Methanobacterium*-dominated niche (Figure 5). Both genera are hydrogenotrophic methanogens with some psychrotolerant and acidotolerant species, but *Methanoregula* isolates require acetate as carbon source for growth (Imachi & Sakai, 2016), while *Methanobacterium* isolates are autotrophs and cannot use organic compounds for growth (Boone, 2015). Therefore, the resulting methanogenic community would suffer less from organic substrate limitation due to the activity of acetate utilisers at non-acidic pH.

Within methanotrophic guilds, all acidic and water-saturated ($\text{dry_wgh} < 0.061$) samples are projected to exceed the annual mean temperature (bio_01) threshold of -8.1°C in the 2021–2040 period (Figure 5) hence suggesting a shift from a *Methylomonas*- to a *Methylocystis*-dominated niche (Figure 4C). *Methylocystis* is characterised by a high metabolic diversity using

substrates other than CH_4 and the ability to oxidise CH_4 at very low (atmospheric) concentration (Knief, 2015). The predominance of *Methylocystis* may thus imply a change in atmospheric CH_4 oxidation, and its effect on the global methane budget in the future (Oh et al., 2020). Within methanotroph communities in non-acidic solid samples (conductivity $< 56 \mu\text{S}/\text{cm}$), the bio_13 tipping point (precipitations of the wettest month) would be exceeded in 50% and 95% of the samples by, respectively, 2021–2040 and 2041–2060 (Figure 5). This niche shift might favour *Methylomirabilaceae* to the detriment of *Methylobacter* (Figure 4C), enhancing the environmental significance of denitrification-coupled anaerobic methane oxidation (attributed to *Methylomirabilaceae*, Wei et al., 2022). Our study thus supports recent efforts in CH_4 cycle modelling for integrating anaerobic methanotrophy (Gauthier et al., 2015; Ricciuto et al., 2021) and eventually its coupling with the nitrogen cycle.

CONCLUSION

Our study investigated the biogeography of Arctic, sub-Arctic and sub-Antarctic prokaryotic communities as well as the two main microbial guilds impacting the CH_4

cycle. Results showed that the geographic distance had more impact on methanogen community composition than on methanotrophs and the overall prokaryotic community. Across all polar samples analysed, physicochemical variables (especially pH) were the main drivers of microbial distribution. However, geography could be as important as physicochemistry or climate for certain combinations of guilds and habitats, notably in sediments or for methanogens. This work provided major insights into CH₄ cycling at high latitude by (i) defining specific environmental niches characteristic of high latitude terrestrial and aquatic ecosystems, (ii) identifying the key microbial bioindicators characterising the niches and (iii) documenting the expected shifts of key CH₄ cycling microbes under climate change projections. These results gave insight into the present and future contributors and processes of the CH₄ cycle at high-latitudes. This microbial information is of crucial importance to improve process-based models of ecosystem methane flux responses to shifts in environmental and climatic parameters (Aronson et al., 2013; Kharitonov et al., 2021). The niche-specific bioindicators identified in this work could represent relevant candidates for further analyses, in order to (i) refine their taxonomy and explore their metabolic potential and versatility through whole genome sequencing; (ii) better resolve the genetic differentiation, dispersal capacity and gene flow connectivity of methane-cycling key-players between high-latitude provinces through intra-population phylogeographic approaches (Schwob et al., 2021) and (iii) evaluate their physiological response to environmental changes through culturing approaches thus providing deeper insights into the tight relationship between high-latitude microbiome and global climate.

AUTHOR CONTRIBUTIONS

Christophe Sepey: Formal analysis (lead); visualization (lead); writing – original draft (equal); writing – review and editing (equal). **Léa Cabrol:** Conceptualization (lead); data curation (equal); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead); supervision (lead); writing – original draft (equal); writing – review and editing (equal). **Frederic Thalasso:** Conceptualization (supporting); funding acquisition (supporting); investigation (equal); methodology (equal); project administration (supporting); writing – review and editing (supporting). **Laure Gandois:** Conceptualization (supporting); investigation (supporting); methodology (supporting); writing – review and editing (supporting). **Céline Lavergne:** Data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); writing – review and editing (supporting). **Karla Martinez-Cruz:** Data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); writing – review and editing (supporting). **Armando**

Sepulveda-Jauregui: Data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); writing – review and editing (supporting). **Polette Aguilar-Muñoz:** Investigation (supporting); methodology (supporting). **María Soledad Astorga-España:** Funding acquisition (supporting); project administration (supporting). **Rolando Chamy:** Funding acquisition (supporting); project administration (supporting). **Bruna Martins Dellagnezze:** Investigation (equal); methodology (equal). **Claudia Etchebehere:** Conceptualization (supporting); funding acquisition (supporting); investigation (supporting); methodology (supporting); project administration (supporting). **Gilberto J. Fochesatto:** Investigation (supporting); resources (supporting); writing – review and editing (supporting). **Oscar Gerardo-Nieto:** Investigation (supporting). **Andrés Mansilla:** Resources (supporting). **Alison Murray:** Conceptualization (supporting); funding acquisition (supporting); investigation (supporting); writing – review and editing (supporting). **Maxime Sweetlove:** Data curation (equal). **Nikita Tananaev:** Investigation (supporting); resources (supporting). **Roman Teisserenc:** Investigation (supporting). **Alexander Tveit:** Investigation (supporting); writing – review and editing (supporting). **Anton Van de Putte:** Data curation (supporting); project administration (supporting); resources (supporting). **Mette Svenning:** Conceptualization (supporting); funding acquisition (supporting); project administration (supporting); supervision (supporting); writing – review and editing (supporting). **Maialen Barret:** Conceptualization (lead); data curation (equal); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead); supervision (lead); writing – original draft (equal); writing – review and editing (equal).

ACKNOWLEDGEMENTS

The authors would like to thank the French Ministries of Foreign Affairs and International Development (MAEDI) and National Education, Superior Education and Research (MENESR), the Chilean National Commission for Scientific and Technological Research (CONICYT) and the Research Council of Norway (grant no. 256132/H30) for the financial support provided through the ERANet-LAC program project METHANOBASE (ELAC2014_DCC-0092). We gratefully thank the Mexican National Council for Science and Technology (CONACYT) for the grant no. 277238 to Oscar Gerardo-Nieto, Christophe V.W. Sepey would also like to thank WISNA program from the German Federal Ministry of Education and Research for financial support. L. Cabrol acknowledges support from Millennium Science Initiative Program ICN2021_002, ANID (Chile). The fieldwork was financially supported by the University of Toulouse and Toulouse National Polytechnic Institute (INP) and the ECOS sud-CONICYT Project “MATCH” C16B03. We thank Anatoli Pimov for fieldwork assistance and Erwin Domínguez Díaz for access

to the Agricultural Research Institute (INIA) Patagonian field sites. Analyses were performed in the University of Alaska in Fairbanks (US), thanks to Mary-Beth Leigh and Katey Walter Anthony for the access to the facilities of the Institute of Arctic Biology—Department of Biology and Wildlife and in the Water and Environmental Research Center (WERC) respectively. We thank Karin Gerard and Claudio Gonzalez-Wevar for accessing the Laboratory of Antarctic and Sub-Antarctic Marine Ecosystems in the University of Magallanes (Punta Arenas; Chile). The sequencing was performed thanks to the Nutrition and Digestive Ecosystems team (INRA, University of Toulouse; France) for library preparation and GeT-PlaGe Genotoul platform (Toulouse; France) for Illumina MiSeq sequencing and bioinformatic support. Computation was performed thanks to the UNINETT Sigma2 Data storage project NS9593K.



CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad repository at <https://datadryad.org/stash/dataset/doi:10.5061/dryad.rfj6q57dp>.

ORCID

Léa Cabrol  <https://orcid.org/0000-0003-0417-2021>
Nikita Tananaev  <https://orcid.org/0000-0003-2997-0169>

REFERENCES

- Abdalla, M., Hastings, A., Truu, J., Espenberg, M., Mander, U. & Smith, P. (2016) Emissions of methane from northern peatlands: a review of management impacts and implications for future management options. *Ecology and Evolution*, 6, 7080–7102.
- Aronson, E.L., Allison, S.D. & Helliker, B.R. (2013) Environmental impacts on the diversity of methane-cycling microbes and their resultant function. *Frontiers in Microbiology*, 4, 225.
- Astorga, A., Oksanen, J., Luoto, M., Soininen, J., Virtanen, R. & Muotka, T. (2012) Distance decay of similarity in freshwater communities: do macro- and microorganisms follow the same rules? *Global Ecology and Biogeography*, 21, 365–375.
- Baani, M. & Liesack, W. (2008) Two isozymes of particulate methane monooxygenase with different methane oxidation kinetics are found in *Methylocystis* sp strain SCZ. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 10203–10208.
- Baas Becking, L.G.M. (1934) *Geobiologie of inleiding tot de milieukunde*. The Hague: W.P. Van Stockum & Zoon.
- Baldwin, S.A., Khoshnoodi, M., Rezadehbashi, M., Taupp, M., Hallam, S., Mattes, A. et al. (2015) The microbial community of a passive biochemical reactor treating arsenic, zinc, and sulfate-rich seepage. *Frontiers in Bioengineering and Biotechnology*, 3, 27.
- Baptiste, E., Brochier, C. & Boucher, Y. (2005) Higher-level classification of the archaea: evolution of methanogenesis and methanogens. *Archaea*, 1, 353–363.
- Barret, M., Gandois, L., Thalasso, F., Martinez Cruz, K., Sepulveda Jauregui, A., Lavergne, C. et al. (2022) Combined microbial and biogeochemical characterisation of terrestrial and aquatic ecosystems in three high-latitude regions (North Siberia, Alaska and Chilean Patagonia) in the perspective of methane cycle. *Scientific Data*, 9, 674.
- Bashenkhaeva, V.M., Galachyants, Y.P., Khanaev, V.I., Sakirko, V.M., Petrova, D.P., Likhoshway, V.Y. et al. (2020) Comparative analysis of free-living and particle-associated bacterial communities of Lake Baikal during the ice-covered period. *Journal of Great Lakes Research*, 46, 508–518.
- Bastviken, D., Cole, J.J., Pace, M.L. & Van de Bogert, M.C. (2008) Fates of methane from different lake habitats: connecting whole-lake budgets and CH₄ emissions. *Journal of Geophysical Research – Biogeosciences*, 113, G02024.
- Belova, S.E., Baani, M., Suzina, N.E., Bodelier, P.L.E., Liesack, W. & Dedysh, S.N. (2011) Acetate utilization as a survival strategy of peat-inhabiting *Methylocystis* spp. *Environmental Microbiology Reports*, 3, 36–46.
- Biderre-Petit, C., Dugat-Bony, E., Mege, M., Parisot, N., Adrian, L., Mone, A. et al. (2016) Distribution of *Dehalococcoidia* in the anaerobic deep water of a remote meromictic crater lake and detection of *Dehalococcoidia*-derived reductive dehalogenase homologous genes. *PLoS One*, 11, e0145558.
- Biskaborn, B.K., Smith, S.L., Noetzli, J., Matthes, H., Vieira, G., Streletskiy, D.A. et al. (2019) Permafrost is warming at a global scale. *Nature Communications*, 10, 264.
- Boone, D.R. (2015) Methanobacterium. In: Whitman, W.B. (Ed.) *Bergey's manual of systematics of archaea and bacteria*. New York: Wiley.
- Borcard, D. & Legendre, P. (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, 153, 51–68.
- Borrel, G., Adam, P.S., McKay, L.J., Chen, L.X., Sierra García, I.N., Sieber, C.M.K. et al. (2019) Wide diversity of methane and short-chain alkane metabolisms in uncultured archaea. *Nature Microbiology*, 4, 603–613.
- Borrel, G., O'Toole, P.W., Harris, H.M.B., Peyret, P., Brugere, J.F. & Gribaldo, S. (2013) Phylogenomic data support a seventh order of methylotrophic methanogens and provide insights into the evolution of methanogenesis. *Genome Biology and Evolution*, 5, 1769–1780.
- Bräuer, S., Cadillo-Quiroz, H., Kyrpidides, N., Woyke, T., Goodwin, L., Detter, C. et al. (2015) Genome of *Methanoregula boonei* 6A8 reveals adaptations to oligotrophic peatland environments. *Microbiology*, 161, 1572–1581.
- Brouillette, M. (2021) How microbes in permafrost could trigger a massive carbon bomb. *Nature*, 591, 360–363.
- Cabrol, L., Thalasso, F., Gandois, L., Sepulveda-Jauregui, A., Martinez-Cruz, K., Teisserenc, R. et al. (2020) Anaerobic oxidation of methane and associated microbiome in anoxic water of Northwestern Siberian lakes. *Science of the Total Environment*, 736, 139588.
- Camacho, C., Coulouris, G., Avagyan, V., Ma, N., Papadopoulos, J., Bealer, K. et al. (2009) BLAST plus: architecture and applications. *BMC Bioinformatics*, 421, 1–19.
- Carere, C.R., Hards, K., Houghton, K.M., Power, J.F., McDonald, B., Collet, C. et al. (2017) Mixotrophy drives niche expansion of verrucomicrobial methanotrophs. *ISME Journal*, 11, 2599–2610.
- Cavicchioli, R., Ripple, W.J., Timmis, K.N., Azam, F., Bakken, L.R., Baylis, M. et al. (2019) Scientists' warning to humanity: microorganisms and climate change. *Nature Reviews Microbiology*, 17, 569–586.
- Cervantes, F.J., van der Velde, S., Lettinga, G. & Field, J.A. (2000) Competition between methanogenesis and quinone respiration for ecologically important substrates in anaerobic consortia. *FEMS Microbiology Ecology*, 34, 161–171.
- Choudoir, M.J., Barberan, A., Menninger, H.L., Dunn, R.R. & Fierer, N. (2018) Variation in range size and dispersal capabilities of microbial taxa. *Ecology*, 99, 322–334.

- Chu, H., Fierer, N., Lauber, C.L., Caporaso, J.G., Knight, R. & Grogan, P. (2010) Soil bacterial diversity in the Arctic is not fundamentally different from that found in other biomes. *Environmental Microbiology*, 12, 2998–3006.
- Conant, R.T., Ryan, M.G., Agren, G.I., Birge, H.E., Davidson, E.A., Eliasson, P.E. et al. (2011) Temperature and soil organic matter decomposition rates—synthesis of current knowledge and a way forward. *Global Change Biology*, 17, 3392–3404.
- Conrad, R. (2007) Microbial ecology of methanogens and methanotrophs. *Advances in Agronomy*, 96, 1–63.
- Conrad, R. (2009) The global methane cycle: recent advances in understanding the microbial processes involved. *Environmental Microbiology Reports*, 1, 285–292.
- Cozannet, M., Borrel, G., Roussel, E., Moalic, Y., Allieux, M., Sanvoisin, A. et al. (2021) New insights into the ecology and physiology of Methanomassiliicoccales from terrestrial and aquatic environments. *Microorganisms*, 30, 1–31.
- Crevecoeur, S., Ruiz-González, C., Prairie, Y.T. & del Giorgio, P.A. (2019) Large-scale biogeography and environmental regulation of methanotrophic bacteria across boreal inland waters. *Molecular Ecology*, 28, 4181–4196.
- Danilova, O.V., Kulichevskaya, I.S., Rozova, O.N., Detkova, E.N., Bodelier, P.L.E., Trotsenko, Y.A. et al. (2013) *Methylomonas paludis* sp. nov., the first acid-tolerant member of the genus *Methylomonas*, from an acidic wetland. *International Journal of Systematic and Evolutionary Microbiology*, 63, 2282–2289.
- De'Ath, G. (2002) Multivariate regression trees: a new technique for modeling species-environment relationships. *Ecology*, 83, 1105–1117.
- Dedysh, S.N., Beletsky, A.V., Ivanova, A.A., Danilova, O.V., Begmatov, S., Kulichevskaya, I.S. et al. (2021) Peat-inhabiting *Verrucomicrobia* of the order Methyloacidiphilales do not possess methanotrophic capabilities. *Microorganisms*, 2566, 1–13.
- Dedysh, S.N., Didriksen, A., Danilova, O.V., Belova, S.E., Liebner, S. & Svenning, M.M. (2015) *Methylocapsa palarum* sp. nov., a methanotroph isolated from a sub-Arctic discontinuous permafrost ecosystem. *International Journal of Systematic and Evolutionary Microbiology*, 65, 3618–3624.
- Dedysh, S.N. & Dunfield, P.F. (2011) Chapter three—facultative and obligate methanotrophs: how to identify and differentiate them. In: Rosenzweig, A. & Ragsdale, S. (Eds.) *Methods in enzymology*, Elsevier Inc. US (NY), Vol. 495, 31–44.
- Dedysh, S.N., Kulichevskaya, I.S., Serkebaeva, Y.M., Mityaeva, M. A., Sorokin, V.V., Suzina, N.E. et al. (2012) *Bryocella elongata* gen. nov., sp. nov., a member of subdivision 1 of the Acidobacteria isolated from a methanotrophic enrichment culture, and emended description of *Edaphobacter aggregans* Koch et al. 2008. *International Journal of Systematic and Evolutionary Microbiology*, 62(Pt_3), 654–664. Available from: <https://doi.org/10.1099/ijs.0.031898-0>
- Dellagnezze, B.M., Bovio-Winkler, P., Lavergne, C., Menoni, D.A., Mosquillo, F., Cabrol, L. et al. (2023) Acetoclastic archaea adaptation under increasing temperature in lake sediments and wetland soils from Alaska. *Polar Biology*, 46, 259–275.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carre, G. et al. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27–46.
- Dufrene, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67, 345–366.
- Dunfield, P.F., Yuryev, A., Senin, P., Smirnova, A.V., Stott, M.B., Hou, S. et al. (2007) Methane oxidation by an extremely acidophilic bacterium of the phylum *Verrucomicrobia*. *Nature*, 450, 879–882.
- Escudie, F., Auer, L., Bernard, M., Mariadassou, M., Cauquil, L., Vidal, K. et al. (2018) FROGS: find, rapidly, OTUs with galaxy solution. *Bioinformatics*, 34, 1287–1294.
- Esson, K.C., Lin, X., Kumaresan, D., Chanton, J.P., Murrell, J.C. & Kostka, J.E. (2016) Alpha- and gammaproteobacterial methanotrophs codominate the active methane-oxidizing communities in an acidic boreal peat bog. *Applied and Environmental Microbiology*, 82, 2363–2371.
- Evans, P.N., Boyd, J.A., Leu, A.O., Woodcroft, B.J., Parks, D.H., Hugenholtz, P. et al. (2019) An evolving view of methane metabolism in the Archaea. *Nature Reviews Microbiology*, 17, 219–232.
- Evans, P.N., Parks, D.H., Chadwick, G.L., Robbins, S.J., Orphan, V.J., Golding, S.D. et al. (2015) Methane metabolism in the archaeal phylum *Bathyarchaeota* revealed by genome-centric metagenomics. *Science*, 350, 434–438.
- Fick, S.E. & Hijmans, R.J. (2017) orldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315.
- Fierer, N., Colman, B.P., Schimel, J.P. & Jackson, R.B. (2006) Predicting the temperature dependence of microbial respiration in soil: a continental-scale analysis. *Global Biogeochemical Cycles*, 20, GB3026, 1–10.
- Fu, L., Song, T. & Lu, Y. (2015) Snapshot of methanogen sensitivity to temperature in Zoige wetland from Tibetan plateau. *Frontiers in Microbiology*, 6, Article 131
- Gao, G.F., Peng, D., Tripathi, B.M., Zhang, Y. & Chu, H. (2020) *Distinct community assembly processes of abundant and rare soil bacteria in coastal wetlands along an inundation gradient*. *mSystems*, 5, e01150–2.
- Gauthier, M., Bradley, R.L. & Šimek, M. (2015) More evidence that anaerobic oxidation of methane is prevalent in soils: is it time to upgrade our biogeochemical models? *Soil Biology and Biochemistry*, 80, 167–174.
- Gies, E.A., Konwar, K.M., Beatty, J.T. & Hallam, S.J. (2014) Illuminating microbial dark matter in meromictic Sakinaw Lake. *Applied and Environmental Microbiology*, 80, 6807–6818.
- Gonzalez-Valencia, R., Magana-Rodriguez, F., Gerardo-Nieto, O., Sepulveda-Jauregui, A., Martinez-Cruz, K., Anthony, K.W. et al. (2014) In situ measurement of dissolved methane and carbon dioxide in freshwater ecosystems by off-axis integrated cavity output spectroscopy. *Environmental Science & Technology*, 48, 11421–11428.
- Graef, C., Hestnes, A.G., Svenning, M.M. & Frenzel, P. (2011) The active methanotrophic community in a wetland from the High Arctic. *Environmental Microbiology Reports*, 3(4), 466–472. Portico. Available from: <https://doi.org/10.1111/j.1758-2229.2010.00237.x>
- Guggenheim, C., Freimann, R., Mayr, M.J., Beck, K., Wehrli, B. & Burgmann, H. (2020) Environmental and microbial interactions shape methane-oxidizing bacterial communities in a stratified lake. *Frontiers in Microbiology*, 11, 579427.
- Gupta, V., Smemo, K.A., Yavitt, J.B., Fowle, D., Branfireun, B. & Basiliro, N. (2013) Stable isotopes reveal widespread anaerobic methane oxidation across latitude and peatland type. *Environmental Science & Technology*, 47, 8273–8279.
- Gwak, J.H., Awala, S.I., Nguyen, N.L., Yu, W.J., Yang, H.Y., von Bergen, M. et al. (2022) Sulfur and methane oxidation by a single microorganism. *Proceedings of the National Academy of Sciences*, 119, e2114799119.
- Hanson, C.A., Fuhrman, J.A., Homer-Devine, M.C. & Martiny, J.B.H. (2012) Beyond biogeographic patterns: processes shaping the microbial landscape. *Nature Reviews Microbiology*, 10, 497–506.
- Hanson, C.A., Mueller, A.L., Loy, A., Dona, C., Appel, R., Jorgensen, B.B. et al. (2019) Historical factors associated with past environments influence the biogeography of thermophilic endospores in Arctic marine sediments. *Frontiers in Microbiology*, 10, 245.
- He, R., Wang, J., Pohlman, J.W., Jia, Z., Chu, Y.X., Wooller, M.J. et al. (2022) Metabolic flexibility of aerobic methanotrophs under

- anoxic conditions in Arctic lake sediments. *The ISME Journal*, 16(1), 78–90.
- He, Y., Li, M., Perumal, V., Feng, X., Fang, J., Xie, J. et al. (2016) Genomic and enzymatic evidence for acetogenesis among multiple lineages of the archaeal phylum *Bathyarchaeota* widespread in marine sediments. *Nature Microbiology*, 16035.
- Hijmans, R.J. (2017) Geosphere: spherical trigonometry 1.5–7 edn. <https://CRAN.R-project.org/package=geosphere>
- Horn, M.A., Matthies, C., Kusel, K., Schramm, A. & Drake, H.L. (2003) Hydrogenotrophic methanogenesis by moderately acid-tolerant methanogens of a methane-emitting acidic peat. *Applied and Environmental Microbiology*, 69, 74–83.
- Hunger, S., Schmidt, O., Hilgarth, M., Horn, M.A., Kolb, S., Conrad, R. et al. (2011) Competing formate- and carbon dioxide-utilizing prokaryotes in an anoxic methane-emitting fen soil. *Applied and Environmental Microbiology*, 77, 3773–3785.
- Imachi, H. & Sakai, S. (2016) Methanoregulaceae. In: *Bergey's manual of systematics of archaea and bacteria*. John Wiley & Sons, Hoboken, United States, pp. 1–4.
- Jansen, J., Woolway, R.I., Kraemer, B.M., Albergel, C., Bastviken, D., Weyhenmeyer, G.A. et al. (2022) Global increase in methane production under future warming of lake bottom waters. *Global Change Biology*, 28, 5427–5440.
- Jassey, V.E.J., Reczuga, M.K., Zielinska, M., Slowinska, S., Robroek, B.J.M., Mariotte, P. et al. (2018) Tipping point in plant-fungal interactions under severe drought causes abrupt rise in peatland ecosystem respiration. *Global Change Biology*, 24, 972–986.
- Juottonen, H. (2020) Disentangling the effects of methanogen community and environment on peatland greenhouse gas production by a reciprocal transplant experiment. *Functional Ecology*, 34 (6), 1268–1279. Portico. Available from: <https://doi.org/10.1111/1365-2435.13536>
- Kalyuzhnaya, M.G., Khmelenina, V.N., Kotelnikova, S., Holmquist, L., Pedersen, K. & Trotsenko, Y.A. (1999) *Methylomonas scandinavica* sp. nov., a new methanotrophic psychrotrophic bacterium isolated from deep igneous rock ground water of Sweden. *Systematic and Applied Microbiology*, 22, 565–572.
- Kaupper, T., Hetz, S., Kolb, S., Yoon, S., Horn, M.A. & Ho, A. (2020) Deforestation for oil palm: impact on microbially mediated methane and nitrous oxide emissions, and soil bacterial communities. *Biology and Fertility of Soils*, 56(3), 287–298. Available from: <https://doi.org/10.1007/s00374-019-01421-3>
- Kharitonov, S., Semenov, M., Sabrekov, A., Kotsyurbenko, O., Zhelezova, A. & Schegolkova, N. (2021) Microbial communities in methane cycle: modern molecular methods gain insights into their global ecology. *Environments*, 8, 16.
- Kleinteich, J., Hildebrand, F., Bahram, M., Voigt, A.Y., Wood, S.A., Jungblut, A.D. et al. (2017) Pole-to-pole connections: similarities between Arctic and Antarctic microbiomes and their vulnerability to environmental change. *Frontiers in Ecology and Evolution*, 137, 1–11.
- Knief, C. (2015) Diversity and habitat preferences of cultivated and uncultivated aerobic methanotrophic bacteria evaluated based on *pmoA* as molecular marker. *Frontiers in Microbiology*, 6, 1346.
- Kotsyurbenko, O.R., Friedrich, M.W., Simankova, M.V., Nozhevnikova, A.N., Golyshin, P.N., Timmis, K.N. et al. (2007) Shift from acetoclastic to H₂-dependent methanogenesis in a West Siberian peat bog at low pH values and isolation of an acidophilic Methanobacterium strain. *Applied and Environmental Microbiology*, 73(7), 2344–2348.
- Kurth, J.M., op den Camp, H.J.M. & Welte, C.U. (2020) Several ways one goal-methanogenesis from unconventional substrates. *Applied Microbiology and Biotechnology*, 104, 6839–6854.
- Langenheder, S. & Lindstrom, E.S. (2019) Factors influencing aquatic and terrestrial bacterial community assembly. *Environmental Microbiology Reports*, 11, 306–315.
- Lavergne, C., Aguilar-Munoz, P., Calle, N., Thalasso, F., Astorga-Espana, M.S., Sepulveda-Jauregui, A. et al. (2021) Temperature differently affected methanogenic pathways and microbial communities in sub-Antarctic freshwater ecosystems. *Environment International*, 154, 106575.
- Lazar, C.S., Baker, B.J., Seitz, K., Hyde, A.S., Dick, G.J., Hinrichs, K.U. et al. (2016) Genomic evidence for distinct carbon substrate preferences and ecological niches of *Bathyarchaeota* in estuarine sediments. *Environmental Microbiology*, 18, 1200–1211.
- Lenoir, J., Virtanen, R., Oksanen, J., Oksanen, L., Luoto, M., Grytnes, J.A. et al. (2012) Dispersal ability links to cross-scale species diversity patterns across the Eurasian Arctic tundra. *Global Ecology and Biogeography*, 21, 851–860.
- Lindstrom, E.S. & Langenheder, S. (2012) Local and regional factors influencing bacterial community assembly. *Environmental Microbiology Reports*, 4, 1–9.
- Litchman, E. (2010) Invisible invaders: non-pathogenic invasive microbes in aquatic and terrestrial ecosystems. *Ecology Letters*, 13, 1560–1572.
- Liu, K., Hou, J., Liu, Y., Hu, A., Wang, M., Wang, F. et al. (2019) Biogeography of the free-living and particle-attached bacteria in Tibetan lakes. *FEMS Microbiology Ecology*, 95, fuz088.
- Liu, N., Hu, H., Ma, W., Deng, Y., Wang, Q., Luo, A. et al. (2021) Relative importance of deterministic and stochastic processes on soil microbial community assembly in temperate grasslands. *Microorganisms*, 9, 1929.
- Looby, I.C. & Martin, P.H. (2020) Diversity and function of soil microbes on montane gradients: the state of knowledge in a changing world. *FEMS Microbiology Ecology*, 96(9), fiaa122.
- Lv, X., Yu, J., Fu, Y., Ma, B., Qu, F., Ning, K. et al. (2014) A meta-analysis of the bacterial and archaeal diversity observed in wetland soils. *The Scientific World Journal*, 2014(437684), 1–12. Available from: <https://doi.org/10.1155/2014/437684>
- Lyu, Z. & Lu, Y. (2018) Metabolic shift at the class level sheds light on adaptation of methanogens to oxidative environments. *ISME Journal*, 12, 411–423.
- Mahé, F., Rognes, T., Quince, C., de Vargas, C. & Dunthorn, M. (2014) Swarm: robust and fast clustering method for amplicon-based studies. *PeerJ*, 2, e539.
- Malard, L.A., Anwar, M.Z., Jacobsen, C.S. & Pearce, D.A. (2019) Biogeographical patterns in soil bacterial communities across the Arctic region. *FEMS Microbiology Ecology*, 95(9), fiz128.
- Martiny, J.B.H., Bohannan, B.J.M., Brown, J.H., Colwell, R.K., Fuhrman, J.A., Green, J.L. et al. (2006) Microbial biogeography: putting microorganisms on the map. *Nature Reviews Microbiology*, 4, 102–112.
- Martiny, J.B.H., Eisen, J.A., Penn, K., Allison, S.D. & Horner-Devine, M.C. (2011) Drivers of bacterial beta-diversity depend on spatial scale. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 7850–7854.
- Meyer, K.M., Memiaghe, H., Korte, L., Kenfack, D., Alonso, A. & Bohannan, B.J.M. (2018) Why do microbes exhibit weak biogeographic patterns? *The ISME Journal*, 12, 1404–1413.
- Miller, K.E., Lai, C.T., Dahlgren, R.A. & Lipson, D.A. (2019) Anaerobic methane oxidation in high-Arctic Alaskan peatlands as a significant control on net CH₄ fluxes. *Soil Systems*, 7, 1–21.
- Miroshnikov, K.K., Didriksen, A., Naumoff, D.G., Huntemann, M., Clum, A., Pillay, M. et al. (2017) Draft genome sequence of *Methylocapsa palsarum* NE2(T), an obligate methanotroph from subarctic soil. *Microbiology Resource Announcements*, 5(24), doi:10.0128/genomea.
- Nazaries, L., Karunaratne, S.B., Delgado-Baquerizo, M., Campbell, C.D. & Singh, B.K. (2018) Environmental drivers of the geographical distribution of methanotrophs: insights from a national survey. *Soil Biology and Biochemistry*, 127, 264–279.
- Nguyen, N.L., Yu, W.J., Gwak, J.H., Kim, S.J., Park, S.J., Herbold, C.W. et al. (2018) Genomic insights into the acid

- adaptation of novel methanotrophs enriched from acidic forest soils. *Frontiers in Microbiology*, 9.
- Ochsenreiter, T., Selezi, D., Quaiser, A., Bonch-Osmolovskaya, L. & Schleper, C. (2003) Diversity and abundance of Crenarchaeota in terrestrial habitats studied by 16S RNA surveys and real time PCR. *Environmental Microbiology*, 5, 787–797.
- Oh, Y., Zhuang, Q., Liu, L., Welp, L.R., Lau, M.C.Y., Onstott, T.C. et al. (2020) Reduced net methane emissions due to microbial methane oxidation in a warmer Arctic. *Nature Climate Change*, 10, 317–321.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGinn, D. et al. (2018) Vegan: community ecology package. <https://CRAN.R-project.org/package=vegan> R Package Version 2.5–2.
- Olefeldt, D., Goswami, S., Grosse, G., Hayes, D., Hugelius, G., Kuhry, P. et al. (2016) Circumpolar distribution and carbon storage of thermokarst landscapes. *Nature Communications*, 7, 13043.
- Op den Camp, H.J.M., Islam, T., Stott, M.B., Harhangi, H.R., Hynes, A., Schouten, S. et al. (2009) Environmental, genomic and taxonomic perspectives on methanotrophic Verrucomicrobia. *Environmental Microbiology Reports*, 1(5), 293–306.
- Pohlert, T. (2022) PMCMRplus: calculate pairwise multiple comparisons of mean rank sums tended. <https://CRAN.R-project.org/package=PMCMRplus> R package version 1.9.6.
- Putkinen, A., Larmola, T., Tuomivirta, T., Siljanen, H.M.P., Bodrossy, L., Tuittila, E. et al. (2014) Peatland succession induces a shift in the community composition of *Sphagnum*-associated active methanotrophs. *FEMS Microbiology Ecology*, 88, 596–611.
- Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P. et al. (2013) The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Research*, 41, D590–D596.
- Ricciuto, D.M., Xu, X., Shi, X., Wang, Y., Song, X., Schadt, C.W. et al. (2021) An integrative model for soil biogeochemistry and methane processes: I. Model structure and sensitivity analysis. *Journal of Geophysical Research: Biogeosciences*, 126, e2019JG005468.
- Rissanen, A., Saareheimo, J., Tirola, M., Peura, S., Aalto, S., Karvinen, A. et al. (2018) Gammaproteobacterial methanotrophs dominate methanotrophy in aerobic and anaerobic layers of boreal lake waters. *Aquatic Microbial Ecology*, 81(3), 257–276. Available from: <https://doi.org/10.3354/ame01874>
- Roberts, D.W. (2013) labdsv: ordination and multivariate analysis for ecology 1.6-1 edn. <http://CRAN.R-project.org/package=labdsv>
- Rognes, T., Flouri, T., Nichols, B., Quince, C. & Mahé, F. (2016) VSEARCH: a versatile open source tool for metagenomics. *PeerJ*, 4, e2584, 1–22.
- Rößger, N., Sachs, T., Wille, C., Boike, J. & Kutzbach, L. (2022) Seasonal increase of methane emissions linked to warming in Siberian tundra. *Nature Climate Change*, 12(11), 1031–1036. Available from: <https://doi.org/10.1038/s41558-022-01512-4>
- Rousk, J., Baath, E., Brookes, P.C., Lauber, C.L., Lozupone, C., Caporaso, J.G. et al. (2010) Soil bacterial and fungal communities across a pH gradient in an arable soil. *ISME Journal*, 4, 1340–1351.
- Rozzi, R., Armesto, J.J., Goffinet, B., Buck, W., Massardo, F., Silander, J. et al. (2008) Changing lenses to assess biodiversity: patterns of species richness in sub-Antarctic plants and implications for global conservation. *Frontiers in Ecology and the Environment*, 6, 131–137.
- Saunois, M., Staver, A.R., Poulter, B., Bousquet, P., Canadell, J.G., Jackson, R.B. et al. (2020) The global methane budget 2000–2017. *Earth System Science Data*, 12, 1561–1623.
- Schmidt, O., Dyckmans, J. & Schrader, S. (2016) Photoautotrophic microorganisms as a carbon source for temperate soil invertebrates. *Biology Letters*, 12, 20150646, 1–4.
- Schuur, E.A.G., Abbott, B.W., Commane, R., Ernakovich, J., Euskirchen, E., Hugelius, G. et al. (2022) Permafrost and climate change: carbon cycle feedbacks from the warming Arctic. *Annual Review of Environment and Resources*, 47, 343–371.
- Schuur, E.A.G., McGuire, A.D., Schaedel, C., Grosse, G., Harden, J.W., Hayes, D.J. et al. (2015) Climate change and the permafrost carbon feedback. *Nature*, 520, 171–179.
- Schwob, G., Segovia, I.N., Gonzalez-Wevar, C., Cabrol, L., Orlando, J. & Poulin, E. (2021) Exploring the microdiversity within marine bacterial taxa: toward an integrated biogeography in the southern ocean. *Frontiers in Microbiology*, 12, 703792, 1–18.
- Segarra, K.E.A., Schubotz, F., Samarkin, V., Yoshinaga, M.Y., Hinrichs, K.U. & Joye, S.B. (2015) High rates of anaerobic methane oxidation in freshwater wetlands reduce potential atmospheric methane emissions. *Nature Communications*, 6, 7477, 1–8.
- Shi, Y., Xiang, X., Shen, C., Chu, H., Neufeld, J.D., Walker, V.K. et al. (2015a) Vegetation-associated impacts on Arctic tundra bacterial and microeukaryotic communities. *Applied and Environmental Microbiology*, 81, 492–501.
- Shi, Y., Grogan, P., Sun, H., Xiong, J., Yang, Y., Zhou, J. et al. (2015b) Multi-scale variability analysis reveals the importance of spatial distance in shaping Arctic soil microbial functional communities. *Soil Biology and Biochemistry*, 86, 126–134. Available from: <https://doi.org/10.1016/j.soilbio.2015.03.028>
- Singh, B.K., Bardgett, R.D., Smith, P. & Reay, D.S. (2010) Microorganisms and climate change: terrestrial feedbacks and mitigation options. *Nature Reviews Microbiology*, 8, 779–790.
- Sizova, M.V., Panikov, N.S., Tourova, T.P. & Flanagan, P.W. (2003) Isolation and characterization of oligotrophic acido-tolerant methanogenic consortia from a *Sphagnum* peat bog. *FEMS Microbiology Ecology*, 45, 301–315.
- Smith, G.J., Angle, J.C., Solden, L.M., Borton, M.A., Morin, T.H., Daly, R.A. et al. (2018) Members of the genus *Methylobacter* are inferred to account for the majority of aerobic methane oxidation in oxic soils from a freshwater wetland. *MBio*, 9(6), e00815–18, 1–17.
- Smith, G.J. & Wrighton, K.C. (2019) Metagenomic approaches unearth methanotroph phylogenetic and metabolic diversity. *Current Issues in Molecular Biology*, 57–84. Available from: <https://doi.org/10.21775/cimb.033.057>
- Stams, A.J.M. & Plugge, C.M. (2009) Electron transfer in syntrophic communities of anaerobic bacteria and archaea. *Nature Reviews Microbiology*, 7, 568–577.
- Tate, K.R. (2015) Soil methane oxidation and land-use change—from process to mitigation. *Soil Biology & Biochemistry*, 80, 260–272.
- Thalasso, F., Sepulveda-Jauregui, A., Gandois, L., Martinez-Cruz, K., Gerardo-Nieto, O., Astorga-Espana, M.S. et al. (2020) Sub-oxycline methane oxidation can fully uptake CH₄ produced in sediments: case study of a lake in Siberia. *Scientific Reports*, 10, 3423, 1–7.
- Therneau, T.M. & Atkinson, B. (2014) mvpart: multivariate partitioning 1.6-2 edn. <https://CRAN.R-project.org/package=mvpart>
- Thottathil, S.D., Reis, P.C.J., del Giorgio, P.A. & Prairie, Y.T. (2018) The extent and regulation of summer methane oxidation in northern lakes. *Journal of Geophysical Research: Biogeosciences*, 123, 3216–3230.
- Tian, J., Shu, C., Chen, H., Qiao, Y., Yang, G., Xiong, W. et al. (2015) Response of archaeal communities to water regimes under simulated warming and drought conditions in Tibetan plateau wetlands. *Journal of Soils and Sediments*, 15, 179–188.
- Tveit, A.T., Hestnes, A.G., Robinson, S.L., Schintmeister, A., Dedysh, S.N., Jehmlich, N. et al. (2019) Widespread soil bacterium that oxidizes atmospheric methane. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 8515–8524.
- Tveit, A.T., Ulrich, T., Frenzel, P. & Svenning, M.M. (2015) Metabolic and trophic interactions modulate methane production by Arctic

- peat microbiota in response to warming. *Proceedings of the National Academy of Sciences of the United States of America*, 112, E2507–E2516.
- Valentine, D.L. (2007) Adaptations to energy stress dictate the ecology and evolution of the archaea. *Nature Reviews Microbiology*, 5, 316–323.
- van Teeseling, M.C.F., Pol, A., Harhangi, H.R., van der Zwart, S., Jetten, M.S.M. & den Camp, H.J.M.O. (2014) Expanding the verrucomicrobial methanotrophic world: description of three novel species of *Methyloacidimicrobium* gen. Nov. *Applied and Environmental Microbiology*, 80, 6782–6791.
- Vorobev, A.V., Baani, M., Doronina, N.V., Brady, A.L., Liesack, W., Dunfield, P.F. et al. (2011) *Methyloferula stellata* gen. nov., sp. nov., an acidophilic, obligately methanotrophic bacterium that possesses only a soluble methane monooxygenase. *International Journal of Systematic and Evolutionary Microbiology*, 61, 2456–2463.
- Vorob'ev, A.V., de Boer, W., Folman, L.B., Bodelier, P.L.E., Doronina, N.V., Suzina, N.E. et al. (2009) *Methylovirgula ligni* gen. nov., sp. nov., an obligately acidophilic, facultatively methylotrophic bacterium with a highly divergent *mxoF* gene. *International Journal of Systematic and Evolutionary Microbiology*, 59, 2538–2545.
- Wang, K., Ye, X., Zhang, H., Chen, H., Zhang, D. & Liu, L. (2016) Regional variations in the diversity and predicted metabolic potential of benthic prokaryotes in coastal northern Zhejiang, East China Sea. *Scientific Reports*, 6, 38709.
- Wang, Y. & Qian, P.Y. (2009) Conservative fragments in bacterial 16S rRNA genes and primer design for 16S ribosomal DNA amplicons in metagenomic studies. *PLoS One*, 4(10), e7401, 1–9.
- Wei, H., Wang, M., Ya, M. & Xu, C. (2022) The denitrifying anaerobic methane oxidation process and microorganisms in the environments: a review. *Frontiers in Marine Science*, 9, 1038400.
- Wen, X., Yang, S., Horn, F., Winkel, M., Wagner, D. & Liebner, S. (2017) Global biogeographic analysis of methanogenic archaea identifies community-shaping environmental factors of natural environments. *Frontiers in Microbiology*, 8, 1339, 1–13.
- Winder, J.C., Braga, L.P.P., Kuhn, M.A., Thompson, L.M., Olefeldt, D. & Tanentzap, A.J. (2023) Climate warming has direct and indirect effects on microbes associated with carbon cycling in northern lakes. *Global Change Biology*, 29(11), 3039–3053.
- Wrighton, K.C., Castelle, C.J., Wilkins, M.J., Hug, L.A., Sharon, I., Thomas, B.C. et al. (2014) Metabolic interdependencies between phylogenetically novel fermenters and respiratory organisms in an unconfined aquifer. *ISME Journal*, 8, 1452–1463.
- Wu, L., Han, C., Zhu, G. & Zhong, W. (2019) Responses of active ammonia oxidizers and nitrification activity in eutrophic lake sediments to nitrogen and temperature. *Applied and Environmental Microbiology*, 85(18), e00258–19, 1–12.
- Wu, W., Lu, H., Sastri, A., Yeh, Y., Gong, G., Chou, W. et al. (2018) Contrasting the relative importance of species sorting and dispersal limitation in shaping marine bacterial versus protist communities. *The ISME Journal*, 12, 485–494.
- Xiang, X., Wang, R., Wang, H., Gong, L., Man, B. & Xu, Y. (2017) Distribution of Bathyarchaeota communities across different terrestrial settings and their potential ecological functions. *Scientific Reports*, 7, 45028, 1–11.
- Yang, J., Jiang, H., Wu, G., Liu, W. & Zhang, G. (2016) Distinct factors shape aquatic and sedimentary microbial community structures in the lakes of western China. *Frontiers in Microbiology*, 7, 1782.
- Yang, S., Liebner, S., Winkel, M., Alawi, M., Horn, F., Doerfer, C. et al. (2017) In-depth analysis of core methanogenic communities from high elevation permafrost-affected wetlands. *Soil Biology & Biochemistry*, 111, 66–77.
- Yavitt, J.B., Yashiro, E., Cadillo-Quiroz, H. & Zinder, S.H. (2012) Methanogen diversity and community composition in peatlands of the central to northern Appalachian Mountain region, North America. *Biogeochemistry*, 109, 117–131.
- Ye, R., Jin, Q., Bohannon, B., Keller, J.K., McAllister, S.A. & Bridgman, S.D. (2012) pH controls over anaerobic carbon mineralization, the efficiency of methane production, and methanogenic pathways in peatlands across an ombrotrophic-minerotrophic gradient. *Soil Biology & Biochemistry*, 54, 36–47.
- Zakharova, Y., Bashenkhaeva, M., Galachyants, Y., Petrova, D., Tomberg, I., Marchenkov, A. et al. (2021) 34. *Microbial Ecology*, 84, 958–973.
- Zalman, C.A., Meade, N., Chanton, J., Kostka, J.E., Bridgman, S.D. & Keller, J.K. (2018) Methylotrophic methanogenesis in Sphagnum-dominated peatland soils. *Soil Biology & Biochemistry*, 118, 156–160. Available from: <https://doi.org/10.1016/j.soilbio.2017.11.025>
- Zhang, L., Adams, J.M., Dumont, M.G., Li, Y., Shi, Y., He, D. et al. (2019) Distinct methanotrophic communities exist in habitats with different soil water contents. *Soil Biology & Biochemistry*, 132, 143–152.
- Zhou, Z., Zhang, C., Liu, P., Fu, L., Laso-Pérez, R., Yang, L. et al. (2022) Non-syntrophic methanogenic hydrocarbon degradation by an archaeal species. *Nature*, 601, 257–262.
- Zhu, Y., Purdy, K.J., Eyice, O.Z.G.E., Shen, L., Harpenslager, S.F., Yvon-Durocher, G. et al. (2020) Disproportionate increase in freshwater methane emissions induced by experimental warming. *Nature Climate Change*, 10, 685–690.
- Zinger, L., Boetius, A. & Ramette, A. (2014) Bacterial taxa-area and distance-decay relationships in marine environments. *Molecular Ecology*, 23, 954–964.
- Zu, Q., Zhong, L., Deng, Y., Shi, Y., Wang, B., Jia, Z. et al. (2016) Geographical distribution of methanogenic archaea in nine representative paddy soils in China. *Frontiers in Microbiology*, 7, 1447.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Seppey, C.V.W., Cabrol, L., Thalasso, F., Gandois, L., Lavergne, C., Martinez-Cruz, K. et al. (2023) Biogeography of microbial communities in high-latitude ecosystems: Contrasting drivers for methanogens, methanotrophs and global prokaryotes. *Environmental Microbiology*, 1–23. Available from: <https://doi.org/10.1111/1462-2920.16526>