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

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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-latitudes regions (Siberia, Alaska and Patagonia) focusing on mineral/organic soils (wetlands, peatlands,

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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 (CH_4; Schuur et al., 2015). The role of microbial communities in CH_4 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 CH_4 arises from natural sources, among which wetlands and lakes contribute to up to 70% of natural biogenic emissions (Saunois et al., 2020). Most of this CH_4 is produced by methanogenic archaea under anoxic conditions in wetlands or lake sediments. Nonetheless, a substantial fraction of this CH_4 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 CH_4 emissions result from an interplay between CH_4 producing and consuming microorganisms. Deciphering the physicochemical, geographical and climatic factors driving the abundance and composition of methanogens and CH_4 oxidisers is therefore important for understanding their contribution to the CH_4 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 CO_2, 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 (CO_2/H_2, 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 CH_4-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 CH_4 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 CH_4 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 CH_4 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 $7.05*10^6$, $2.15*10^6$ 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

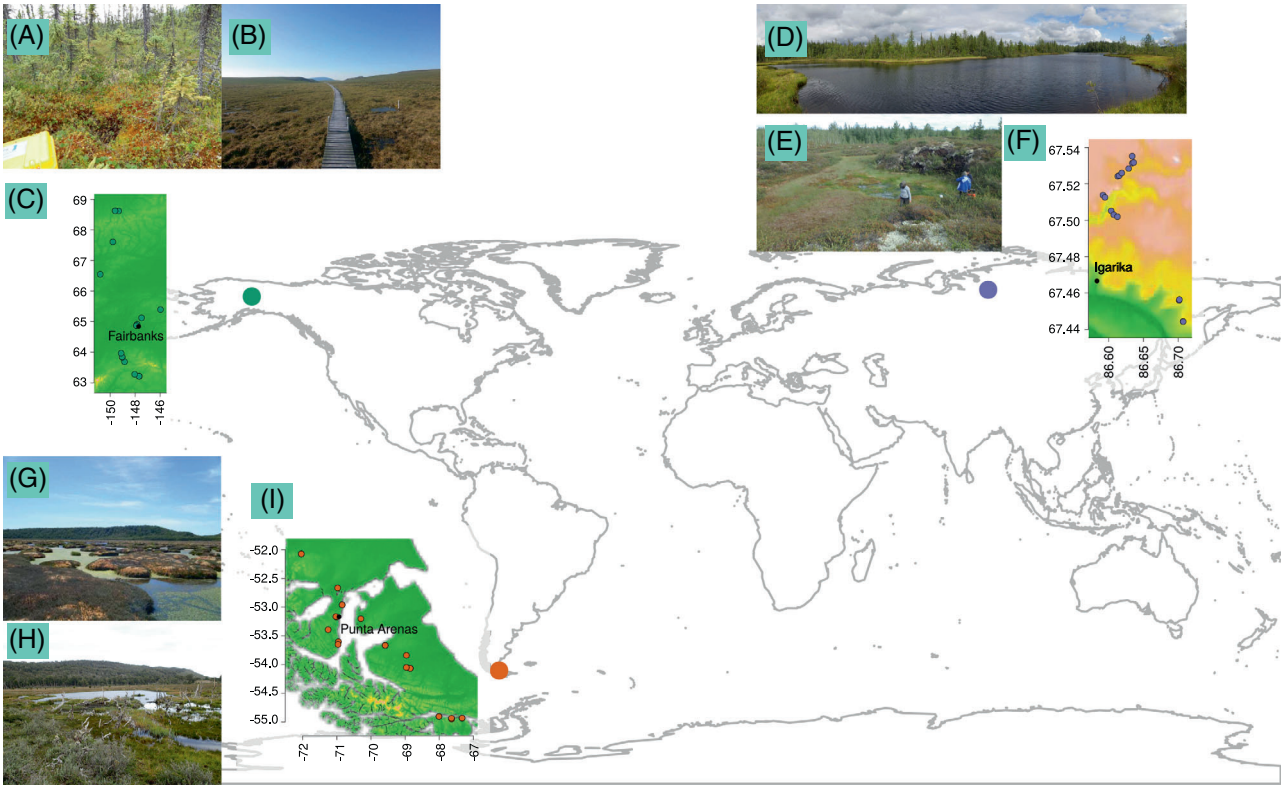

FIGURE 1 Global map showing the location of the sampling regions and pictures of some characteristic studied ecosystems (Alaska: A, B, C; Siberia: D, E, F; Patagonia: G, H, I). The three sub-maps (C, F, I) show the sampling sites locations. The colour scales of the sub-maps (from green to light pink) 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 CH_4 concentrations (diss_CH4) and CH_4 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 (Schuur 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 (CCCCGYCAATTCMTTTRAGT; 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*, *Methanimicrococcus*, *Methanococcoides*, *Methanohalobium*,

Methanohalophilus, *Methanolobus*, *Methanomethylovorans*, *Methanosalsum*, *Methanosarcina*, *Methermicoccaceae*, Methanomethyliales, Methanomassiliicoccales, 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 methylotroph *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 sub setting 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 assignation 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 (Bapteste 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 biassed 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).

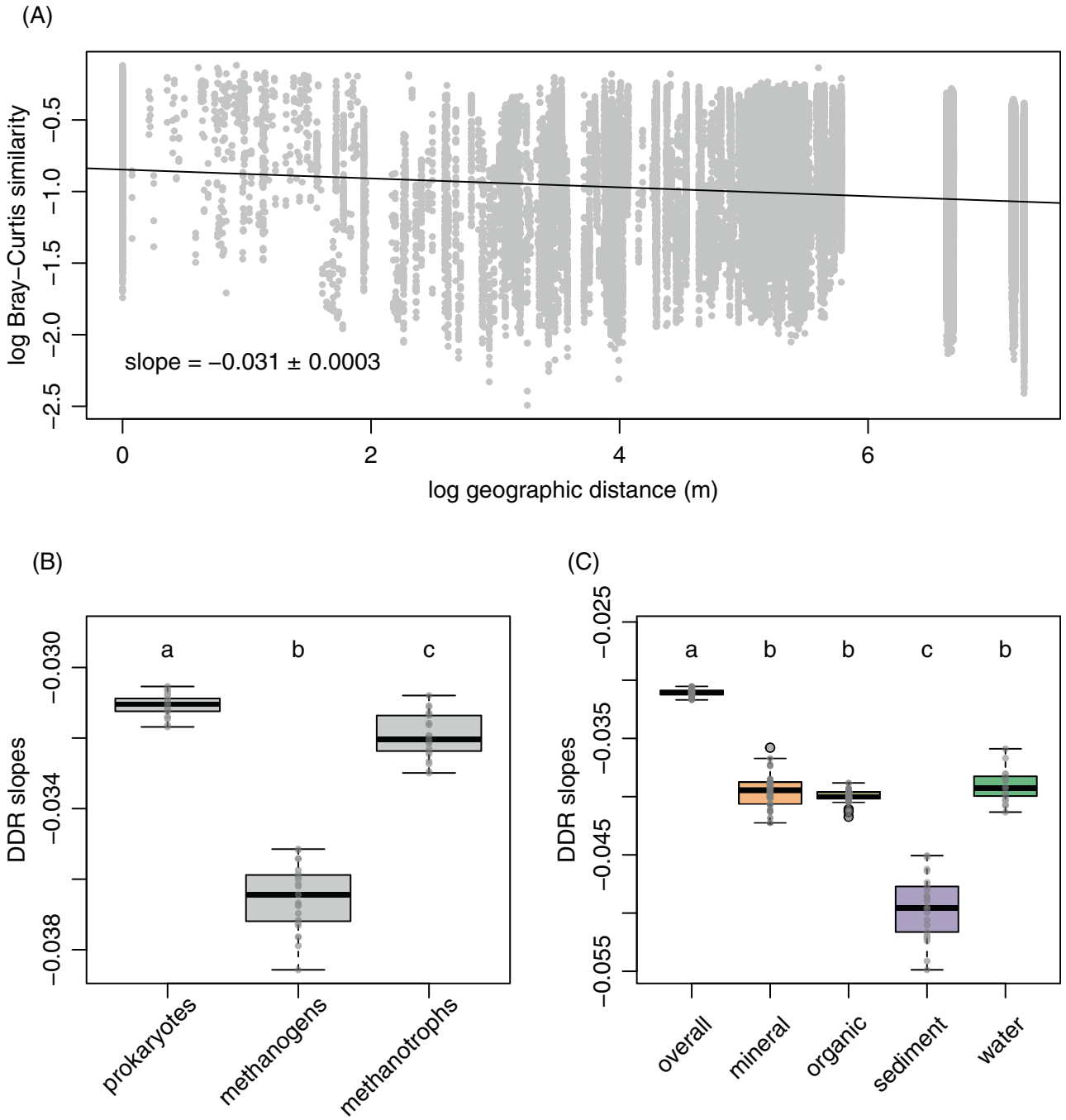

FIGURE 2 (A) Distance decay relationship (DDR) of 387 prokaryotic communities retrieved from four habitats (mineral soils, organic soils, sediments and waters) in Northern Siberia, North-central Alaska and Southern Patagonia. (B) Distribution of DDR slopes for the prokaryotic, methanogenic and methanotrophic 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% w/w ± 20% SD) than in other habitats (organic soils: 14% ± 12% SD, sediments: 17% ± 18% SD, water: $1*10^{-4} \pm 3*10^{-4}$, 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

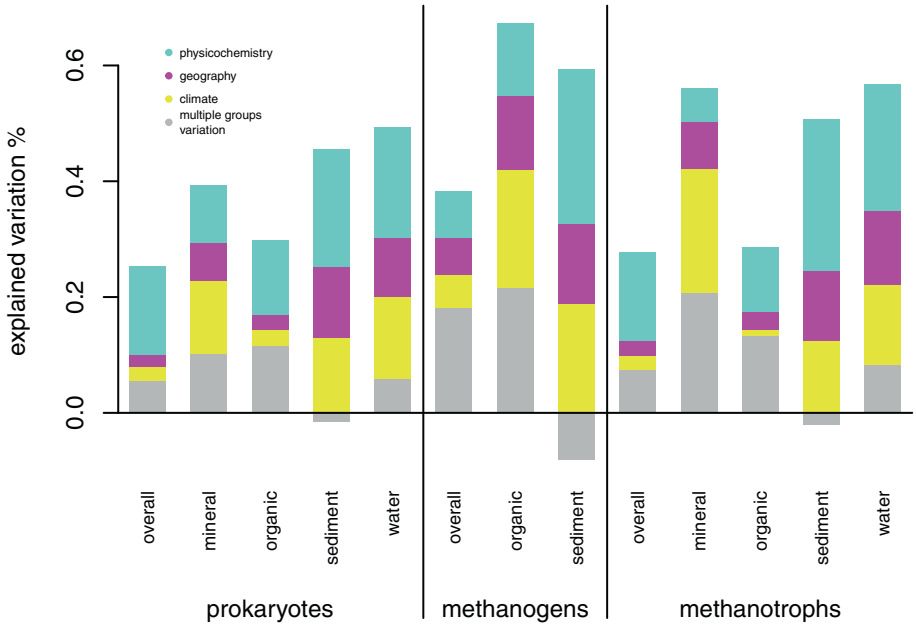

FIGURE 3 Variation partitioning analysis showing the variation explained exclusively by physicochemistry, geography and climatic variables for prokaryotic, methanogenic and methanotrophic communities retrieved in four habitat types (mineral soils, organic soils, sediments and waters) from Northern Siberia, 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, Jassey 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

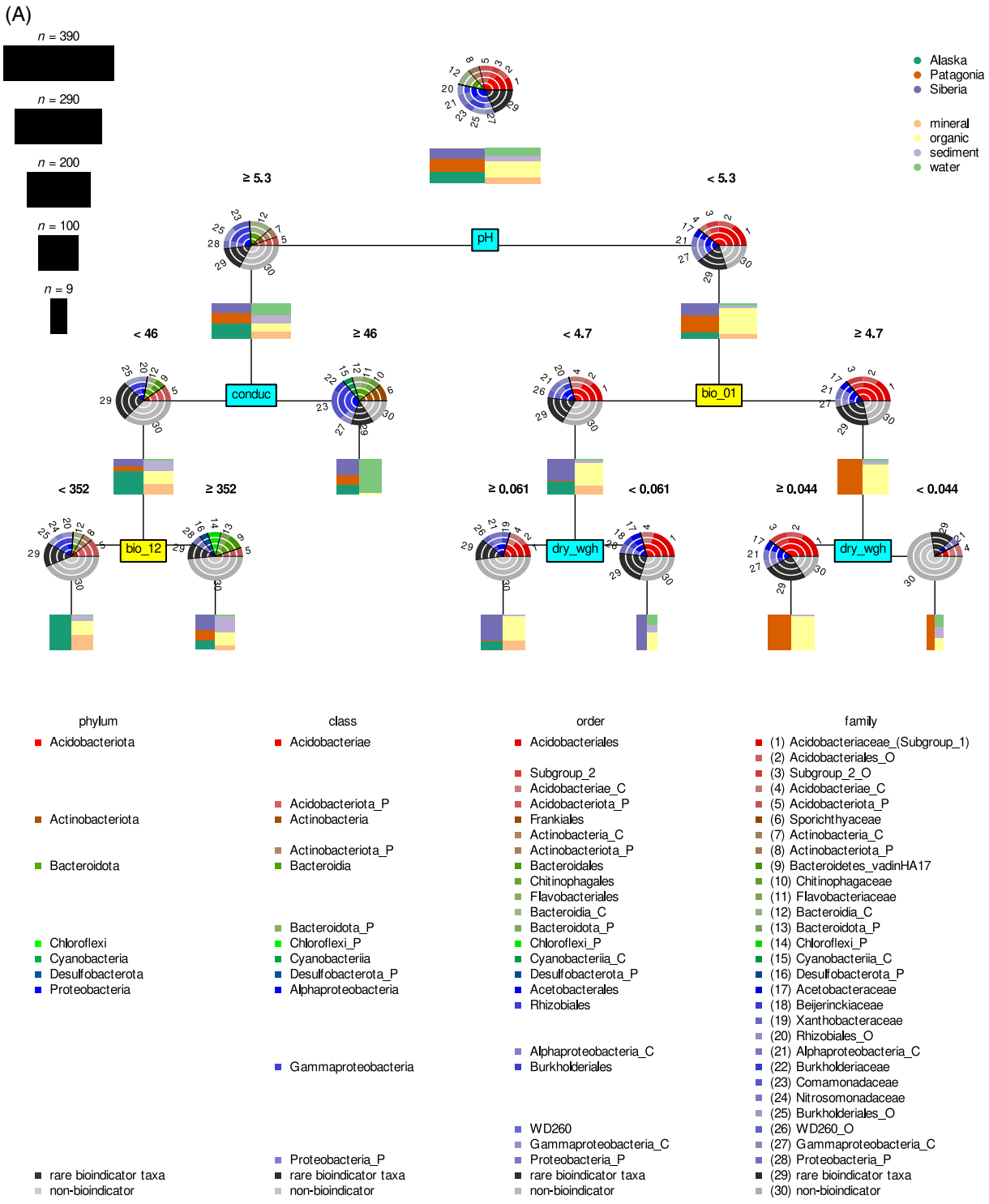

FIGURE 4 Multivariate recursive partitioning tree (MRT) from 387 prokaryotic communities (A, only Bacteria shown here), 125 methanogenic communities (B) and 261 methanotrophic communities (C) from all habitats (mineral soils, organic soils, sediments and water) and all regions (Northern Siberia, North-central 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.

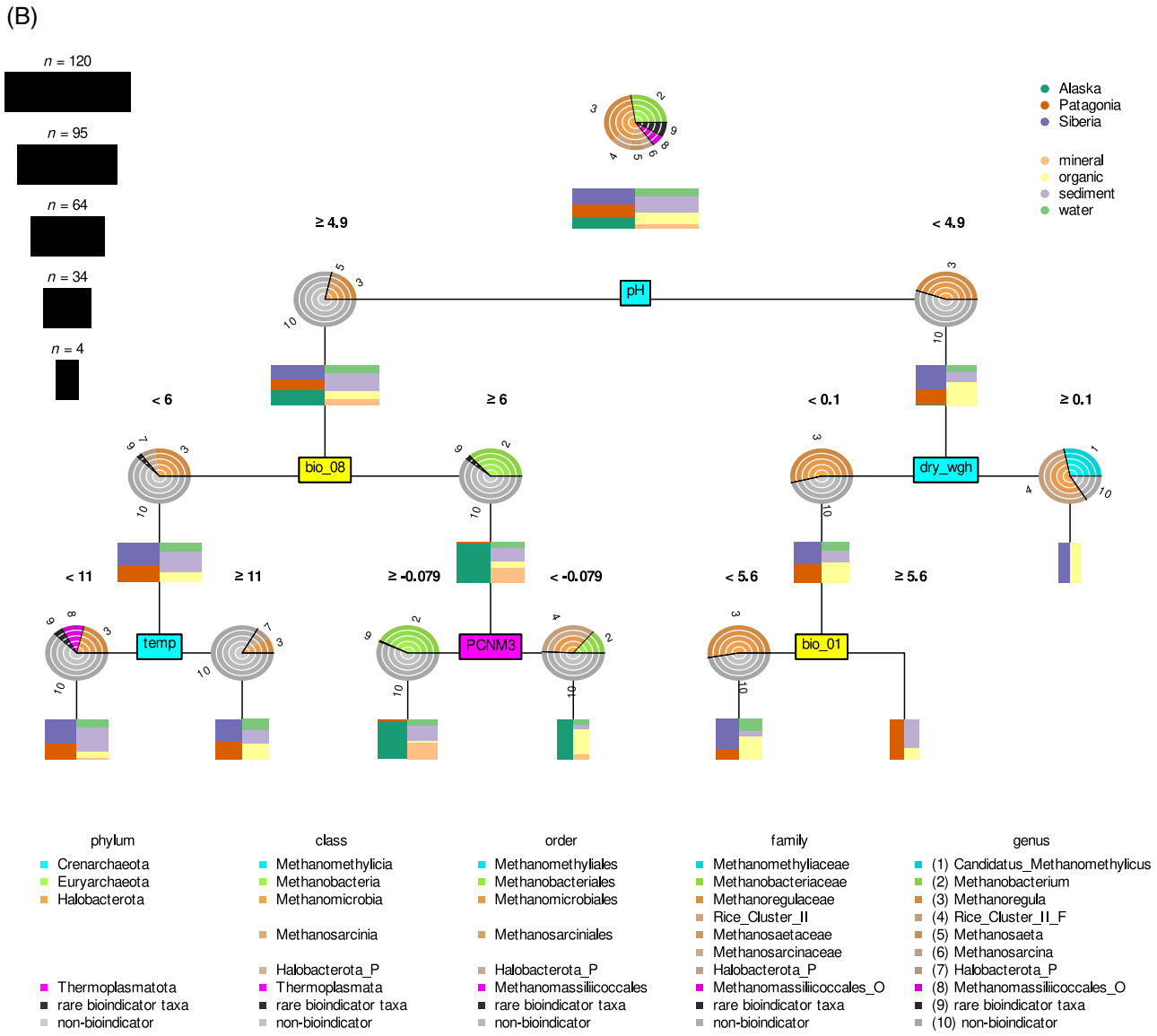

FIGURE 4 (Continued)

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 CH_4 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).

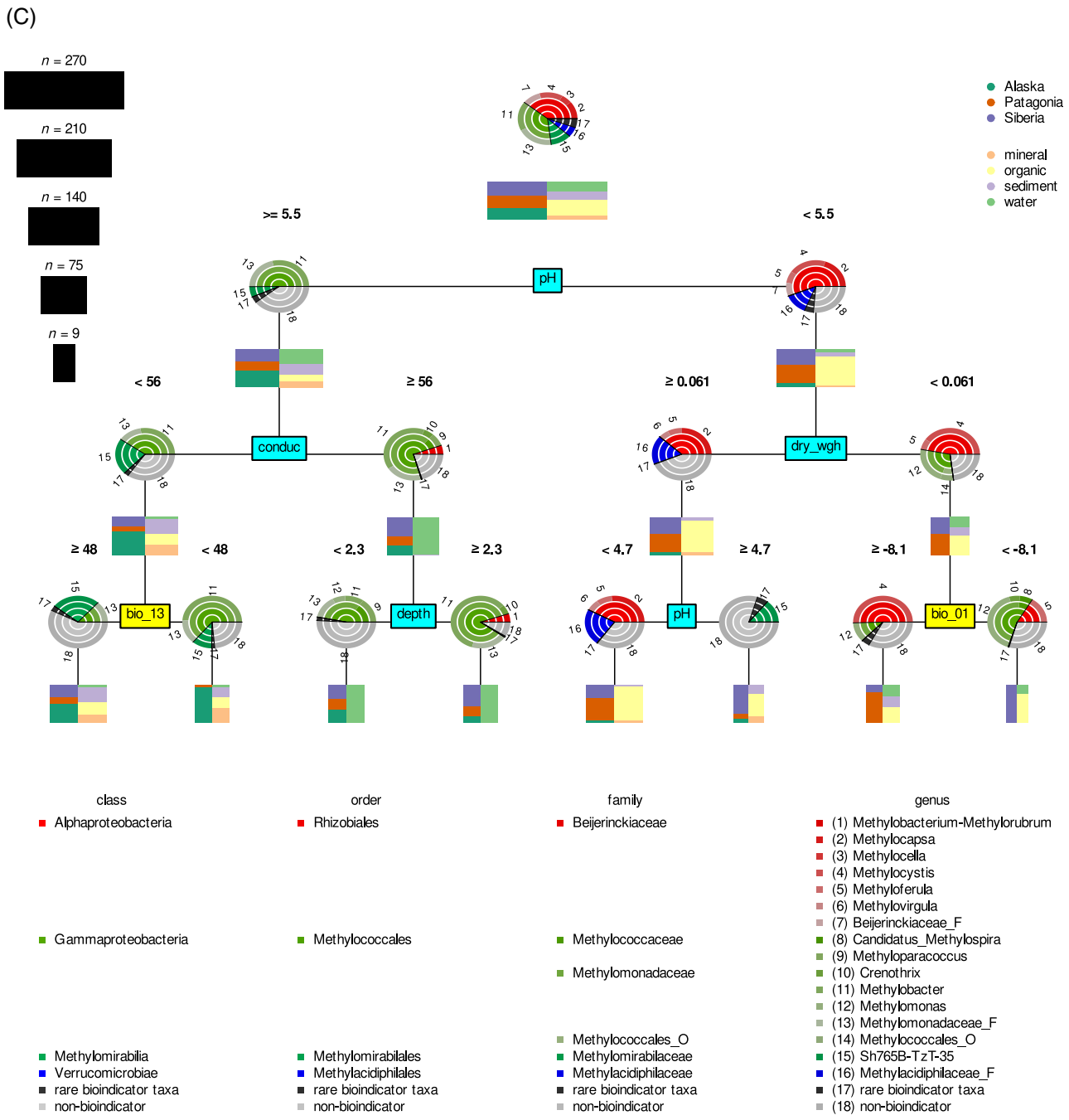

FIGURE 4 (Continued)

In situ temperature only occurred as a determinant at a lower level (third rank) in the methanogenic guild. It mainly separated lake sediments (<11°C) from wetland soils (>11°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 CH_4 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 CH_4 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. Methanoregulaceae 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°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°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. palsarum* (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 CH_4 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 CH_4-oxidiser *Methylomirabilaceae* as bioindicators).

Prokaryotic bioindicators

Several prokaryotic bioindicators identified in the Bacteria MRT can act as partners of CH_4-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 CH_4 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). Bathyarcheota 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 CH_4 cycle either as acetate producer (He et al., 2016; Lazar et al., 2016), or more directly as a potential methanogen or anaerobic CH_4 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 (Schuur 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 CH_4 emissions (Schuur 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 CH_4 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 CH_4.

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

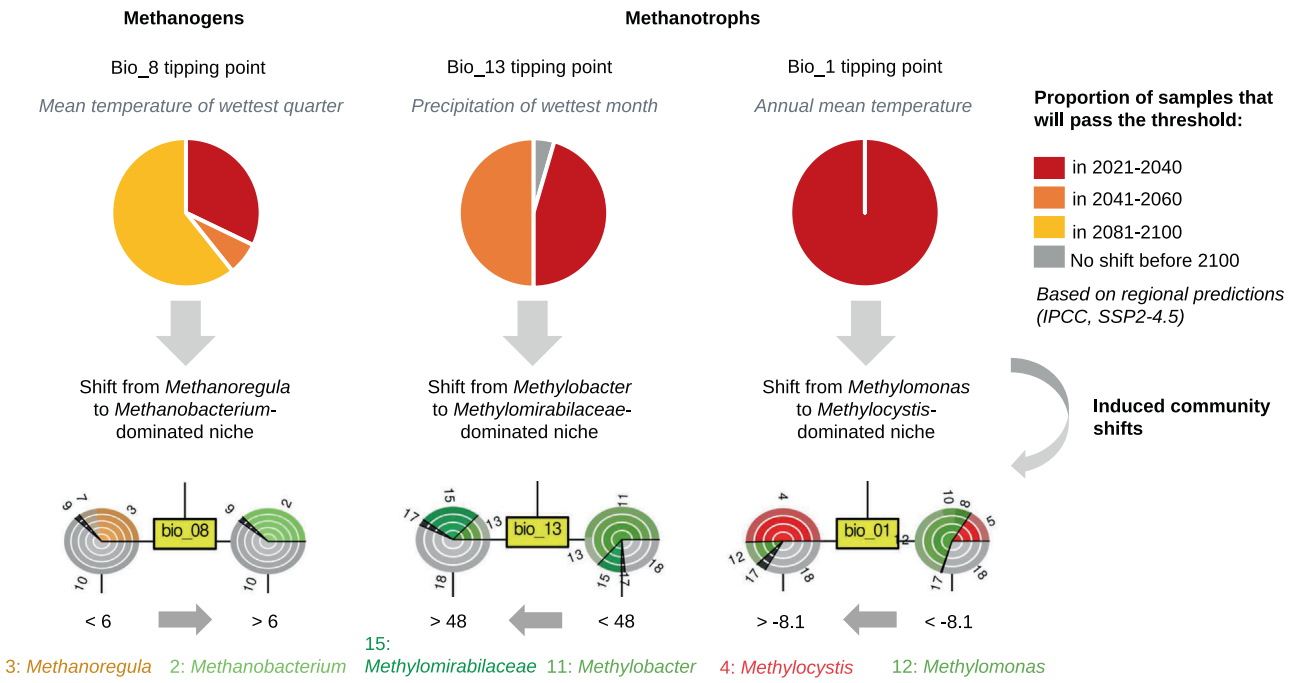

FIGURE 5 Predictions of community shifts with climate change. The top pie charts show the percentage of samples currently below the tipping point for bioclimatic variables 1, 8 and 13 in methanogenic and methanotrophic MRT trees (Figure 4B,C) that are expected to pass the corresponding climatic threshold 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 (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 (conduc <56 μS/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 CH_4 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 CH_4 cycling microbes under climate change projections. These results gave insight into the present and future contributors and processes of the CH_4 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 Seppey: 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).

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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.

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SUPPORTING INFORMATION

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