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Review

Microbial Communities in Methane Cycle: Modern Molecular Methods Gain Insights into Their Global Ecology

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Abstract: The role of methane as a greenhouse gas in the concept of global climate changes is well known. Methanogens and methanotrophs are two microbial groups which contribute to the biogeochemical methane cycle in soil, so that the total emission of CH_4 is the balance between its production and oxidation by microbial communities. Traditional identification techniques, such as selective enrichment and pure-culture isolation, have been used for a long time to study diversity of methanogens and methanotrophs. However, these techniques are characterized by significant limitations, since only a relatively small fraction of the microbial community could be cultured. Modern molecular methods for quantitative analysis of the microbial community such as real-time PCR (Polymerase chain reaction), DNA fingerprints and methods based on high-throughput sequencing together with different "omics" techniques overcome the limitations imposed by culture-dependent approaches and provide new insights into the diversity and ecology of microbial communities in the methane cycle. Here, we review available knowledge concerning the abundances, composition, and activity of methanogenic and methanotrophic communities in a wide range of natural and anthropogenic environments. We suggest that incorporation of microbial data could fill the existing microbiological gaps in methane flux modeling, and significantly increase the predictive power of models for different environments.

Keywords: methane; greenhouse gases; microbial communities; high-throughput sequencing; mcrA; pmoA; methanogens; methanotrophs

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1. Introduction

The global methane cycle is one of the basic components of the total biogeochemical carbon cycle directly influencing the climate on Earth [1–3]. Methane is considered the second most important greenhouse gas in the atmosphere. Its concentration is directly correlated with anthropogenic activity [4,5]. According to various estimations, methane accounts for 16–30% of the radiative forcing by long-lived greenhouse gases [6,7]. Additionally, the growth of CH_4 content in the atmosphere is associated with about half of the increase in the concentration of tropospheric ozone adversely affecting living organisms [8]. Before the industrial age, methane concentration in the atmosphere was ca. 700 ppb, whereas it reached 1845 ppb in 2016 [9]. In the last three decades, the growth rate of atmospheric methane concentration varied significantly stimulating interest in factors controlling the global methane budget [10]. The total annual methane emission from all sources was calculated to be 600 Tg, with natural and anthropogenic sources accounting

for 40 and 60%, respectively [4,5,11]. Natural methane sources are soil (mostly soil of wetlands), lake sediments, oceans, termites and some geological sources (seeps, microseeps, mud volcanoes and methane hydrates). Plant cover could also valuably contribute to the total methane dynamics of the landscape [12–15]. Wetlands are the potent source of CH_4 accounting for 62% of the natural sources the total methane emission into the atmosphere. Anthropogenic sources are rice fields, ruminants, landfills, biomass burning and combustion of fossil fuels [2].

The main microbial agents responsible for biological methane production are methanogenic archaea operating under anaerobic conditions [16]. Classically, methanogens belong exclusively to Euryarchaeota. However, the genes that encode the key enzymes of methyl-reducing methanogenesis were detected in the genomes of archaeal candidate phyla "Candidatus Bathyarchaeota" and "Candidatus Verstraetearchaeota" which are phylogenetically distant from Euryarchaeota [17–21]. Methanogens are not able to consume complex organic compounds themselves and need close symbiotic relationships with bacteria producing either acetate (acetogens), or carbon dioxide and hydrogen (synthrophs), or methylated compounds such as methanol, methylamines and methyl-sulfides [22,23]. Chemical structure of each methane precursor defines, in turn, four main methanogenic pathways: acetoclastic, hydrogenotrophic, methylotrophic and methyl-reducing [2,20,24,25] (Table 1). In addition, there are several recently discovered pathways of methane production in aerobic conditions by various bacterial species from methylated compounds such as phosphonates [26,27], methylated-sulfur compounds [28], and methylamines [29]. Marine algae, freshwater and marine Cyanobacteria could produce methane as a byproduct of photosynthesis [30–32].

The final methane flux is also dependent on the activity of methanotrophs using methane as a carbon and energy source. Currently, methanotrophs belong to phyla Gammaproteobacteria (also known as type I), Alphaproteobacteria (type II) and Verrucomicrobia (type III). The *pmoA* gene encodes the large subunit of the copper- or iron-containing oxidoreductase enzyme, methane monooxygenase (MMO); it is most commonly used as a marker for methanotrophs [33]. *pxmA* is a gene marker of uncultured methanotrophs [34–37]. Type I methanotrophs assimilate C via the ribulose monophosphate pathway, while type II methanotrophs use the serine pathway [34]. Methanotrophs belonging to Verrucomicrobia are autotrophic and use methane as an energy source [38]. The most detailed description of aerobic methanotrophs is done in the review of Knief and co-workers [36]. Anaerobic methanotrophic archaea (ANME) use anaerobic oxidation of methane as an energy source [39].

The effect of methanotrophs on the total methane emission is variable in different publications [40–48]. Classical identification and enumeration techniques, such as selective enrichment and pure-culture isolation, have been long used to study diversity and activity of methanogenic and methanotrophic communities. However, these traditional techniques are characterized by significant limitations, since only a relatively small fraction (less than 1%) of the microbial community can generally be cultured and identified [49]. Therefore, nucleic acids or proteins may be used as the primary source of information for uncultured but viable and active methanogens and methanotrophs. Culture-independent nucleic acid approaches include analyses of whole genomes or selected genes (16S rRNA; *pmoA*, *mmoX*, *mxaF* for methanotrophs; *mcr*, *mtd*, *mth*, *mrt*, *frh* for methanogens) [50,51]. Over the last few decades, a wide variety of molecular techniques have been developed for describing and characterizing the phylogenetic and functional diversity of methanogenic and methanotrophic communities.

In this review, we aimed at compiling and analyzing experimental data on activity and structure of methanogenic and methanotrophic communities in various natural and anthropogenic environments obtained by modern molecular biological methods such as:

- New generation (high throughput) sequencing (NGS);
- Real-time PCR, or qPCR (RT-PCR);

- DNA-stable isotope probing (DNA-SIP).

Table 1. Main biochemical reactions of methanogenesis and methanotrophy [20,33,52–54].

Methanogenesis Pathway	Biochemical Reaction	ΔG⁰', kJ/mol CH4	Taxa
Acetoclastic	$CH_3COO^- + H_2O \rightarrow CH_4 + HCO_3^-$	−31	Phylum Euryarchaeota, order Methanosarcinales (genera *Methanosarcina, Methanothrix* (*Methanosaeta*))
Hydrogenotrophic	$4H_2 + HCO_3^- + H^+ \rightarrow CH_4 + 3H_2O$ $4HCOO^- + H^+ + H_2O \rightarrow CH_4 + 3HCO_3^-$	−135 −145	Phylum Euryarchaeota, orders Methanosarcinales, Methanobacteriales, Methanococcales, Methanomicrobiales, Methanopyrales, Methanocellales
Methylotrophic	$4CH_3OH \rightarrow 3CH_4 + HCO_3^- + H_2O + H^+$ $4CH_3NH_2 + 2H_2O \rightarrow 3CH_4 + CO_2 + 4NH_3$	−104 −75	Order Methanosarcinales (family *Methanosarcinaceae*)
Methyl -reducing	$CH_3OH + H_2 \rightarrow CH_4 + H_2O$	−113	Order Methanobacteriales, Methanomassiliicoccales
Methane Oxidation Pathway	**Biochemical Reaction**	**ΔG0', kJ/mol CH4**	**Taxa**
Aerobic methane oxidation	$CH_4 + 2O_2 \rightarrow CO_2 + 2H_2O$ $CH_4 + O_2 + 2e^- + 2H^+ \rightarrow CH_3OH + H_2O$	−778 −322 (sMMO) −284 (pMMO)	Type I (phylum γ-proteobacteria, order Methylococcales, family *Methylococcaceae*) Type II (phylum *α*-proteobacteria, families *Methylocystaceae, Beijerinckiaceae*) Type III (phylum Verrucomicrobia, class *Methylacidiphilum*)
Anaerobic methane oxidation	$CH_4 + SO_4^{2-} \rightarrow HCO_3^- + HS^- + H_2O$	−16.6	anaerobic methanotrophic archaea (ANME, clusters 1—order Methanosarcinales, 2—order Methanomicrobiales, 3—order Methanococcoides)
Nitrite-dependant methane oxidation (N-DAMO)	$3CH_4 + 8NO_2^- + 8H^+ \rightarrow 3CO_2 + 4N_2 + 10H_2O$	−928	Candidatus phylum NC10 (*Methylomirabilis oxyfera*) Archaea: Candidatus "*Methanoperedens nitroreducens*"

In our review, we focused mostly on publications where any correlation between physicochemical parameters of methane cycle measured in field experiments and molecular data on methanogenic and methanotrophic communities functioning in the same research sites was established. We also considered landscape and ecological features of ecosystems which can influence the structure of microbial communities.

2. Natural Sources of Methane

2.1. Soils

Cell counting in samples from different soils revealed that methanogens and methanotrophs are successfully coexisting in different environments [55,56]. Coupling of methanogenesis and methanotrophy in aerated soils as well as high sensitivity of microorganisms driving these processes to environmental conditions are the reasons of temporal and spatial variability in emission or consumption of methane in soils. This fact should be always taken into account in estimations of contribution of various soil ecosystems to methane turnover [57].

Methanogenesis and methanotrophy are strongly dependent on soil water regime, organic carbon and total nitrogen in the environment [58]. Extremely low soil moisture reduces the rate of both microbial processes [59–63]. Decrease in soil sample moisture by 10% results in reduction in methane oxidation by 1.2–1.3 times due to moisture deficit stress or accumulation of mineral nitrogen compounds in soil [64]. Soil waterlogging favors the development of methanogens and declines the number of methanotrophs because of reduction in the size of aerobic zones. In all types of soils studied, the maximum rates of methane oxidation were detected at moderate moisture [65–70].

A negative logarithmic correlation has been established between the water table level and soil methane emission: the lower the water table level, the higher the rate of methane oxidation and hence the lower the rate of methane emission [71]. In arctic coastal plains, the rate of methane production in water-logged sites was 12 times higher than that in sites where the water table level was 5 cm below the soil surface [72]. These results were predictable since the low water table level was associated with more oxidative conditions in the upper soil layers and facilitated diffusion of atmospheric oxygen and methane to soil. The rate of methane oxidation is also significantly decreased at very low soil moisture conditions [58,60,73].

Optimal temperature for methane production by certain microorganisms correlates with climate conditions of their habitat. In support of that fact, the optimal temperature increased from 19 to 38 °C along the direction from north to south [74]. At low soil temperature, the rate of methane production decreases due to reduced activity of both methanogens and other microbial groups composing the methanogenic community. Methanotrophs seem to be less sensitive to temperature, than methanogens. The relationship between temperature and methane oxidation rates in soil is mostly uncertain. The clear correlation between these parameters can be observed at temperatures lower than 10 °C or higher than 40 °C, presumably owing to the decrease in activity of mesophilic methanotrophs [75–77].

The assertion that the highest activity of methanogens is observed in soil at neutral or slightly alkaline pH and is very sensitive to changes in pH values was recently prevalent because of the lack of data on isolation of acidophilic methanogens [55]. Intensive studies of methanogenesis and methane emissions in acidic oligotrophic and mesotrophic bogs as well as in lakes led to the conclusion that soil pH may play only a small role in spatial variability due to the adaptations of microbial communities to local average pH [78–81].

Methane oxidation was proved to occur in various soil ecosystems in a wide range of pH conditions [82–86]. This fact can be explained by adaptation of methanotrophic bacteria or the whole microbial community to slowly varying pH values in an ecosystem. In other words, microbial communities developing in acidic soils oxidize methane with rates almost similar to those in neutral or slightly alkaline soils. However, methanotrophs can be quite sensitive to pH in case of deviation from its optimum values in a certain site. As an example, methanotrophs in clay-loam soil were highly sensitive to pH decreasing from 8.0 to 7.1 caused by nitrification of ammonium fertilizers [87]. Deviation of pH by 1.0 from its original level of 6.8 resulted in a reduction in methane oxidation [88]. Thus, methane-oxidizing activity is affected by either deviation of pH from its optimum specific level to

the predominant methanotrophic species (directly) or changes in composition of nitrogen transformation products (indirectly).

Nitrifying capacity of methanotrophs and participation of chemoautotrophic nitrate bacteria in methane oxidation suggest nitrogen soil regime parameters as the key factors for regulating microbial oxidation of CH_4 [89]. Ammonium nitrogen is a competitive inhibitor of methane oxidation. Moreover, its inhibitory effect can be enhanced by hydroxylamine and nitrate formed as a result of NH_4^+ oxidation by methanotrophs [87]. Nitrates can also suppress microbial methane-oxidizing activity by transforming into nitrites in the process of denitrification. Although the contribution of nitrifying bacteria to methane oxidation is estimated to be minor, their influence on the methane-oxidizing capacity of soil is generally recognized [90].

Soil use in the farming industry leads to reducing the methane-oxidizing capacity of soil. It can be due to several reasons such as destruction of ecological niches inhabited by methanogenic and methanotrophic microbial communities, impeded permeability of water and air in soil as a result of use of soil-tilling implements, disruption of mineralization and immobilization turnover of nitrogen after mineral fertilization and changes in other physicochemical soil parameters [91].

Water and temperature regimes, acidity, mineral composition, granulometric texture and some other soil characteristics are used for building models predicting methane cycle dynamics. Such models are in strong demand because of the great importance of methane for the climate system of the Earth. The simulation results on methane emissions into the atmosphere can be used by climatologists for predicting global climate changes since it is impossible to make in situ measurements of the rates of CH_4 fluxes at every relevant geographic site. Nevertheless, these models do not take into account the composition and the functional structure of methanogenic and methanotrophic microbial communities [2]. The majority of models consider the microbial community as a "black box" so that characteristics attributable to microorganisms in soils are not included in the calculations due to ambiguity and inhomogeneity of such data. However, there is an increase in the number of publications pointing out the importance of data on microbial communities for developing predictive models describing more adequately the in situ situation [2,92]. Modern molecular "-omics" technologies bring about great opportunities to quantitatively evaluate the temporal dynamics of microbial communities [93,94]. There is an immense amount of data on methanogenic and methanotrophic microorganisms in the literature. By now, main groups of methanogens in different soil types are identified. In most cases, the majority of methanogens found were assigned to the genera *Methanosarcina* and *Methanocella* as well as to class Methanobacteria to a smaller extent [95,96]. In forest soil, orders Methanococcales and Methanomicrobiales and *Methanocella spp.* were detected to be dominant methanogens whereas *Methanosarcina* was less abundant compared to other soil types [97].

Molecular biology studies have revealed significant changes in the structure of methanotrophic microbial communities in arid and semiarid ecosystems [98]. The results of such studies are of a great importance since arid and semiarid zones account for ca. 50% of the terrestrial part of the earth. Nevertheless, most of the current global models either simply ignore or underestimate the role of these ecosystems in the methane cycle [99,100].

Potential CH_4 oxidation rate was linked with the composition and the abundance of methanotrophs from 21 sites at the regional scale across three steppes of China analyzed by quantitative PCR and high-throughput sequencing techniques [101]. In this study, type I methanotrophs were predominant in soils from the Inner Mongolia steppe and Xinjiang Autonomous Region, whereas *pxmA* methanotrophs were mainly distributed in the Tibetan alpine steppe soil. The authors revealed that at the regional scale, total nitrogen was the environmental variable mainly explained the potential CH_4 oxidation rate, and its influence was associated with its effects on plant growth and methanotrophic community traits [101].

Another study was carried out in a young Arctic landscape on Disko Island (West Greenland), where *in situ* fluxes of CH_4 between upland and wetland soils and potential rates of CH_4 oxidation and production were integrated with the abundances and diversity of the methanotrophs and methanogens measured with pyrosequencing of 16S rRNA gene and rRNA fragments in soil and permafrost layers [102]. The magnitude of CH_4 oxidation and the direction of the flux were linked to different methanotrophic communities in upland and wetland soils. In the active layer of upland soils, only activity of Type II methanotrophs was detected, whereas the active layer of the wetland soils possessed both Type I and Type II methanotrophs. In addition, the observed link between production/consumption rates and the microbial abundance and activity indicated that the age of an Arctic landscape could play an important role for CH_4 production [102]. In upland tundra soils, high-affinity USCα methanotrophs (belonging to Type II) dominate the methane-oxidizing community; these bacteria inhabit a thin organic layer of soil and provide atmospheric CH_4 sink from −0.4 to −0.6 mg CH_4-C m^{-2} day^{-1} [103].

2.2. Wetlands

Wetlands are the most active sources of methane among natural ecosystems due to their permanent waterlogging favorable for methanogenic microorganisms. According to various estimations, wetlands contribute from 20 to 39% to the total atmospheric methane, and their potential increase due to the climate warming could be 50–80% [104,105]. The rate of methane production varies significantly depending on wetland and vegetation types, acidity, organic matter content, mineral composition and climate. The influence of the above factors are considered in detail in different reviews [55,106–109].

Several studies have shown that water level and temperature are the key factors affecting the activity and community of both methanogens and methanotrophs in peatlands [110–112]. Impacts of warming in different moisture regimes on the activity and community of methanogenic and methanotrophic communities are not straightforward [113].

The analysis of 16S-rRNA revealed specific features of localization of methanogens and methanotrophs within a wetland biocenosis. Methanogens were negatively correlated with nitrate-, sulfate-, and metal-reducing bacteria and were most abundant at sampling sites with the highest methane production. Besides, microbial phylogeny based on marker genes as well as quantitative analysis of data obtained by shotgun sequencing gave insights into competitive relationships between methanogens and other anaerobic microorganisms. It has been shown that anaerobic competitors can suppress methanogenesis [104].

2.3. Aquatic Environments

The authors studying methanogenesis and methanotrophy deal mostly with three basic water ecosystems such as oceans/seas (salty water), lakes/rivers (fresh water) and estuaries (mixture of salty and fresh waters). These ecosystems differ significantly from each other in relation to microbial community structures and, hence, to biochemical pathways leading to methane production and consumption. This is the reason why most studies are focused on only one particular water ecosystem.

Marine environments produce relatively small amounts of methane (0.7–1.4 Tg $year^{-1}$) [114]. Moreover, almost all CH_4 produced in marine sediments is consumed anaerobically in adjacent water layers. A small part of methane can pass to the upper layers and is further oxidized by aerobic methanotrophs [39]. This natural bacterial trap limits escaping methane from the sediment to the atmosphere [115–118]. Methane could also be produced in upper oxygenated water layers from methylated compounds in case of limited nutrient supply [26,28]. Additionally, some portion of methane formed in the sediments is converted into gas hydrates.

Microbial communities responsible for biochemical processes leading to formation of gas hydrates are being now intensively studied by modern molecular methods. The sediment samples from the eastern part of Pacific Ocean were examined for both methane

production and structure of methanogenic and methanotrophic microbial communities [119]. Sequencing of functional genes specific for methanogens (methyl coenzyme M reductase (*mcrA*)) and methanotrophs (methane monooxygenase subunit A (*pmoA*)) in extracted DNA samples allowed for proper identification of all agents driving these microbial processes. The results of the study indicated that the samples taken from different depths differed both in methane production rates and microbial community structures. The highest (0.016 mg $m^{-2}day^{-1}$) and the lowest (0.0026 mg $m^{-2}day^{-1}$) rates of methanogenesis were observed in the samples from the depths of 550 and 300 m, respectively. The analysis of the *mcrA* gene sequences revealed that *Methanococcoides*-like microorganisms were predominant in all samples independently of the sampling depth. Additionally, the representatives of some other methanogenic taxa were found at different depths: Methanosarcinales (222 m), Methanomicrobiales and Methanocellales (650 m). Phylogenetic analysis of methanotrophic microorganisms made by sequencing *pmoA* genes showed that most of the sequence variants belonged to uncultivated species of the type 1 marine methanotrophs. The representatives of the family *Methylococcaceae* including species of genera *Methylococcus* and *Methylomonas* have also been identified. In contrast to methanogens, any substantial changes in the structure of the methanotrophic community along the sampling depth were not observed.

In situ measurements of production and oxidation of methane have also been made in other marine ecosystems. Kruger with co-authors studied these processes in eight locations in the Arctic, Atlantic and Pacific oceans as well as in the North and Baltic seas, whereas Crill and Martens published the results of their measurements in the gulf of Cape Lookout Bight [114,120]. Importantly, the results obtained by different researchers in various ecosystems and at different times are quite similar in terms of their values.

Analysis of methane turnover in sediments of the Aarhus Bay, Denmark, revealed that methane emission varied within a year from 0.035 mg m^{-2} d^{-1} in December to 0.34 mg m^{-2} d^{-1} in May [121]. Besides, the analysis of the 16S rRNA sequences was made to identify the microbial community structure in this environment. Archaeal community was represented by phyla Woesearchaeota, Euryarchaeota, Thaumarchaeota and Bathyarchaeota. Methanogens belonging to Euryarchaeota accounted for ca. 1.4% from the total amount of archaea detected, with their absolute number being decreased along the sediment depth. Methanogens were not detected at the depth of 13 cm and below. Most of the 16S rRNA sequences were identified with Methanomicrobiales, Methanococcoides and Methanococcus. Methylotrophic and hydrogenotrophic methanogens were predominant in the samples, whereas acetoclastic methanogens were rare.

No correlation between the structure of the microbial community and the rate of methanogenesis or methanotrophy was found in any study mentioned above. The most likely reasons for that are low spatial resolution and lack of information on the classification of microorganisms [121].

In contrast to marine environments, freshwater ecosystems are the main sources of atmospheric methane [122]. Estimations of the total methane emission from 733 lakes located to the north of 50° N give an approximate value of 16.5 Tg $year^{-1}$ [123]. Methane is oxidized anaerobically in both freshwater and marine environments with the participation of certain microorganisms using different terminal electron acceptors such as SO_4^{2-}, NO_3^-/NO_2^-, Fe^{3+} and Mn^{4+} [124–128]. In contrast with marine ecosystems, the influence of anaerobic methane oxidation on CH_4 emission from freshwater environments is poorly studied and differently interpreted.

Rissanen and co-workers used the label dilution method to measure the rates of methanogenesis, methanotrophy and methane emission in two boreal mesotrophic lakes [129]. They found that anaerobic oxidation of methane insignificantly influenced the methane emission in these lakes. Other researchers using the same method revealed that the anaerobic methane oxidation accounted for ca. 15% of the total methane production or was proportional to the whole amount of CH_4 produced [126–128,130].

According to many researchers, the determination of the structure of microbial communities driving methanogenesis and methanotrophy is necessary for proper explanation of the observed scatter in results. The main modern method used to determine the community structure is the next-generation sequence (NGS). The analysis of 16S rRNA sequences allows for the description of taxonomical composition of bacteria and archaea participating in the methane cycle whereas the analysis of *mcrA* and *pmoA* genes enables detecting and quantifying the potential activity of these microbial groups. For example, the most abundant methanogens in the sediments of boreal lakes were representatives of the family *Methanobacteriaceae* driving hydrogen-dependent methanogenesis [129]. The abundance of acetoclastic family *Methanosaetaceae* and hydrogenotrophic family *Methanoregulaceae* increased along the depth. Members of phyla Bacteroidetes, Chloroflexi and Deltaproteobacteria represented mostly by families *Desulfobacteraceae*, *Syntrophaceae*, *Syntrophobacteraceae*, and *Syntrophorhabdaceae* were dominant bacteria in both surface and deep sediment samples.

Oversaturation of oxygen-rich water layers with methane was observed for freshwater lakes [29,131]. However, the question about the main source of methane emissions from lake ecosystems (sediments or oxic methane production) remains unsolved [122,132,133]. The contribution of oxic methanogenesis in total methane emission depends on lake size [122]. Methane production has been linked to the photosynthesis of phytoplankton in a phosphorous-depleted meso-to-oligotrophic lake [134]. Methane could also be produced as a byproduct of nitrogen fixation via Fe-only nitrogenase [135]. The study of a pelagic methane-enriched zone in an oligotrophic-mesotrophic lake showed that in the laboratory conditions, methane was mostly generated from methylphosphonate. The analysis of 16S rRNA gene sequences showed that the dominants of the bacterial community in this zone were *Pseudomonas sp.* capable of methylphosphonate degradation using C-P lyases. Notably, no *mcrA* genes were detected using qPCR in the studied zone, suggesting the absence of "classical" methanogenes [27]. Demethylation of methylphosphonates that leads to methane production was also observed in a freshwater lake, but methane was mainly produced by another pathway from trimethylamines [29].

In contrast to marine ecosystems, estuaries are productive sources of atmospheric methane. Their main feature as intermediate ecosystems is the inflow of both fresh and salty waters with the salinity gradient, affecting the microbial community structure. Methanogens, in particular, inhabit mostly fresh zones of estuaries and decrease their number with the increase in salinity [136]. However, the key factor influencing the distribution of methanogens in estuaries is the level of sulfate reduction [137–140]. Sulfate reducers outcompete methanogens for common substrates and hence suppress methanogenesis. Nevertheless, some methanogens use "non-competitive" substrates and can therefore produce methane even at high concentrations of sulfate [141,142]. Moreover, the relationship between methanogens and sulfate reducers competing for common substrates is not limited by this competition and more complicated [143].

Evaluation of the clone libraries and T-RFLP analysis of 16S rRNA genes allowed for the description of the composition of methanogenic and methanotrophic communities in the estuary of the river Juilong River [144]. The major part of the 16S rRNA gene sequences was assigned to genus *Methanosaeta* and orders Methanomicrobiales and Methanosarcinales / anaerobic methanotrophic archaea (ANME). The order Methanosarcinales was predominant in all samples accounting for an average of 51% of the total sequences analyzed and was represented mostly by ANME-2 microbial cluster. The members of genus *Methanosaeta* and order Methanomicrobiales accounted for 21 and 28%, respectively. According to the community profile studied in this ecosystem, acetoclastic and hydrogenotrophic methanogeneses and anaerobic methane oxidation were considered to be the predominant microbial processes in the methane cycle. The analysis of the microbial community from the estuary of the Yangtze River, made by using 454 pyrosequencing and RT-PCR of *mcrA*, also revealed the prevalence of Methanosarcinales and Methanomicrobiales [145].

The study of the microbial community in the estuary of the Severn river (UK) has been conducted by the PCR-DGGE analysis of 16S rRNA genes in ^{12}C- and ^{13}C-DNA (stable isotope probing—SIP). The combination of various molecular techniques and DNA-SIP method allowed for the identification of an active pool of microorganisms in the estuary. In the aerobic and anaerobic zone slurries with ^{13}C-glucose, the prokaryotic populations were dominated by Gammaproteobacteria and Marine Group 1 Archaea, whereas both anaerobic sediment slurries incubated with ^{13}C-acetate showed incorporation into Epsilonproteobacteria and other bacteria, with the sulfate reduction zone slurry also showing ^{13}C-acetate utilization by Miscellaneous Crenarchaeotic Group Archaea. The lower potential energy methanogenesis zone slurries were the only conditions where no ^{13}C-incorporation into Archaea occurred, despite Bacteria being labeled [146].

3. Anthropogenic Sources of Methane

Agricultural activities account for more than 50% of the total anthropogenic methane emission where CH_4 is the product of degradation of organic matter used for human needs. In the calculation of the rates of methane emissions, the values characterizing organic sources of methane such as mass of the animal fodder, the rice field square, the amount of wastes produced and some others are used rather than the mass of organic matter itself.

3.1. Rice Fields

Rice fields account for about 20% of agricultural methane emissions [147]. The structure of methanogenic and methanotrophic microbial communities in rice fields is influenced by various interrelated factors such as soil organic matter content [148,149], soil pH [150–152], texture of soil [153], redox potential of soil [154], fertilizers [98,155,156] and soil temperature [157]. CH_4 emission processes are also affected by diurnal variation [158], seasonal variation [158,159], elevated ozone [160,161] and elevated CO_2 [162] along with management practice such as rice cultivar [12,163], nutrient application [148], water management [164,165] and application of pesticides [166]. The influence of all the above-mentioned factors are reviewed in detail by Malyan with co-workers [167].

The correlation between methane emission and the structure of the microbial community has been established for the rice field before its exploitation, at sowing the field with rice and on day 120 of its growth before the maturity [168]. The rate of methane emission has been measured to increase from 7.2 (before sowing) to 552 mg $m^{-2}d^{-1}$ (maturity). The analysis of 16S rRNA sequences by using RT-PCR revealed that methanogens of genera *Methanosaeta*, *Methanocella*, *Methanosarcina* and *Methanobacterium* accounted for 68.3 to 86.6% of the total number of archaea in the microbial community inhabiting the studied rice field. In the course of the rice maturity, the abundance of methanogens was continuously increasing and reached its maximum by the 90th day of the experiment. The abundance of methanotrophs in the microbial community was much lower and accounted for 0.79 to 1.75% of the total 16S rRNA genes sequences. The representatives of methanotrophs exhibited different dynamics of the population change. The abundance of genus *Methylocystis* (type II methanotrophs) noticeably decreased after the rice sowing, whereas the number of *Methylosinus* and unclassified type II methanotrophs was almost constant during the whole experiment. Genera *Methylocaldum*, *Methylobacter*, *Methylomonas* and *Methylosarcina* (type I methanotrophs) were only rarely detected before the rice sowing and at the early stage of its growth. However, the significant increase in the number of all the above-mentioned methanotrophs has been detected on the 60th day and reached a maximum by days 90 to 120 of rice growth. In the meantime, the abundance of anaerobic methanotrophs was low and accounted for only 0.25–3.27% of the total 16S rRNA genes sequences indicating the negligible role of the anaerobic methane oxidation in the rice field soil. Multiple factor analyses revealed that the ratio of *mrcA*/*pmoA* could be a parameter allowing for the exact prediction of the amount of methane emitted from a rice field into the atmosphere.

In a similar study, the researchers took soil samples at every stage of the rice growth: vegetative, reproductive and maturing. The main result of the molecular analysis was that the microbial community of the rice field was relatively stable at different stages of rice growing. The changes in its composition have only been established at periods of shifting in the agriculture strategy. In another study, the method of radiolabeled carbon has been applied to determine the portion of methane produced via the acetoclastic pathway in the rice fields of North Italy and emitted into the atmosphere [169]. Similar to the above-mentioned study, the structure of the methanogenic community in the Italian rice fields did not change in the whole course of the vegetation period.

The influence of water regime on methanogen community was studied in two paddy soils from rain-fed and irrigated rice fields in Thailand [165]. While chemical characteristics and total CH_4 production from these soils was similar, the slight difference was observed for the methanogenic communities and for the amount of methane produced by aceticlastic and other types of methanogenesis. In rain-fed soil, approximately 30% of methane was produced from CO_2 compared to 45% for irrigated soil; dessication and reincubation in anaerobic conditions lead to higher stimulation of methane production in rain-fed soil. In both soils, *mcrA* gene copy number was similar, while the number of *mcrA* gene transcripts increased significantly after the reincubation. Soil treatments in the laboratory condition influenced the composition of methanogenic communities of both soils: *Methanobacteriales* abundance was highest after desiccation and *Methanosarcinaceae* was highest after desiccation and rewetting. The combination of metagenome- and proteome-based analyses (metaproteogenomics), which allowed the identification of members of methanogens and methanotrophs within the microbial community, gave insight into the physiological potential of the community and enabled the identification of the metabolic pathways in rice phyllosphere and rhizosphere. Based on metagenome data, archaeal rice rhizosphere inhabitants comprised, in particular, diverse methanogens—orders Methanobacteriales, Methanomicrobiales, Methanosarcinales, and Methanocellales. Although the methanogens contributed only about 3% to the total microbial community, numerous proteins of strictly anaerobic archaea were identified and were dominant in the metaproteomes of the root samples. Proteome data analysis showed that methanogenesis was a dominant one-carbon conversion process in the rice root samples. At the same time, alpha- and gamma-proteobacterial enzymes involved in aerobic methane oxidation were detected only in the rice root samples [170].

3.2. Livestock Animals

Molecular "-omics" technologies can be effectively used for estimation of the amount of methane produced in intestinal tracts of various livestock animals, in particular in ruminants. According to a recent report [171], the contribution of ruminant animals in USA to anthropogenic methane emission accounts for 25%. Thus, the reasons for the special attention of the researchers towards rumen methanogenesis are its high productivity and high global population of ruminants. Besides, the rate of methanogenesis in ruminants is the indicator of their health and productivity [172,173]. However, there is scarce information about the effect of amount and type of feeding stuff on the methanogenesis rate [174].

In a number of publications, three major (genera *Methanobrevibacter*, *Methanomicrobium* and *Methanosphaera*) and three minor (genera *Methanosarcina*, *Methanobacterium* and order Methanomassiliicoccales, or Rumen Cluster C) groups of methanogens in ruminants are described [175–177]. In the rumen, methanogenesis is proved to occur mostly via a hydrogen-dependent pathway; other pathways are negligible. The diversity of microbial taxa provides an opportunity for changing over from H_2-dependent methanogenesis to its other pathways (acetoclastic and methylotrophic) in the rumen resulting in reducing methane emissions [175,176].

Presently, different strategies of the reduction in methane emission by ruminants considering the role of various factors such as type of feedstuff, selective breeding of animals, recombinant protein vaccination and some others are discussed [178–185]. First knowledge of the relationship between characteristics of a microbial community and the amount of produced methane has been obtained.

Recently, the whole-genome sequencing of methanogenic strain ISO4-H5 isolated from the ovine rumen has been performed [186]. Shortly after, the draft sequences of genomes of methanogenic archaea *Methanobacterium bryantii*, *Methanosarcina spelaei*, *Methanosphaera cuniculi* and *Methanocorpusculum parvum* were published. These methanogens collectively drive all three basic methanogenesis pathways: acetoclastic, methylotrophic and hydrogenotrophic. The whole-genome sequencing gives insight into functioning methanogenic archaea in natural environments since parameters of a cell can be changed after its isolation [187].

A metabolically active methanogenic community was described in the different rumen fractions of Xiangdong black goats using RNA isolation and further analysis of synthetized cDNA by qPCR and sequencing of archaeal 16S rRNA genes [188]. The metabolically active methanogenic communities differed in four fractions (solid- and liquid-phase, epithelium- and protozoa-associated) and changed with the feeding (before and after weaning, after rhubarb addition). The diversity of methanogenic community increased in epithelium-associated fraction with the goat age from days 1 to 60.

In a number of studies, the effect of sodium nitrate used as a supplement feed on methane production has been revealed [189–193]. The mechanism of the action of sodium nitrate reducing methane production has already been described: nitrate anions decrease availability of H_2 for hydrogenotrophic methanogens and are reduced to nitrite that in turn inhibits growth of methanogens [191,194]. This theory was also confirmed in another study where RT-PCR with the primers specific to different groups of methanogens and methanotrophs in the dairy goat rumen was performed. The researchers found that the use of nitrate as a supplement feed did not lead to a significant change in the abundance of the whole microbial community in the goat rumen. Nevertheless, the portion of methanogens in the community decreased by 20%, whereas the abundance of methanotrophs increased by one third. It was hypothesized that the increase in nitrates in the feed stuff could result in the higher abundance of methanotrophs belonging to clusters Anammox and ANME-2d that in turn would lead to the reduction in methane emission. Importantly, methanotrophs from the above-mentioned clusters were not detected in this study [195].

3.3. Landfills

Solid waste landfills account for 10–19% of the total anthropogenic methane emission into the atmosphere. Studies of landfill methane can be methodologically divided into two main groups: evaluating and modeling methane emission using physicochemical methods and investigating the structure of the microbial communities involved in the methane cycle by modern molecular techniques. The studies where these two methodologies comprehensively complement each other are still deficient, although each direction of the study provides insights into our understanding of the CH_4 cycle processes.

Fielding and co-workers have isolated and identified methanogenic strains *Methanobacterium formicicum*, *Methanosarcina barkeri* and *Methanobacterium bryantii* from landfills [196]. At that time, this discovery initiated the intensive classical microbiological studies of landfills since the implementation of molecular techniques was only at the early stage. Later, Mori and co-workers isolated one more methanogenic archaeon *Methanobacterium pumilus* from a waste-disposal site [197]. Introduction of 16S rRNA sequencing and fingerprinting methods for analyzing the microbial diversity allowed for identifying the major taxa of methanogenic archaea inhabiting landfills: *Methanosarcina*, *Methanoculleus*, *Methanothermobacter* and *Methanosaeta* [53,198–200]. Eventually, *mcrA* gene analysis was confirmed as an alternative phylogenetic tool in the detection and identification of meth-

anogens. In this study, the orders Methanosarcinales, Methanobacteriales and Methanomicrobiales were found to be the dominant methanogens in landfills [201]. Recently, comparative study of 11 landfills in different geographical zones of China has been conducted [202]. The study revealed that hydrogenotrophic methanogens were predominant in all landfills. This finding was confirmed by another study of the methanogenic community based on methyl coenzyme M reductase A gene amplicons. The analysis showed that most clones (92%) were related to the hydrogenotrophic methanogens, Methanomicrobiales. The majority of these retrieved clones were members of the genus *Methanoculleus*. The remaining clones were assigned to the genera *Methanofollis* and *Methanosarcina*. Besides, T-RFLP analysis revealed 22 methanogenic taxa accounting for 69–96% of the microbial community in the landfill.

One of the few studies where physicochemical methods and "-omics" technologies are used as complementary approaches was performed by Lie and co-workers. The researchers found that methane emission from the landfill was correlated with the abundance of type II methanotrophs [203]. It was also shown that small arid landfills (SALs) being semi-aerobic ecosystems emit less methane into the atmosphere, than typical anaerobic landfills. The reason is the increase in methanotrophic microbial population including type II methanotrophs in the presence of oxygen. Thus, the study confirmed the connection of the microbial community structure with the landfill methane emission. Similar regularities are found for the wastewater treatment processes.

3.4. Wastewater Treatment Systems

The capacity of the methanogenic microbial community to degrade complex organic compounds is used in the process of wastewater treatment [204]. Anaerobic microbial processes applied for the treatment of industrial wastewaters are the most cost-effective technologies [205–207]. They are widely accepted for the wastewaters from pulp and paper, food, chemical and petrochemical industries [206,208]. The study of the methanogenic diversity in 10 different wastewater treatment systems by 16S rRNA gene sequencing with the primers specific for archaea was performed by Kuroda and co-workers and revealed the methanogens responsible for the methane production in these environments. The order Methanobacteriales was predominant in all samples and accounted for 9.4 to 97.9% of the total microbial abundance. Methanosarcinales and Methanomicrobiales were also found to be among dominant methanogenic orders accounting for 0.4–43.6% and 0.1–46.8%, respectively [209].

In the study of synthetic soft drink wastewater, three main methanogenic groups specializing in hydrogenotrophic (*Methanobacterium*) and acetoclastic (*Methanosaeta*) methanogenesis as well as nutritionally versatile *Methanosarcina* have been detected by applying 16S rRNA pyrosequencing [210]. The main species of synthrophic bacteria as the important microbial group in the methanogenic community have been also identified.

In contrast to methanogens, the role of methanotrophic bacteria in the wastewater treatment systems is still uncertain. However, recent data clearly indicated their active involving in the process of treatment. Siniscalchi and co-workers have detected the major groups of methanotrophs in a sequencing batch reactor (SBR) and described their cultivation conditions [52]. Moreover, a new species of methanotrophs, *Candidatus Methylomirabilis oxyfera*, able to oxidize both methane and nitrite in the wastewaters has been enriched. The authors suggested the concept of using such methanotrophs for the treatment of municipal wastewaters. Implementation of such an approach could solve two problems at once: removing an access of nitrate leading to eutrophication of water reservoirs and dissolved methane preventing its emission into the atmosphere. Additionally, the methodology of enriching the denitrification zones in aerotanks with the above-mentioned type of methanotrophs has been developed that would provide more effective treatment of wastewaters [211]. The technology of wastewater treatment using the potential of denitrifying anaerobic methane oxidation (DAMO) and Annamox for effective simultaneous nitrogen and methane removal was recently tested [212].

Examples of methanogens and methanotrophs found in different environments are summarized in Table 2.

Table 2. Examples of methanogens and methanotrophs found in different environments.

Location	Methanogens	Methanotrophs	Detection type	Link
Soils				
Forest soil (Germany)		USCα type ((1.2-0.2) × 10^8 *pmoA* genes per g of dry weight)	qPCR of *pmoA* genes; sequencing of 16S rRNA genes	[213]
Deglaciated soils in high-altitude cold deserts (India)	*Methanosarcina, Methanocella, Methanobacterium; mcrA* gene copies per dry weight soil 5 × 10^2 to 1.5 × 10^4		T-RFLP of archaeal 16S rRNA genes; qPCR of *mcrA* gene	[95]
Saline alkaline soils (Mexico)		type I (Gammaproteobacteria), *Methylomicrobium sp.*	*pmoA* gene cloning and sequencing	[98]
Alpine grassland and forest soil	Methanococcales (dominated the forest soil), Methanomicrobiales, *Methanocella* spp, Methanosarcinales		qPCR	[97]
Steppe soil (China)		type I and *pxmA* methanotrophs	qPCR and high-throughput sequencing of *pmoA*, *amoA* and *pxmA*-like gene,	[101]
Alluvial meadow soil (Russia)	genera *Methanobacterium, Methanobrevibacter, Methanocella, Methanolinea, Methanomassiliicoccus, Methanoregula, Methanosarcina, Methanospirillum, Methanothrix*.		sequencing of 16S rRNA genes	[58]
Middle taiga subzone forest (Russia)		The *pmoA* gene numbers per g of dry weight varied from 10^7 to 10^9.	qPCR of *pmoA* genes	[51]
Amazon rainforest (Brazil)	Methanogens diversity and number increased in soil under pasture compared to rainforests (both primary and secondary)	Type II methanotrophs (Alphaproteobacteria) dominated the active methanotroph community	DNA-SIP, qPCR of *mcrA, pmoA* genes; sequencing of 16S rRNA, *mcrA, pmoA* genes	[214]
Subarctic sandy upland soil (Russia)		USCα type (*Candidatus* Methyloaffinis lahnbergensis; "*Methylocapsa gorgona*" MG08)	qPCR of *pmoA* genes; sequencing of 16S rRNA genes	[103]
Wetlands				
Acidic bog peat	*Methanobacteriaceae, Methanomicrobiales, Methanosarcinaceae*		DGGE and sequencing	[79]

Peatland (Alaska)	Methanogen abundances showed a positive relationship with mean daily CH_4 fluxes		qPCR of *mcrA* gene	[111]
Boreal fen (Finland)	*Methanosarcinacea*, Methanocellales Fen cluster	*Methylocystis*	T-RFLP of *mcrA* and *pmoA* genes	[112]
Restored wetland (China)	anaerobic Euryarchaeota; order Methanomicrobiales, Methanobacteriales, Methanosarcinales	*Methylocystis, Methylosinus* within *Methylocystaceae* (type II), *Methylococcaceae* (type I).	16S rRNA gene sequencing; Shotgun metagenomics and analysis of *pmoA*, *mcrA*	[104]
Boreal fens (Finland)	Methanogen abundance decreased after warming	type Ib, genus *Methylocapsa*	*pmoA* microarray data, TRFLP of *mcrA*, qPCR of *mcrA* and *pmoA* genes and gene transcripts	[113]
Zoige wetland (China)	The *mcrA* gene numbers per g of soil varied from 10^3 to 10^6; methanogen community dominants were fam. *Methanobacteriaceae, Methanosaetaceae, Methanoregulaceae, Methanosarcinaceae*	The *pmoA* gene numbers varied from 10^5 to 10^6; methanotroph community dominants were gen. *Methylocystis*, *Methylocaldum*	qPCR and sequencing of *mcrA* and *pmoA* genes	[215]
Aquatic environments				
Acidic bog lake	Acetate-using methanogens		Fluorescence in situ hybridization (FISH)	[78]
Cold seeps in the river		type I and type II methanotrophs *Methylobacter psychrohilus; Methylobacter tundripaludum; Crenothrix polyspora*	*pmoA* gene cloning and sequencing	[85]
River estuary (China)	Acetoclastic and hydrogenotrophic methanogeneses	ANME	T-RFLP analysis of 16S rRNA gene	[144]
River estuary (China)	Methanosarcinales, Methanomicrobiales		454-pyrosequencing of 16S rRNA gene, qPCR of *mcrA* gene	[145]
Lake sediments (Germany)		Candidatus Methylomirabilis oxyfera peak in anoxic layers that coincided with the zone of methane oxidation	T-RFLP analysis of NC10 bacterial 16S rRNA genes; qPCR of *pmoA* genes	[125]
Marine sediments (Denmark)	Methanomicrobiales, genera *Methanococcoides* and *Methanococcus*; Mostly methylotrophic and hydrogenotrophic methanogens		Sequencing of archaeal 16S rRNA gene	[121]
Eastern part of Pacific Ocean	Methanosarcinales, Methanomicrobiales Methanocellales	type 1, genera *Methylococcus*, *Methylomonas*	Sequencing of *mcrA* and *pmoA* genes	[119]

Oxic layer of oligotrophic-mesotrophic lake	no *mcrA* genes were detected, relative abundance of *Pseudomonas sp.* (with potential for methane production in oxic conditions) was 11%		Sequencing of 16S rRNA gene, qPCR of *mcrA* genes	[27]
Boreal lake sediments (Finland)	hydrogenotrophic *Methanobacteriaceae, Methanoregulaceae*, *Methanocellales;* acetoclastic *Methanosaetaceae*; methyl-consuming *Methanomassiliicoccales, Verstraetearchaeota*	ANME-2D archaea	Sequencing of 16S rRNA gene, *mcrA* genes and transcripts	[129]
Estuary sediments (Israel)	3.4×10^7 copies per gr of dry sediment		qPCR of *mcrA* gene	[143]
Rice fields				
Rice field, two seasons (Italy)	*Methanosaetaceae, Methanosarcinacea, Methanobacteriaceae*		T-RFLP of archaeal SSU rRNA genes	[169]
Phyllosphere and rhizosphere of rice cultivars	Methanogens contributed 3% to the total microbial community	*Methylobacterium* in phyllosphere	Sequencing of bacterial and archaeal 16S rRNA genes, metagenomics, metaproteomics	[170]
Rice paddy soil with 8 cultivars (Korea)	Highest *mcrA* abundance was observed under rice cultivar with highest CH_4 emission rates	Highest *pmoA* abundance was observed under rice cultivar with lowest CH_4 emission rates	qPCR of *mcrA* and *pmoA* genes	[163]
Rice microcosms, different soil compartments (roots, rhizosphere) and seasons (China)	*Methanobacteriales*, *Methanosarcinaceae* and *Methanocellales*		qPCR, T-RFLP, sequencing of archaeal *mcrA*, 16S rRNA genes	[147]
Flooded rice ecosystem	*Methanosaeta, Methanocella, Methanosarcina, Methanobacterium*	*Methylocystis, Methylosinus*, unclassified *Methylocystaceae* (type II), *Methylocaldum, Methylobacter, Methylomonas*, *Methylosarcina* (type I), negligible amount of anaerobic methanotrophs	qPCR of *pmoA* and *mcrA* genes and gene transcripts, sequencing of 16S rRNA gene	[168]
Paddy soils of irrigated and rain-fed rice fields (Thailand)	Transcript copy numbers of *mcrA* increased, relative abundances of *Methanomicrobiales* decreased, *Methanocellales* increased after desiccation and reincubation		qPCR of *mcrA* genes and gene transcripts, sequencing of 16S rRNA gene, T-RFLP of archaeal 16S rRNA genes	[165]

Pot experiment with biochar addition (China)	Methanocella, Methanomassiliicoccus, Methanobacterium, Methanosarcina; biochar led to decrease in methanogenic archaea	Methylococcaceae, Methylocystis, Methyloparacoccus	qPCR and sequencing of methanogenic archaea (*mcrA*) and methanotrophic bacteria (*pmoA*) genes	[156]
Rumen of livestock animals				
Rumen of cows fed on different forage	*Methanobrevibacter spp*		cDNA-based length heterogeneity PCR, qPCR of bacterial rrs RNA and archaeal *mcrA* genes and transcripts	[179]
Ovine rumen	Isolate of order Methanomassiliicoccales – hydrogenotrophic methanogenesis		Isolate genome study	[186]
Goat ruminal fluid	Supplementation of $NaNO_3$ decreased the relative proportion of methanogens	Supplementation of $NaNO_3$ increased the relative proportion of NC10; ANME were not detected	qPCR of *mcrA* gene, NC10 and ANME-2d-specific primers	[195]
Goat rumen fractions	Most abundant genera were *Methanobrevibacter*, Candidatus *Methanomethylophilus*, *Methanosphaera*; methanogenic community was distinct in rumen solid- and liquid phase, protozoa- and epithelium-associated fractions		RNA-based qPCR, sequencing of archaeal 16S rRNA genes	[188]
Steer rumen microbiota	*Methanosphaera*, *Methanobrevibacter* (ord. Methanobacteriales); Thermoplasmata (*VadinCA11*)		Sequencing of 16S rRNA gene	[193]
Holstein dairy cows rumen	Ruminotype cluster associated with higher CH_4 was characterized by lower abundance of *Methanosphaera*		Sequencing of 16S rRNA gene, shotgun metagenomic sequencing	[216]
Landfills				
Municipal solid waste landfill (Taiwan)	Mostly thermophilic species, *Methanothermobacter thermautotrophicu*		Sequencing of archaeal 16S rDNA clone libraries	[198]
Leachate of a closed municipal solid waste landfill	hydrogenotrophic *Methanomicrobiales* and the methylotrophic and acetoclastic *Methanosarcinales*		Cloning and phylogenetic analysis of archaeal 16SrRNA gene sequences	[199]
Municipal solid waste landfill	Families *Methanosaetaceae, Methanosarcinaceae*; hydrogenotrophic order		Cloning and phylogenetic analysis of archaeal 16SrRNA gene sequences	[53]

leachates (France)	Methanomicrobiales (genera *Methanoculleus*, *Methanofollis)*			
Municipal landfill (India)	*Methanosarcinales*, *Methanomicrobiales*		Sequencing of archaeal 16S rRNA gene	[200]
Cover soils of semi-aerobic landfills (China)		*Methylobacter*, *Methylosarcina*, *Methylomicrobium* (Type I) *Methylocystis* (Type II)	qPCR, DGGE of 16S rRNA genes	[203]
Leachate of municipal waste landfill sites (China)	Hydrogenotrophic methanogens *Methanomicrobiales*, *Methanobacteriales*		454 pyrosequencing of archaeal community (V3–V5 region of the 16S rRNA gene)	[202]
Landfill cover soil		genus *Methylobacter* (type I) dominated the cover soil	16S rRNA gene amplicon sequencing and shotgun metagenome sequencing	[217]
WWTP				
Enriched municipal wastewater sludge		ANME-I and II, *Methylocaldium*, *Methanobacteria*, *Methylosinus*, *Methylocistis*, Verrucomicrobia	qPCR, pyrosequencing	[52]
Anoxic Wastewater Treatment Sludge	methanogens belonging to Euryarchaeota		Sequencing of archaeal 16S rRNA gene	[209]
Membrane Aerated Membrane Bioreactor (MAMBR)		Candidatus *Methanoperedens*, Candidatus *Methylomirabilis*	Sequencing of 16S rRNA gene, FISH	[212]
Leach field soils	*mcrA* gene copies were highest (10^7 copies per g of dry weight soil) near the wastewater inlet in both soil columns; Methanosaetaceae, Methanosarcinaceae, Methanobacteriaceae, Methanomassillicoccaceae	Methylococcaceae (Type I), Methylocystaceae (Type II)	qPCR and sequencing of 16S rRNA, *mcrA*, and *pmoA* genes and gene transcripts	[218]

4. Methanogenic and Methanotrophic Communities in Modeling the Methane Cycle

Methane cycle modeling aroused the scientific interest in the late 20th century. In spite of the fact that dynamic models of methane production were applied for the control strategy evaluation of the degradation processes in methane tanks [219], the first true model was created for studying methane emission from freshwater ecosystems [220]. Later, many actual models adjusted to both natural and anthropogenic ecosystems have been created. Most advanced models developed for methane emission from wetlands were also successfully applied for other environments. Normally, basic factors used for modeling are climate related and include precipitation, soil properties, solar radiation, temperature, vegetation type, root spread and water table level. The information regarding seasonal dynamics of methane emissions and its sources could also improve models

[105,221–223]. In the fundamental review, Xu and co-authors suggested dividing all the models of methane cycle into three groups according to their structure [224]:

(1) The group of simple empirical models calculating the resulting methane flux as a function of such environmental parameters as temperature, water table level, organic matter content, net primary production [225–227]. These models do not consider methanogenesis and methanotrophy as separate microbial processes. They are mostly point models not dealing explicitly with microbial factors.

(2) The group of models explicitly considering the key microbial stages of the methane cycle: methanogenesis, methanotrophy, methane transport and some others. Nevertheless, the effect of environmental factors (temperature, soil moisture, pH, concentration of dissolved organic carbon etc.) on the above microbial processes is described by empirical functions, e.g., Michaelis–Menten kinetics. These models deal with the soil profile and are vertically distributed; they do not directly involve microbial characteristics in their calculations [228–230].

(3) The group of process-oriented models mechanistically describing the methane cycle stages based on their actual mechanisms. In such models, biomass of different microbial groups is an independent variable and has a temporal dynamic. They are also vertically distributed [230–233]. The group also includes models describing incubation experiments and designed to be focused mostly on a certain constituent of the methane cycle in detail. For example, there are detailed mathematical models of methanogenesis for anaerobic incubation experiments where the description of methane transport and methanotrophy is not necessary [234].

By now, the model group 2 is the most relevant and is commonly used for the long-term climate forecasting. The reason is that parameterizing more complex models from the group 3 for different regions would require great efforts. First of all, such efforts are necessary to describe various characteristics of the microbial community involved in the methane cycle, namely, growth constants, efficiency of methane oxidation and threshold concentrations and others. Moreover, the situation is complicated by the fact that diverse methanogens and methanotrophs are dominant in different ecosystems [2,235,236]. In upland soils, the situation is even more complicated because of the lack of pure cultures of methanotrophs inhabiting these environments so that the study of their individual properties is difficult [2,236,237]. However, over the last years, the use of modern molecular biological methods in the laboratory experiments with methanogenic samples resulted in improving and parameterizing the models from the group 3 that are most reliable in forecasting methane emissions for both incubation experiments and field measurements [238]. The major advancement in the methane cycle modeling in this respect is the proper inclusion of molecular biological data into such models [2].

Accuracy of current models of methane cycle in soil could be improved using the new information about methanotrophs obtained by methods of molecular biology [239]. As an example, methanotrophs are traditionally claimed to use methane as the only carbon source and hence are limited by CH_4 concentration in soil. However, facultative methanotrophy was discovered for acidophilic methanotrophic bacteria of the *Methylocella* genus [240]. For a long time, these microorganisms were considered the only facultative methanotrophs. Just recently, researchers studying methanotrophic metabolism by molecular methods revealed that many of these bacteria can use carbon sources other than methane and are truly facultative [241–248]. The facultative methanotrophy should be considered in the models predicting the amount of methane produced and consumed in soils.

As an example, if the high abundance of facultative methanotrophs belonging to the *Methylocella* genus is established in a certain soil system, then we have to consider their capacity of utilizing a wide variety of compounds additional to methane and methanol such as acetate and some organic acids like pyruvate, succinate and malate as well as ethanol. It has been shown that *Methylocella* species consume primarily acetate and begin to oxidize methane only after acetate is exhausted in the system [240]. In this case, the model

taking into account the aforementioned fact would predict significantly smaller methane emission or even its absence, since the increment of methane caused by its CO_2-dependent production could be reduced or compensated by the increased methane-oxidizing activity of facultative methanotrophs once all acetate is consumed.

Molecular biological characteristics of wetlands considered in this review could also be important for methane cycle modeling and for the description of different ecological processes [2,249,250]. In particular, any change in composition of methanogens and their spatial dynamics are basic, but frequently ignored factors for estimations of methane production in wetlands. The information regarding the influence of seasonal vegetation changes on methane production in wetlands usually improves model accuracy [251], as with the information about microbiological parameters. One of the first models referring to some microbiological parameters was built for forest soil and incorporated the module describing methane oxidation [252]. The model includes such parameters as "Michaelis O_2-constant for methanotrophs", "Michaelis CH_4-constant for rhizospheric methanotrophs", "Michaelis CH_4-constant for soil methanotrophs". However, relevant literature values were taken for these parameters to calculate methane uptake in a certain environment instead of analyzing methanotrophic community functioning *in situ* in order to determine the actual values of the above-mentioned constants.

The anaerobic methane oxidation should be also taken into account for correct modeling. This microbial process is still not considered in any models of the methane cycle despite its significance for CH_4 turnover in various environments that is recognized in many publications [243,253,254]. The reasons for this are (i) the absence of the equations formally describing that process, (ii) the lack of information about the factors regulating its intensity and the true pathway of anaerobic methane oxidation including key enzymes involved [255]. The implication of anaerobic methane oxidation in modeling would enable the application of the models to a large number of environments where this microbial process is noticeable.

5. Conclusions and Outlook

The analysis of all the publications presented above shows that the modern molecular methods are widespread for studying methane cycle processes. Nevertheless, there is a lack of works where such methods could properly complement methane flux measurements. In modeling methane turnover, little attention has been paid to the use of the data on microbial community structure in various methanogenic environments that decreases the accuracy and efficiency of the models.

For instance, we create a mathematical model of a certain environment for which two conclusions can be made according to obtained experimental data. The first is that methane is formed both from acetate and via CO_2 reduction. The second is that methanotrophy does not occur in this environment or is negligible. If we assume further that the model with identified parameters is now applied to the environment where acetate is eliminated as a substrate for methanogens, the model would predict the change in methane emission related to production of CH_4 exclusively via a hydrogenotrophic pathway. However, some data on microbial community structure obtained by molecular methods could make a principal contribution to understanding the real situation in an environment.

Quantification of the abundance (qPCR) and determination of the taxonomical structure (NGS) of microbial communities based on 16S rRNA gene are widely used techniques for the study of microorganisms involved in the methane cycle. However, there are some troubles in using 16S rRNA gene for detection of methanogens and methanotrophs in complex microbial communities since both these microbial groups are not monophyletic. The alternative is to study gene sequences specific for methanogens (*mcrA*) and methanotrophs (*pmoA*). Quantification of these specific functional genes allows for evaluating potential activities of methanogenesis and methanotrophy. Nevertheless, the high quan-

tity of a functional gene does not mean the high activity of the microbial process depending on that gene so that interpreting the results is complicated. The gene expression can occur only within quite narrow range of certain ecological conditions. In other words, molecular biological methods based on RNA consider transcripts and have certain advances compared to DNA-based methods dealing with microbial genes. Availability of transcripts in microbial cells is the direct indication of the expression of genes encoding functional proteins. Thus, the quantity of the transcripts of 16S rRNA, *mcrA* and *pmoA* is the indicative microbiological parameter that can have an impact in modeling methane cycle processes.

At the present time, our knowledge of diversity, abundance and potential of methanogens and methanotrophs is still limited and the relationship between these parameters and actual methane fluxes from various ecosystems is not established. The active implementation of modern molecular techniques could fill the gap in studying microbial factors regulating the methane cycle as well as improve the accuracy of current models of methane turnover in different environments.

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