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Review

Methane Biofiltration Processes: A Summary of Biotic and Abiotic Factors

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Abstract: The ongoing yearly rise in worldwide methane (CH_4) emissions is mostly due to human activities. Nevertheless, since over half of these emissions are scattered and have a concentration of less than 3% (*v*/*v*), traditional physical–chemical methods are not very effective in reducing them. In this context, biotechnologies like biofiltration using methane-consuming bacteria, also known as methanotrophs, offer a cost-efficient and practical approach to addressing diffuse CH_4 emissions. The present review describes recent findings in biofiltration processes as one of the earliest biotechnologies for treating polluted air. Specifically, impacts of biotic (such as cooperation between methanotrophs and non-methanotrophic bacteria and fungi) and abiotic factors (such as temperature, salinity, and moisture) that influence CH_4 biofiltration were compiled. Understanding the processes of methanogenesis and methanotrophy holds significant importance in the development of innovative agricultural practices and industrial procedures that contribute to a more favourable equilibrium of greenhouse gases. The integration of advanced genetic analyses can enable holistic approaches for unravelling the potential of biological systems for methane mitigation. This study pioneers a holistic approach to unravelling the biopotential of methanotrophs, offering unprecedented avenues for biotechnological applications.

Keywords: biofiltration; greenhouse gases; methane emission; salinity; temperature

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1. Introduction

The group of six greenhouse gases (GHG) emissions comprises carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), sulfur hexafluoride (SF6), hydrofluorocarbon (HFC), and perfluorocarbon (PFC) [1], collectively known as carbon dioxide equivalents (CO_{2e}) [2]. Methane, the second most significant GHG, contributes 16% of global GHG emissions from both human and natural sources and is 21 times more potent per unit as a GHG compared to CO_2 [3]. In 2005, global GHG emissions totalled over 44 gigatons (Gt) of CO_{2e}, with CH_4 accounting for 7 Gt of CO_{2e} [4,5]. Approximately 60% of CH_4 emissions arise from activities like agriculture, coal mining, landfills, natural gas, and oil, while the rest originate from natural sources [6]. Each GHG has distinct properties regarding infrared absorption and atmospheric lifespan after emission [7]. Since 1750, GHG concentrations in the atmosphere have increased from a CO_{2e} level of 280 ppm to 430 ppm, with a pre-industrial level of 380 ppm [8]. The atmospheric CH_4 concentration has risen 2.5-fold over the past millennium, posing challenges to Earth temperature stability in the 21st century [9]. Currently, methane is emitted at an average rate of 600 teragrams (Tg) per year by both natural and human sources, with 55% of anthropogenic emissions containing less than 3 vol.% (*v*/*v*) methane (CH_4) [10,11].

The annual methane production from landfills worldwide was estimated to be approximately 30 teragrams in 2005, accounting for roughly 5% of the total net methane production [12]. Methane, being a greenhouse gas, is significantly more harmful to the

environment, with its impact estimated to be 21–25 times greater than that of CO_2, and it remains in the atmosphere for approximately 12 years [13,14]. Global warming's indirect effects are contributing to additional methane emissions, such as the thawing of permafrost, which releases long-term stored methane [15]. Moreover, the increased plant productivity resulting from rising atmospheric CO_2 levels may stimulate methane production in wetlands and agriculture due to enhanced production of labile soil carbon [16,17]. The remaining 40% of methane emissions are of natural origin and primarily emanate from wetlands and oceans [18,19].

Global political initiatives, including the Paris Agreement, are pushing nations to curb methane (CH_4) emissions as part of efforts to limit temperature increases to 1.5–2 °C above pre-industrial levels [20]. While technologies like combustion can control CH_4 emissions from landfills, older or smaller landfills often find traditional methods less feasible, making biofiltration a promising alternative [21]. Biofiltration, one of the earliest biotechnologies for treating polluted air, was initially used solely to combat odours [22,23]. However, it has since proven reliable in eliminating volatile organic compounds (VOC_s) and volatile inorganic compounds (VIC_s) in contaminated air [24,25]. Biotechnologies, particularly through methanotroph activity, offer a cost-effective and eco-friendly alternative to physical–chemical methods [26]. Among these, biofilters have gained popularity in recent decades for treating diffuse CH_4 emissions [27,28]. A similar approach for older landfills involves biocovers or soil covers [29,30]. This review summarizes recent information on methane biofiltration processes, various methanotroph species (both methanotrophic and non-methanotrophic bacteria and fungi), and key factors such as salinity and temperature that influence CH_4 biofiltration.

2. Methodology

Multiple academic databases were utilised to conduct a comprehensive literature search, including Web of Knowledge, Scopus, ScienceDirect, Google Scholar, Web of Science Core Collection by Clarivate Analytics, and ResearchGate. The search focused on publications from 2000 to 2023. Several keywords were employed to obtain a wide range of search results. These keywords encompassed various aspects related to methane emissions, methanotrophs, biofiltration, greenhouse gases, methanotrophic bacteria, non-methanotrophic bacteria, fungal methane removal, salt-affected soils and methane emissions, methane oxidation activity, phosphogypsum application and GHG emission, microbial CH_4 oxidation, temperature, and methane oxidation activity. In addition to the initial search, the references cited within the obtained publications were collected to ensure a comprehensive literature review. The chosen keywords were combined using operators like "OR" and "AND" to refine the search and obtain more precise results. Including quotation marks around specific terms, such as "methane biofiltration", ensured accurate retrieval of relevant records. All the keywords were used in all four databases to maximise the search coverage and gather a comprehensive collection of literature on the subject. The keywords and topics that are trending in each specific review section were identified using Bibliometrix.

To address our research question and achieve our review objective, we conducted a thorough search for peer-reviewed studies specifically focused on methane biofiltration processes. Our search was primarily centred on journal articles, excluding grey literature such as books, book chapters, and conference papers, except in rare cases where they provided valuable insights. We screened and evaluated titles and abstracts from over 1000 articles, employing a rigorous selection process to identify relevant papers. A key criterion for inclusion was the presence of quantitative information within the study. We specifically targeted studies that addressed the following topics: (i) methanotrophic and non-methanotrophic bacteria and fungal methane removal; and (ii) the impact of abiotic factors, especially salinity and temperature, on methane biofiltration processes. After comparing and analysing the remaining articles, we categorised them based on relevant keywords. Additionally, we summarised the conducted research, critically evaluated the

content of over 100 studies, extracted essential features, and identified key challenges that warrant further investigation. By following this rigorous methodology, we aimed to provide a comprehensive review that synthesises the current state of knowledge, highlights significant findings, and identifies areas that require additional research attention within the context of methane biofiltration. The bibliometric analysis of the review sections is summarised in Figures 1 and 2. We performed data analysis and generated bibliometric graphs using the Bibliometrix R package (Derviş, 2019).

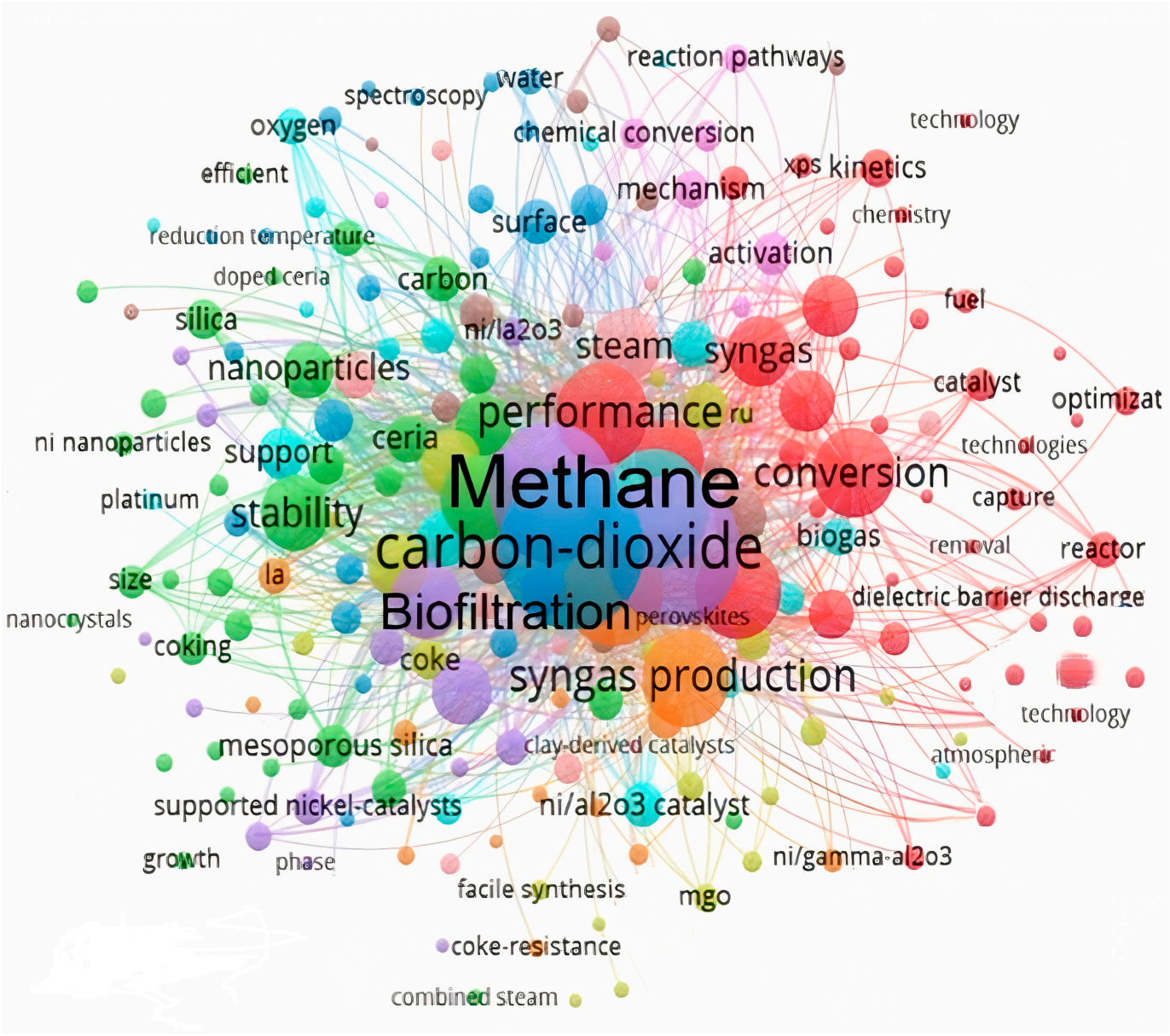

Figure 1. Bibliometric analysis for the author-supplied keywords. The size of nodes presents the frequency of recurrence. The connections between the nodes illustrate their co-occurrence in the same article.

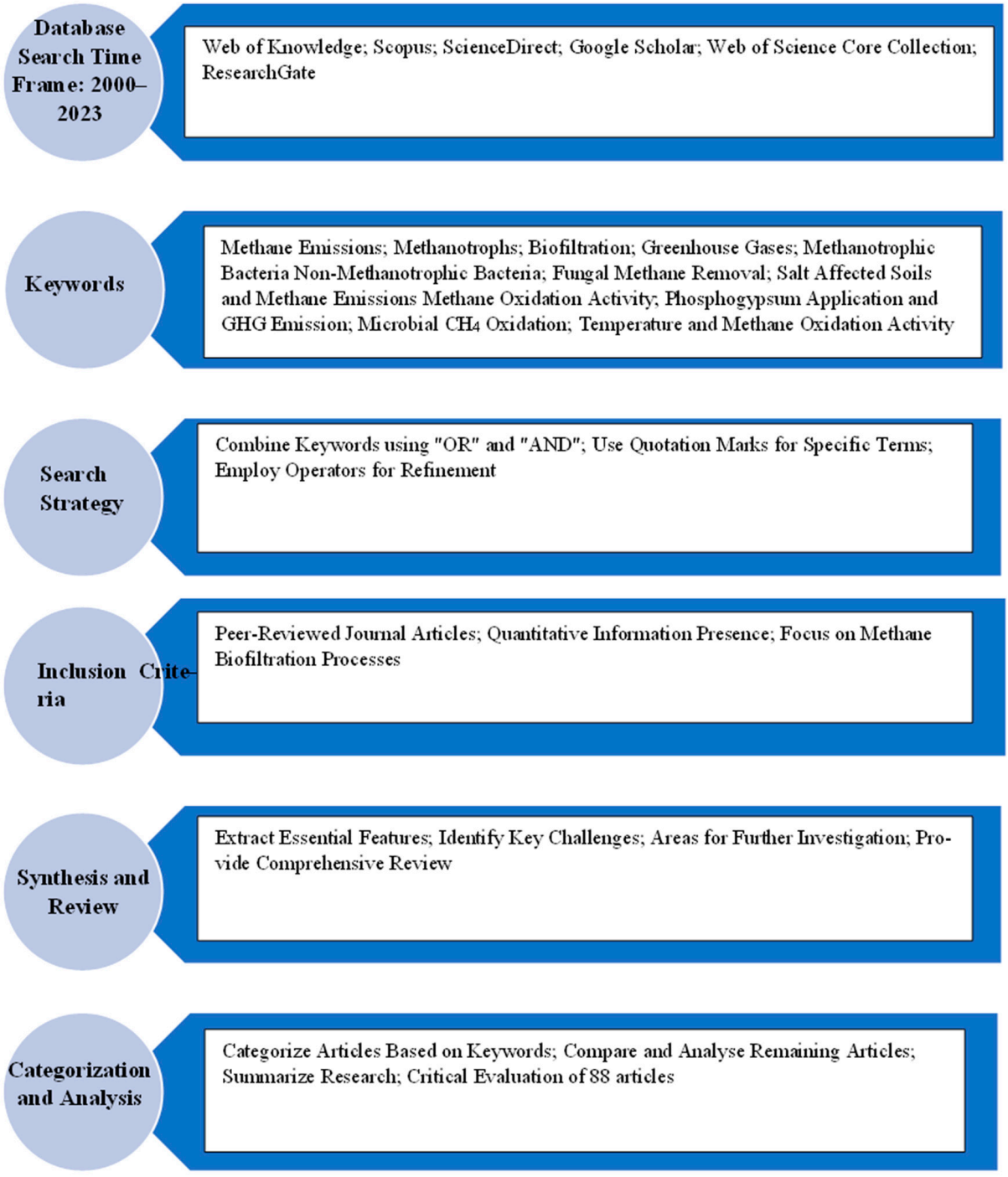

Figure 2. Diagrammatic view of the organisation of the paper.

3. Biofiltration Processes

Biofiltration is a system that harnesses the power of microbes to efficiently break down pollutants in a contaminated exhaust stream [31,32]. For example, methane (CH_4) present in an exhaust stream can be transformed into biomass, carbon dioxide, and water through the action of methanotrophic microbes [33]. Unlike traditional CH_4 removal methods, biofiltration offers several advantages: it is cost-effective to construct and operate, functions under ambient temperature and pressure conditions, and does not require complex safety mechanisms due to its non-electrical nature [34,35]. Biofiltration systems are adaptable to varying input flows and pollutant concentrations, easy to install, and can be made

mobile, making them suitable for a range of applications [36]. These systems have demonstrated high efficiency in treating high-flow waste gases with low pollutant concentrations, typically $\leq$1% (v/v) in the air [37].

Biofiltration represents an environmentally friendly process devoid of harmful emissions such as nitrogen oxides (NO_x), particulate matter, sulfur dioxide (SO_2), or carbon monoxide (CO) in the exhaust gas [38]. Typically, a biofiltration system consists of organic or inorganic packing materials serving as surfaces for microbial growth [39]. Organic beds, rich in macronutrients, sustain biomass growth. Biofiltration has a century-long history of application in treating sewage and other malodourous, waterborne wastes [40], with European countries employing bioreactors for contaminated air treatment for six decades [41,42]. Various biofiltration systems have been used for methane elimination, including conventional biofilters, biotrickling filters, bioscrubbers, membrane bioreactors, and two-liquid-phase bioreactors [43,44]. While many laboratory-scale biofilter studies have employed biotrickling filters, where nutrients are continuously introduced at the top of the unit [45], this paper focuses on conventional biofilters. These are characterised by the absence of continuous liquid-phase feeding, making them easy to install, mobile, and cost-effective [46,47].

Biofiltration harnesses the metabolic activity of microorganisms adhered to various packing materials to effectively treat a broad spectrum of organic and inorganic contaminants [48,49]. Within a biofilter, contaminants in the gas phase diffuse into biofilms, which are thin layers comprising a consortium of microorganisms residing on the packing material, where they are consumed by these microorganisms [50]. Biofilters employ diverse packing materials made from both natural and synthetic sources to provide the necessary surface area for biofilm formation [51,52]. For the successful commercial application of this treatment method to remove methane, leveraging the methane-degrading capabilities of methanotrophs, it is crucial to assess both the engineering and economic viability through model and pilot tests [53]. Additionally, specific conditions pertinent to methanotrophs, such as copper concentration, which controls the expression of pMMO and sMMO, must be considered within the model [54].

Considerable research has been carried out on the biofiltration of volatile organic compounds (VOC_s) and methane (CH_4), revealing promising results in terms of removal efficiency (RE) and elimination capacity (EC) [55]. Moreover, efforts have been dedicated to exploring variations in operating conditions, such as pollutant inlet load (IL), empty bed residence time (EBRT), temperature, and the impact of filter bed materials on the performance of individual VOCs or CH_4 biofilters [56,57]. Figure 3 illustrates a typical schematic of a biofilter used to eliminate either a single pollutant or a mixture of pollutants, and the process of CH_4 utilisation involves several intracellular steps, as depicted in Figure 4. The initial step is the oxidation of CH4 to methanol (CH_3OH), a reaction catalysed by the enzyme CH_4 monooxygenase (MMO) [58,59]. Subsequently, methanol is further oxidised to formaldehyde (HCHO) with the assistance of methanol dehydrogenase (MDH). Formaldehyde can then serve as a substrate for either a dissimilatory pathway leading to the production of formate (HCOOH) and ultimately carbon dioxide (CO_2) for energy generation or various assimilatory pathways that result in the synthesis of cellular components essential for the growth of methanotrophs [60].

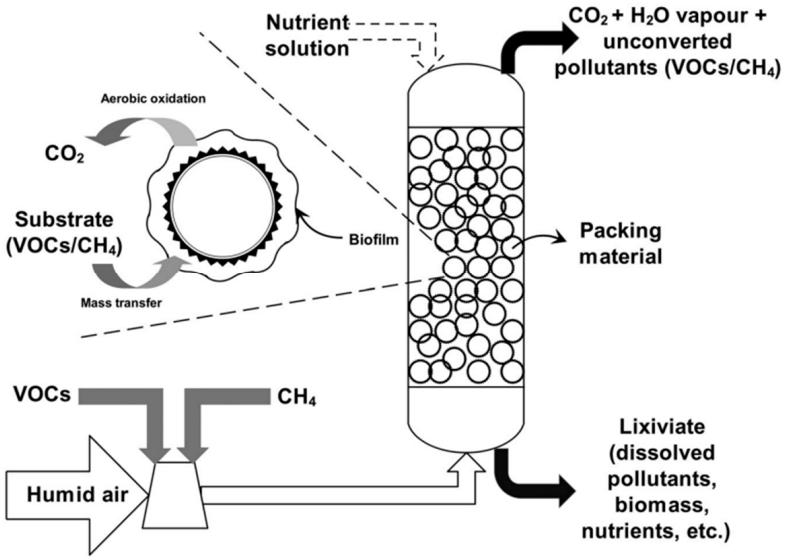

Figure 3. A diagram of typical laboratory biofilter [59].

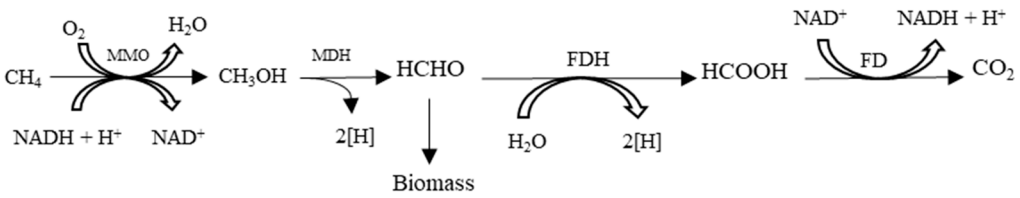

Figure 4. Methane oxidation pathway of methanotrophic bacteria [17]. *NAD^+* nicotinamide adenine dinucleotide oxidised from *NADH* nicotinamide adenine dinucleotide reduced from *MMO* methane monooxygenase, *MDH* methanol dehydrogenase, *FDH* formaldehyde dehydrogenase, and *FD* formate dehydrogenase [17].

4. Microorganisms

4.1. Methanotrophs

Methanotrophs, the particular bacteria tasked with breaking down methane (CH_4), belong to a subset of methylotrophs, which are bacteria specialised in the decomposition of compounds containing just one carbon atom [61,62]. Methanotrophs are categorised into three main types [63]. Type I includes the genera *Methylomonas*, *Methylomicrobium*, *Methylobacter*, *Methylocaldum*, *Methylophaga*, *Methylosarcina*, *Methylothermus*, *Methylohalobius*, and *Methylosphaera*. These methanotrophs utilise the ribulose monophosphate pathway for formaldehyde assimilation and primarily feature cellular membranes composed of fatty acids with either 16 or occasionally 14 carbon atoms [64].

Type II encompasses *Methylocystis*, *Methylocella*, *Methylocapsa*, and *Methylosinus*, which employ the serine pathway for formaldehyde assimilation. These methanotrophs possess cellular membranes consisting of fatty acids with 18 carbon atoms, arranged around the cell periphery [65]. Type X, represented by Methylococcus, combines characteristics from both Type I and Type II methanotrophs. It features fatty acids with 16 carbon atoms and utilises both the ribulose monophosphate cycle and the serine pathway for formaldehyde assimilation. The genomic sequence of *Methylococcus capsulatus* has confirmed the presence of genes associated with both pathways [66]. Generally, aerobic methanotrophic bacteria are considered obligate C1 metabolizers, as they are unable to grow on substrates containing only C–C bonds as the carbon source. However, the genus Methylocella stands out as an exception to this rule, as it can utilise compounds like acetate, pyruvate, succinate, malate, and ethanol [67].

Methanotrophs can be categorised into three types (type I, type II, and type X) based on various characteristics, including cell morphology, assimilatory pathway, growth temperature, nitrogen fixation capability, and membrane arrangement [68]. Type I methanotrophs encompass the genera *Methylomonas*, *Methylomicrobium*, *Methylobacter*, *Methylocaldum*, *Methylophaga*, *Methylosarcina*, *Methylothermus*, *Methylohalobius*, and *Methylosphaera* [69]. These methanotrophs utilize the ribulose monophosphate pathway to assimilate formaldehyde (an intermediate of methane oxidation) and typically have cellular membranes composed of fatty acids containing 16 or sometimes 14 carbon atoms [70]. Type II methanotrophs include the genera *Methylocystis*, *Methylocella*, *Methylocapsa*, and *Methylosinus*. These methanotrophs employ the serine pathway for formaldehyde assimilation and typically feature cellular membranes primarily composed of fatty acids with 18 carbon atoms arranged around the cell periphery [71]. Type X methanotrophs, represented by the genus *Methylococcus*, exhibit a combination of characteristics from both type I and type II methanotrophs [72]. They possess cellular membranes containing fatty acids with 16 carbon atoms and utilize both the ribulose monophosphate and serine pathways for formaldehyde assimilation [73].

In a notable study by Amodeo et al. (2018), they successfully operated a fungal-bacterial biofilter for the reduction of methane (CH_4) emissions and achieved impressive elimination capacities of 878 g per cubic meter per day (g/m^3 d) with an inlet load of 984 g/m^3 d, all under a relatively short empty bed residence time (EBRT) of just 20 min [74]. This biofilter consisted of compost that had been inoculated with the fungal strain *Graphium* sp. and was irrigated using a mineral salt medium containing the antibiotic chloramphenicol, which was added to inhibit the growth of competing bacteria [75]. Interestingly, their study revealed that as the irrigation rate increased, reaching up to 200 mL/day (resulting in excess leachate collected through a drainage system at the bottom of the biofilter), the performance of the fungal-bacterial biofilter improved significantly. Surprisingly, this increase in irrigation did not lead to significant pressure drops or other operational problems [30]. Pressure drop in methane biofiltration is a critical consideration in designing and operating biofilters for the treatment of methane-containing gas streams. The average reasoning behind pressure drop involves factors such as the characteristics of the filter media, flow rate, fouling, moisture content, and biofilm growth. Smaller media particles, higher porosity, and proper humidity can mitigate pressure drop, while higher flow rates and fouling tend to increase it. Theoretical reasoning employs fundamental concepts such as Darcy's Law and the Ergun Equation, as well as computational fluid dynamics (CFD) modelling, to understand and predict pressure drops in biofilters. These theoretical approaches provide a more detailed understanding of pressure drop distribution within the biofilter [76]. The most attractive native product in Type II methanotrophs is polyhydroxy butyrate (PHB), due to its inherent biodegradability, biocompatibility, water resistance, optical purity, and piezoelectric properties (Figure 5) [77].

4.2. Non-Methanotrophic Bacteria

Nitrifying bacteria, which are responsible for breaking down ammonia (NH_3), have the capacity to degrade methane (CH_4) as well. However, their CH_4 degradation performance is notably lower, typically less than 5%, when compared to pure methanotrophic populations [78]. Additionally, certain bacteria involved in the decomposition of methanol can also degrade CH_4, but this occurs effectively only when CH_4 concentrations are maintained below 10% v/v and their optimal growth temperature is around 35 °C [79].

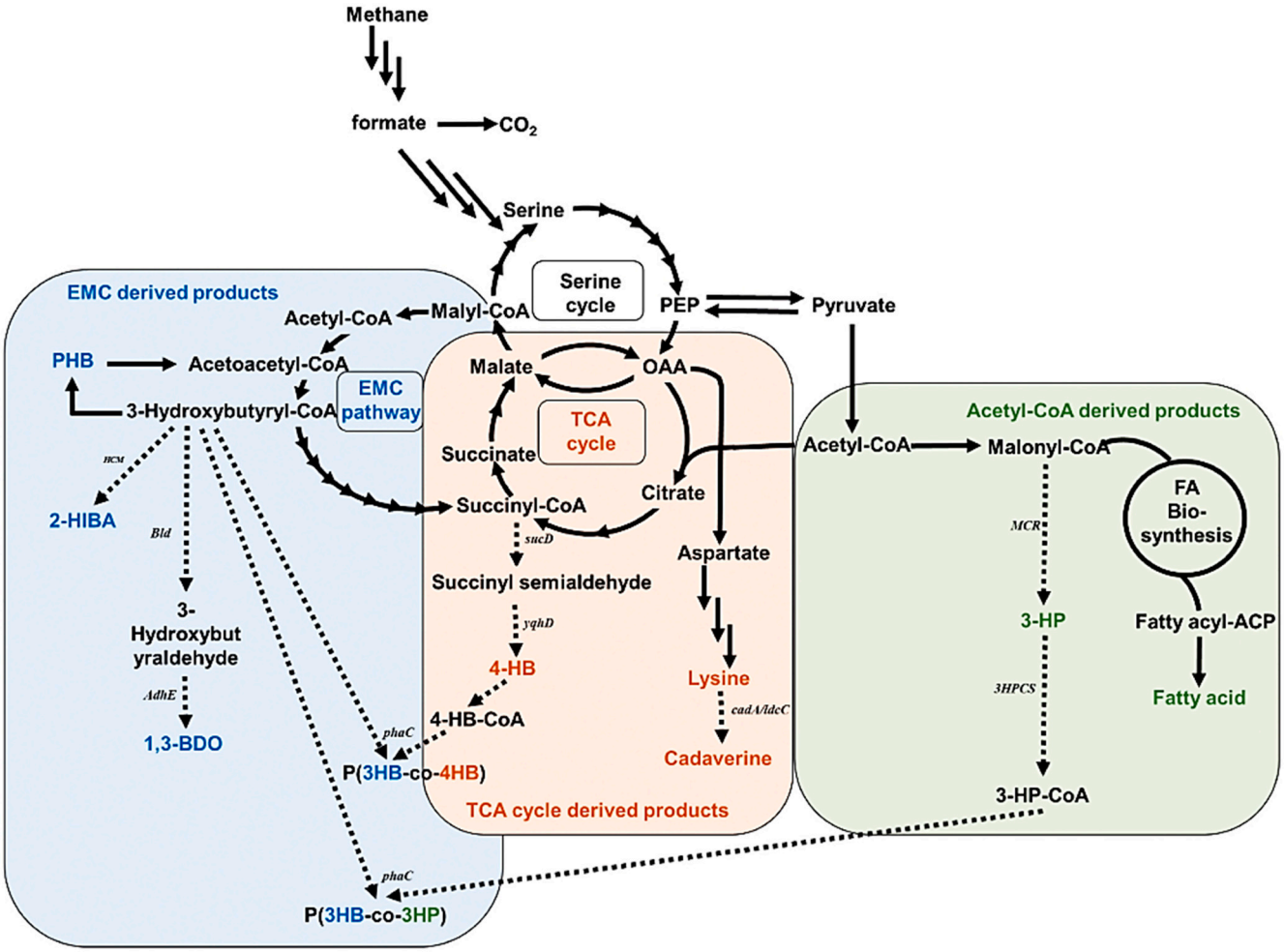

Figure 5. Simplified metabolic pathway for the production of chemicals and fuels from methane in Type II methanotrophs. The dotted arrows represent the non-native pathway, and the interactions mediated by the heterologous enzyme are marked in red. Enzymes (or encoding genes): *MCR*, malonyl-CoA reductase; 3HPCS, 3-HP-CoA synthetase; *sucD*, succinate semialdehyde dehydrogenase; *yqhD*, succinate semialdehyde reductase; *cadA*/*ldcC*, L-lysine decarboxylase; *phaC*, PHA synthase; *HCM*, 2-hydroxyisobutyryl-CoA mutase; *Bld*, butyryl-CoA dehydrogenase; *AdhE*, alcohol/aldehyde dehydrogenase [26].

There are anaerobic bacteria capable of CH_4 degradation as well. These bacteria are active in aqueous environments and often work in conjunction with sulfate-reducing bacteria. This process requires additional carbon sources like acetate or lactate, and the minimum sulfate concentration in the system should be approximately 1 mmol L^{-1} [80]. The concept of a connection between sulfate reduction and anaerobic methane oxidation is supported by studies conducted in landfill-leachate plumes [81] and groundwater [66]. However, attempts to isolate these anaerobic bacteria have been unsuccessful so far [82,83]. Recently, a microbial consortium capable of methane oxidation coupled with nitrate reduction in the absence of oxygen has been isolated.

4.3. Fungal Methane Removal

The utilisation of fungal activities for methane abatement in CH_4 biofiltration has not been widely explored. Casas et al. (2023) attempted to employ fungal strains as a biological adsorption mechanism to enhance CH_4 retention in the system. However, none of the strains they tested survived once the system was operational for CH_4 treatment.

Fungal methane removal, often referred to as fungal biofiltration or mycofiltration, is a promising area of research within the broader field of biofiltration [84]. Biofiltration is a biotechnological process that utilises living organisms to remove or degrade pollutants from the air or water. In the case of fungal methane removal, certain types of fungi are employed to capture and metabolise CH_4, a potent greenhouse gas [85]. Certain fungi are capable of oxidising methane as part of their metabolic processes. These fungi belong to the group of methanotrophic organisms. One well-studied example is *Methylocystis*, a genus of methanotrophic fungi that can utilise methane as a carbon and energy source. Methanotrophic fungi are characterised by their unique ability to utilise methane, a compound traditionally deemed challenging for microbial metabolism due to its low reactivity [86–88]. The genus *Methylocystis* stands out as a well-studied representative of this group, demonstrating remarkable methane-oxidising capabilities that contribute to its significance in biofiltration applications [89]. The key to the methane-oxidising ability of methanotrophic fungi lies in their possession of specialised enzymes, particularly methane monooxygenase (MMO) [25]. This enzyme catalyses the initial and crucial step in methane metabolism, converting methane into methanol. This oxidation process not only facilitates the assimilation of methane-derived carbon into the fungal biomass but also generates energy crucial for the organism's growth and maintenance [29]. While significant progress has been made in understanding the methane-oxidising abilities of methanotrophic fungi, challenges remain. Researchers are working to optimise fungal strains for enhanced methane oxidation efficiency, improve the scalability and stability of biofiltration systems, and explore potential synergies with other microorganisms or plant species to create more robust and resilient biofiltration environments (Table 1).

Nitrifying bacteria, encompassing ammonia-oxidising bacteria (AOB) and nitrite-oxidising bacteria (NOB), play vital roles in the nitrogen cycle by converting ammonia to nitrite and then to nitrate. These microbes, represented by genera such as Nitrosomonas and Nitrobacter, facilitate nutrient availability for plants. In contrast, methane oxidation is primarily driven by methanotrophic bacteria, which is crucial for mitigating methane, a potent greenhouse gas. Methanotrophs, categorised into Type I and Type II, convert methane to carbon dioxide. Although these processes operate independently, their interplay in soils is influenced by factors like soil conditions, microbial competition for oxygen, and broader environmental variables. Understanding these interactions is essential for managing nutrient cycles, greenhouse gas emissions, and overall soil health (Figure 6).

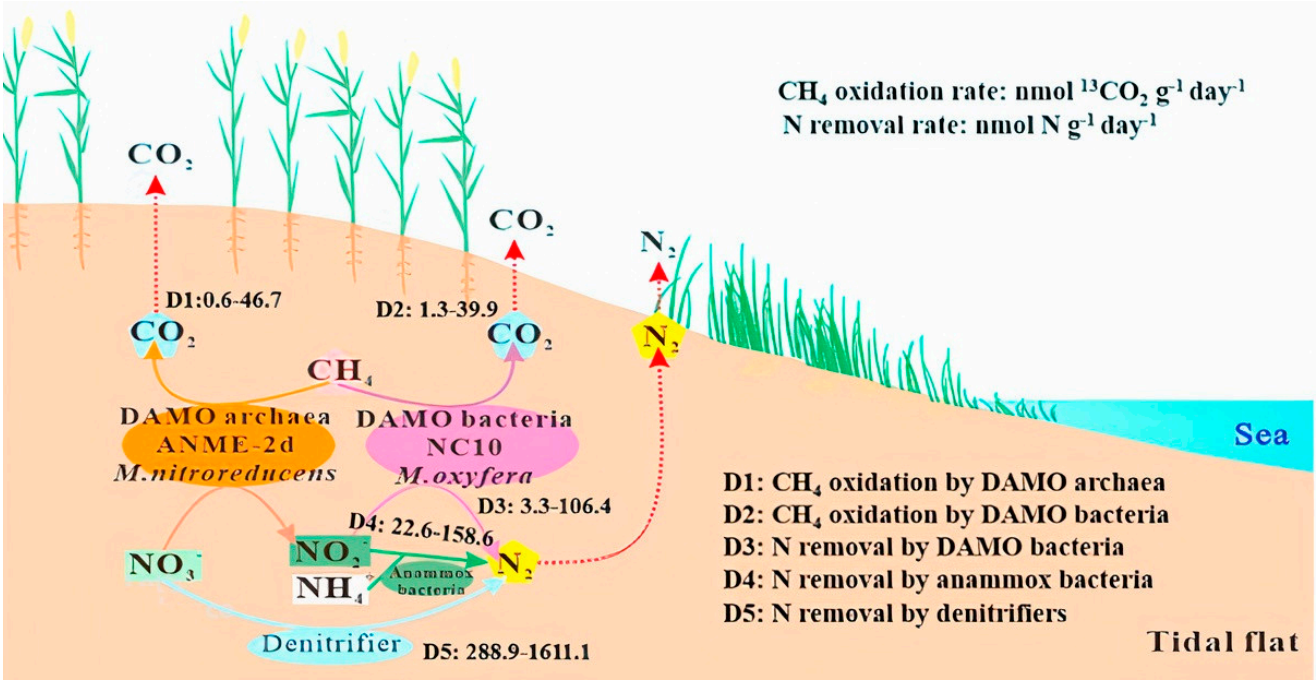

Figure 6. Nitrifying bacteria involved in methane oxidation processes [86].

Table 1. Summary of CH_4 biofiltration (and biotrickling filter, BTF) studies. All studies included in this table are either laboratory or field packed-bed column studies. The studies that rely on atmospheric diffusion are indicated as such.

Media	Nutrient Source	O_2:CH_4	EBRT (min)	Maximum CH_4 Conversion (%)	References
Landfill cover soil: coarse sand; clay top soil	NH_4NO_3, K_2HPO_4, and sewage sludge	13:1	52.1	61%	[67]
Agricultural soil and landfill cover soil	Organic amendments: wheat straw and beet leaves	30:1	7.8	78%	[68]
Soil (70% sand)	None	21:1	92 to 93	83%	[69]
Landfill cover soil (closed landfill)	NH_4Cl, KNO_3, KCl	11.7:1	103	36%	[70]
Alberta, Canada, soils	None	2:1	43	50%	[71]
2:1 compost and perlite	Nutrient solution	12.5:1	57 to 1136	>70%	[72]
Landfill cover soil	None	25:1	40 to 45	40%	[73]
Compost and sand	None	8:1 and 210:1	447 to 1162	88%	[74]
40:60 (by volume) perlite and compost	None	2.6:1 to 52:1	7 to 80	24%	[75]
Inorganic material and compost	Nutrient solution	2:1 to 7:1	4.3	98%	[76]
Compost, wood fibres, peat, and mixture	None	28:1 to 46:1	5.2 (bench)	98%	[77]
Compost; recycling paper pellets	None	28:1 to 30:1	2.4 (pilot)	90%	[78]
4:2:4 (ww) of compost, de-inking waste, and sand	None	6:1 to 70:1	98 to 558	80%	[79]
Gravel	Nutrient solution	10:1	495 to 515	85%	[80]
Stone	Nutrient solution	2.5:1	4.2		[81]
Landfill cover soil and earth worm cast	None	2.7:1 to 3.7:1	3.2 to 7.5	41%	[82]
Compost, 2:1 ceramsite and compost	None	21:1 to 161:1	3.8 to 280	23%	[54]
gravel	Nutrient solution	21:1 to 161:1	884	11%	[63]
Various: compost, sewage sludge, sand, soil, and Mixtures	None	0.4:1, 1.7:1, 3.8:1	4.2	96%	[29]
Stones	Nutrient solution	Atmospheric diffusion	310	97%	[50]

Table 1. *Cont.*

Media	Nutrient Source	O_2:CH_4	EBRT (min)	Maximum CH_4 Conversion (%)	References
BTF: Clay spheres, Polypropylene sphere, Stones	Nutrient solution	840:1	4.2	38%	[36]
1:1 Perlite and volcanic pumice soils from landfill	Nutrient solution	49:1	4.25	>90%	[51]
cap	None	2.5:1	4.2	100%	[42]
Pumice soils (top soil and subsoil)	None	28.5:1	>120	65%	[64]
Soil, compost and mixtures (1:1, 3:1 *w*/*w*)	None	29:1	90	36%	[23]
52.8% plastic waste and 47.2% stabilized organic Waste	Nutrient solution	40:1 to 393:1	15.7	Up to 100%	[17]
GAC and pumice	Mineral Salt Medium	2:1	9425 to 28,274	65%	[29]
BTF: polyurethane foam	Nutrient solution	3:1 to 206:1	20.1	50%	[27]
Perlite	Nutrient solution	6:1	4	43%	[34]
Tobermolite	Nutrient solution	Atmospheric diffusion	20	Up to 100%	[18]
Mixture: wood pine bark chips, perlite, compost	None	3.4:1 to 52.3:1	20	100%	[34]
Mixtures: compost (60%, *v*/*v*), burst furnace slag	Nutrient solution	9:1	4.4	70–100%	[28]
Stone material	Mineral Salt Medium	4:1	7.4 to 42.8	Up to 97%	[18]
Compost and fungal strains	Nitrate Mineral Salts	4:1	1 to 6	91–99%	[30]
Activated carbon, plastic bio-balls, gravel	None	85:1 to 161:1	20 to 40	82.8%	[25]
Fungal strains and spores; bacterial consortium	None	6.7:1 to 59.8:1	200 to 998	12%	[10]
0:50 (*v*/*v*) volcanic pumic soil and perlite	Nitrate Mineral Salts	210:1	0.42 (or 25 s)	51.3%	[39]
BTF: Polyethylene rings	None	161:1	50	33%	[47]
Compost	None	123:1	10 to 100	62%	[14]
Compost	Nitrate Mineral Salts	20:1	54 to 163	90% to 95%	[28]

Estimates presented here are calculated from values provided in the paper and may be different from what is reported. Where temperature is not specifically provided, 25 °C (and 1 atm) is used for the calculations.

5. Influence of Salt Concentration (Sodium and Sulfur) on Methane Oxidation Activity

Soil salinity has the potential to significantly impact the availability of carbon (C) and nitrogen (N) in the soil, affecting various microbial processes and activities [36]. These alterations in soil conditions can lead to changes in soil organic carbon (SOC) levels and emissions of greenhouse gases (GHG_s) such as carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) [9]. Previous research has indicated that soil salinity primarily decreases CO_2 and CH_4 emissions [36]. However, the response of N_2O emissions to soil salinity varies, including linear increases, decreases, or no significant response [37]. Some studies have suggested that the microbial processes involved and certain control factors play a role in determining these different responses to GHG emissions [39]. Furthermore, it has been observed that soil salinity-induced CO_2 and N_2O emissions are sensitive to temperature [40] and can also be influenced by the use of inorganic fertilisers [41]. This implies that under scenarios of warming and intensified fertiliser use, salinized soils may produce more CO_2 and N_2O [42].

In summary, the available research suggests that soil salinity-induced GHG emissions have the potential to influence global GHG dynamics and budgets. However, the results in this field have not been thoroughly synthesised, and there are research gaps and directions for future investigations that have not been clearly identified [43]. Studies have shown that increasing salt concentrations, resulting in electrical conductivity (EC) values greater than 6 mS cm^{-1}, lead to a clear decrease in methane consumption by both *Methylosinus* sp. cultures and biofilter materials [44]. For pure cultures, an increase in salt concentration from EC = 6 to EC = 12 mS cm^{-1} resulted in a six-fold decrease in methane consumption [45]. On the other hand, for biofilter materials, increasing EC values from 4 to 12 mS cm^{-1} led to only a three-fold decline in methane consumption rates [46]. This suggests that the methanotrophic population in the biofilter may adapt better to higher salt concentrations [47].

Interestingly, in both experiments, using biofilter leachate as a medium resulted in methane oxidation rates significantly lower than those achieved with nutrient media solution (NMS-media) adjusted to the corresponding EC values [48]. This indicates that the environmental conditions in situ may not optimally support the activity of the methanotrophic population [49].

Furthermore, the addition of $MgSO_4 \cdot 7\ H_2O$ from 0.5 to 1 g L^{-1} (resulting in EC values of 2.8 and 3 mS cm^{-1}, respectively) greatly enhanced methane consumption by biofilter material. The exact reason for this improvement remains unclear. However, it can be ruled out that the medium or glass bottle contamination was the cause, as the aliquots were from the same lot used to test the *Methylosinus* sp. culture, and all three replicates showed similar methane uptake rates [50]. It is suggested that the increase in methane oxidation rate from EC 2.8 to 3 mS cm^{-1} is likely due to enhanced nutrient availability [51].

Salinization has a significant impact on belowground microbially-mediated biogeochemical processes, including methane cycling in rice paddies. Previous research has demonstrated the adverse direct and indirect effects of salinization on methanogenesis (the production of methane) and methane emissions [52]. However, there is less knowledge about how salt stress affects methane oxidation and the methanotrophic bacteria in wetland rice paddies [53]. This area of research seeks to understand how changes in soil salinity levels may influence the microbial processes responsible for methane consumption in these environments. Salinity can also have an impact on methane (CH_4) flux by affecting plant physiological characteristics. First, an increase in salinity can lead to a decrease in plant species diversity and growth rate. This reduction in plant diversity and growth can, in turn, decrease CH_4 emissions from the soil by reducing the input of organic matter [54].

Second, higher salinity levels may result in increased CH_4 emissions from tree stems. Trees have the capacity to emit CH_4 that is either produced within the tree itself or in the surrounding soils. Frasi et al. (2020) discovered that exposure to seawater in five forests along the United States coastline significantly increased tree-stem CH_4 emissions. It is

possible that dying gymnosperm trees, which can result from seawater exposure, may accumulate higher levels of CH_4 [55]. Interestingly, some studies have not observed any significant response of soil CH_4 emissions to changes in soil salinity in agricultural fields [56]. This suggests that the impact of salinity on CH_4 emissions can vary depending on the specific environmental conditions and ecosystems under consideration. The relationship between the electrical conductivity of saturated paste extraction (EC_e) and soil organic carbon (SOC) contents is shown in Figure 7.

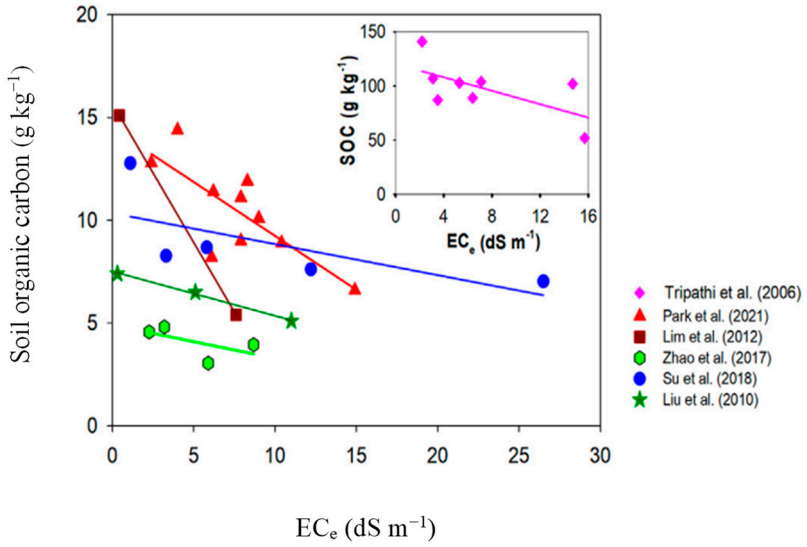

Figure 7. Relationship between electrical conductivity of saturated paste extraction (Ec_e) and soil organic carbon (SOC) contents in natural and agricultural lands [28].

Halophilic and halotolerant methanotrophs, capable of thriving in saline environments, have been identified in various settings such as soda lakes, mangroves, alkaline lakes, and estuaries [57]. These microorganisms often possess specialised mechanisms that allow them to adapt to and overcome salt-stress conditions [58]. Most of these salt-adapted methanotrophs belong to the type of Ia subgroup within the gammaproteobacteria. However, there have been reports of an alphaproteoacterial methanotroph, *Methylocystis*, which has demonstrated the ability to cope with salt stress at salt concentrations below 1% NaCl [59]. While previous studies have focused on methanotrophs indigenous to saline environments and their responses to salt stress at the cellular level [60], less attention has been given to understanding how methanotrophs from non-saline environments respond to increasing salinity and what the resistance and threshold levels are for their methanotrophic activity [61]. Recent research indicates that the NaCl threshold for methanotrophic activity in paddy soil is approximately 0.3 M (approximately 1.75% salinity). This threshold is higher than what has been observed in freshwater planktonic methanotrophs (0.1–0.5% salinity) but lower than the threshold for methanotrophs in estuarine environments (>3.5% salinity) [62]. These findings highlight the variability in salt tolerance among methanotrophic microorganisms and the importance of understanding their responses to changing salinity conditions in different ecosystems.

The inhibitory effect of ammonium on methane oxidation has been a subject of study by various researchers. Zarei et al. (2023) and Vikrant et al. (2018) concluded that this inhibition is due to chloride ions (Cl^-), which are the counter ions of ammonium (NH_4^+). In contrast, previous research [63,64] observed high chloride sensitivity among soil methanotrophs with high chloride concentrations. On the other hand, some authors found no growth inhibition for 135 different methanotrophic strains when exposed to a medium containing 10 g NaCl per litter [65]. These variations in findings suggest that the response of methanotrophs to chloride ions and ammonium can vary among different strains and environmental conditions. Regarding wetlands exposed to high concentrations of sulfate, which is present in seawater,

they often emit methane at relatively low rates. This is because sulfate-reducing bacteria can outcompete methanogens for energy sources in the presence of sulfate, thereby inhibiting methane production [66]. However, the relationship between sulfate concentrations and methane emissions in saline marshes can be complex and influenced by various factors.

Since methane oxidation is influenced by temperature and plant activity, the temporal and spatial variability in these processes, as well as sulfate dynamics, can create conditions where methane production and sulfate coexist in wetland ecosystems [67,68]. Annual methane emissions as affected by salinity are summarised in Table 2. Several researchers (Table 2) found a negative relationship between porewater salinity and methane flux. This trend was only partly supported when the data were grouped by salinity class. Mean methane emissions were significantly lower for polyhaline systems than for the other salinity classes. Methane emissions were generally lower in mesohaline systems than in freshwater (Table 2).

Regarding the tolerance of methanotrophic bacteria to salinity, some cultures have been reported to grow in the presence of up to 15% NaCl [69]. Additionally, in some cases, the addition of cow manure to salt-affected paddy fields enhanced CH_4 emissions significantly due to an increase in the relative abundance of methanogens, which benefited from improved soil properties and nutrient availability [70].

It is important to note that salinity can have different effects on various microbial groups. While methanogens may be more adversely affected by salinity due to their reliance on sodium ions (Na^+) for growth and metabolic processes, methanotrophs and methylotrophs may exhibit more tolerance to salinity [71]. Different types of methanogens, such as acetolactic methanogens and hydrogenotrophic methanogens, may also respond differently to saline conditions, with some being significantly inhibited while others maintain their methanogenesis rates [72]. Overall, the response of methane-producing and methane-consuming microorganisms to salinity is complex and can vary depending on the specific environmental conditions and microbial communities present (Figure 8).

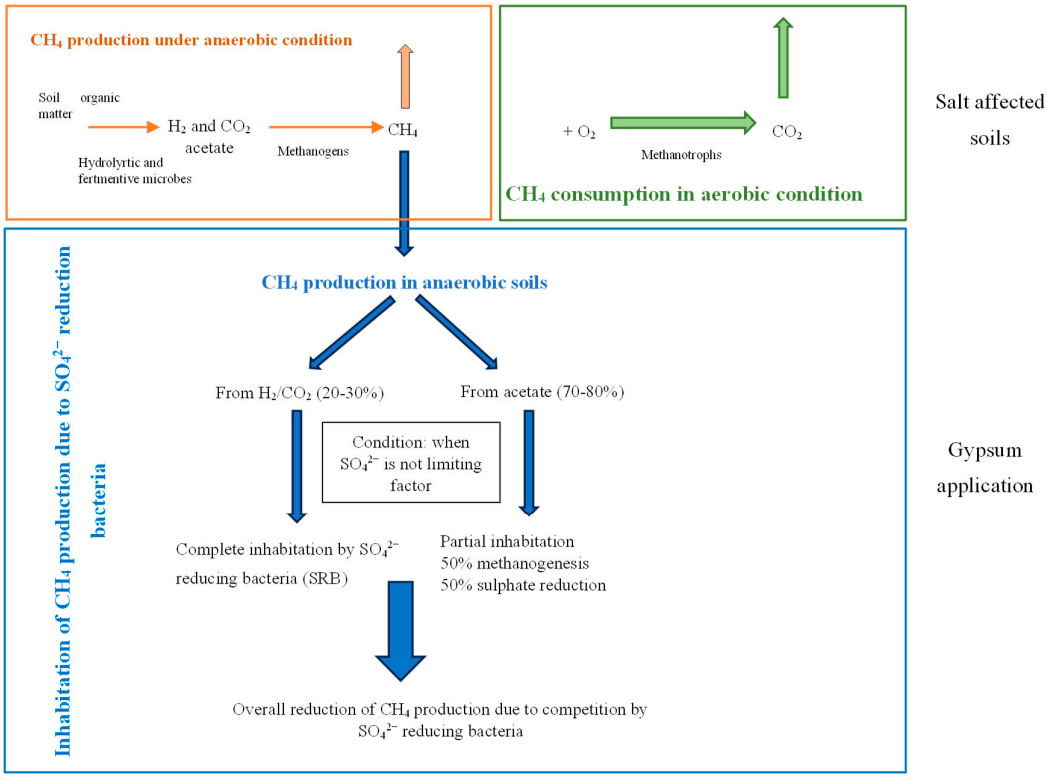

Figure 8. Schematic diagram showing the process of CH_4 production and mechanism of reduction of CH_4 production with the application of gypsum and phosphogypsum through competition with the sulfate-reducing bacteria [19].

Table 2. Summary of data extracted from references on annual methane emissions.

Site Name	Sample Frequency [a]	Salinity (mS m^{-1})	Soil Surface Flooding [b]	Daily Flux Reported	Annual Flux Reported [c]	References
				(mg CH_4 $m^{-2}d^{-1}$)	(g CH_4 m^{-2} yr^{-1})	
Fresh	13 (17 mo)	0.4	not systematic		213.3	[74]
Brackish	13 (17 mo)	1.8	not systematic		97.3	[62]
Salt	13 (17 mo)	18.1	not systematic		5.7	[54]
Creek bank	16 (20 mo)	18.7	exposed		1.2	[33]
High marsh	13 (13 mo)	22.6	exposed		0.4	[20]
Short *Spartina*	21 (24 mo)	26.3	exposed		1.3	[72]
Site 1	11 (12 mo)	5.1	not reported		18.2	[60]
Site 2	11 (12 mo)	12.8	not reported		22.4	[30]
Site 3	11 (12 mo)	16.6	not reported		5.6	[29]
GI Near Bank	8 (13 mo)	0.25	exposed		8.2	[52]
GI Far Bank	8 (13 mo)	0.25	exposed		5.7	[38]
UF Near Bank	8 (13 mo)	0.25	exposed		5.1	[40]
UF Far Bank	8 (13 mo)	0.25	exposed		3.5	[22]
Upland edge	6 (1.5 mo)	23.5	not systematic	3.7		[12]
High marsh	6 (1.5 mo)	31.6	not systematic	0.5		[26]
Middle marsh	6 (1.5 mo)	33.7	not systematic	0.6		[82]
Low marsh	6 (1.5 mo)	35.1	not systematic	0.6		[30]
Scirpus Close	68 (24 mo)	2.5	exposed		4.5	[11]
Phragmites Far	68 (24 mo)	2.5	exposed		75.4	[29]
Sweet Hall	8 (15 mo)	0.25	exposed		96.0	[32]
Lower site	17 (20 mo)	0.25	exposed		1.3	[81]
Upper site	16 (20 mo)	0.25	exposed		1.8	[55]

Table 2. *Cont.*

Site Name	Sample Frequency [a]	Salinity (mS m^{-1})	Soil Surface Flooding [b]	Daily Flux Reported	Annual Flux Reported [c]	References
Alresford Creek	12 (12 mo)	0.25	not reported		0.3	[38]
Colne Point	12 (12 mo)	33.0	not reported		0.4	[62]
C_3 Ambient CO_2	14 (24 mo)	6.8	exposed	13.9		[57]
C_4 Ambient CO_2	7 (24 mo)	6.8	exposed	9.6		[36]
Salt marsh	-	-	flooded	600.0		[84]
Salt marsh 24-h Day	-	2.1	flooded	2365.7		[34]
CD Marsh	-	-	exposed	1585.8	14.4	[21]
CD Marsh 24-h Day	9 (12 mo)	5.5	exposed		13.8	[30]
Wildlife	6 (6 mo)	11.6	exposed	90.0	14.1	[17]
Barbados	6 (6 mo)	12.9	exposed	94.0		[54]
Shanyutan wetland	-	2.3	exposed	122.4		[41]
Shanyutan wetland	-	4.2	flooded	48.0		[68]
Shanyutan wetland	-	2.3	exposed	112.8		[71]
All flood stages	10 (12 mo)	2.3	flooded + exposed	-	32.6	[64]

[a] Number of sampling events (total length of study, mo: month). [b] indicates whether the soil surface was exposed or flooded during emission measurements. In cases deemed "not systematic", fluxes were measured under both flooded and exposed conditions, but flooding was either determined to have no effect on emissions or the effects were not determined. [c] Emissions [4] were based on Table 2 and accounted for the length of time between sample dates.

Gypsum and phosphogypsum have long been employed for soil reclamation in alkali soils due to their ability to dissociate into calcium and sulfur. Calcium's strong affinity for soil particles displaces sodium and enhances soil structure by promoting aggregation. While numerous studies have explored gypsum effects on soil reclamation, only a select few have assessed its impact on greenhouse gas (GHG) emissions. Some investigations [50,51] focused on CH_4 emissions in rice ecosystems and observed reductions in reclaimed soils. Gypsum application increases SO_4^{2-} concentration, leading to competition between sulfate-reducing bacteria (SRB) and methanogens for common substrates such as H_2, CO_2, and acetate. Sulfate-reducing bacteria have a higher affinity for these substrates, which inhibits methanogenesis but does not completely eliminate CH_4 emissions. Gypsum also enhances water infiltration and soil redox potential, mitigating CH_4 emissions from saline/sodic soils. The rate of gypsum application plays a significant role, with higher doses leading to increased CH_4 mitigation due to intensified competition between SRB and methanogens. Gypsum is considered an effective reclamation agent for CH_4 emissions in both sodic and non-sodic soils, with higher application rates resulting in greater mitigation. Approximately 60% CH_4 mitigation was achieved with 8 MG ha^{-1} of by-product gypsum fertiliser (BGF) application [52]. It was found that 18–23% CH_4 mitigation in coastal paddy soils was achieved with the application of 150 kg ha^{-1} silicate slag, which contained high free iron oxide and SO_4^{2-} content acting as electron acceptors [53,54]. Additionally, Sun et al. (2020) explored the potential of gypsum and humic acid on CH_4 and N_2O emissions from coastal saline soils, observing a 19.36% reduction in CH_4 emissions and a 9.43% reduction in N_2O emissions with gypsum-amended N-fertilized soils. The application of humic acid, while stimulating higher N_2O fluxes, enhanced soil redox potential and further impacted GHG emissions in these soils. Impact of different amendments practices on GHG emissions from salt-affected soils is summarised in Table 3. Greenhouse gas (GHG) emissions from salt-impacted soils can be influenced by various improvement methods. Saline soils are characterised by high levels of salts, which can affect microbial activity, nutrient availability, and overall soil health. Regularly monitoring soil conditions, salinity levels, and GHG emissions can help in implementing timely interventions and adjusting management practices accordingly.

Table 3. Impact of different amendment practices on GHG emissions from salt-affected soils.

Experiment Type	Treatment Detail	Observation (GHG Emissions)	Key Findings and Reasoning	References
Pot experiment Initial soil pH = 7.8, EC = 5.6 dS m^{-1}, OC = 1.48%	25 nM salinity. 25 nM + phosphogypsum	Biochar amendment to saline soil reduced CH_4 emission by 16.4% (25 mM) to 19.6% (at 75 mM)	Phospho-gypsum and biochar mitigate CH_4 emission due to improved soil redox potential (Eh), increased SO_4^{2-} and decreased soil EC.	[62]
Field experiment growing rice conducted in Jiangsu Province, China	N1 (300 kg N ha^{-1}). N1 + humic acid. N1 + gypsum. N1 + humic acid + gypsum	CH_4 emissions increased with Humic acid (6.2%), gypsum (19.4%), decreased with gypsum + humic acid (27.3%). Humic acid and gypsum application increase N_2O emission	Humic acid and gypsum application with N300 kg ha^{-1} is the better management for coastal saline soils of China to mitigate CH_4 emission.	[50]
Field experiment with rice.	No by-product gypsum fertiliser (BGF); BGF (2 Mg ha^{-1}); BGF (4 Mg ha^{-1}); BGF (8 Mg ha^{-1})	CH_4 flux decreased with increasing level of BGF, and BGF (8 Mg ha^{-1}) reduced it by 60.6% compared to control.	BGF application could be a better management practice for CH_4 mitigation from paddy soils.	[42]
Field experiment with rice in upland soil.	Urea (250 kg ha^{-1}). Urea + Phosphogypsum (90 kg ha^{-1}). Urea + silicate slag (150 kg ha^{-1})	Silicate slag and phosphogypsum reduced CH_4 emission by 18.0–23.5% and 14.7–18.6%, respectively.	Silicate slag and phosphogypsum decreased CH_4 due to high free iron oxide and SO_4^{2-} content which acted as electron acceptors	[30]
Field experiment with rice.	Urea (165 kg N ha^{-1}); Urea + gypsum (6.60 t ha^{-1})	The CH_4 emissions from gypsum amended plots were reduced by 55–70% compared to non-amended plots.	Inhibition of methanogenesis by sulfate-reducing bacteria caused a reduction in CH_4 emission.	[64]
Field experiment with rice	N1 (300 kg N ha^{-1}). N1 + 20 t biochar ha^{-1}. N1 + 40 t biochar ha^{-1}	Biochar amendment increased N_2O emissions b 13.7–38.1% and had no significant effects on CH_4 emissions	Thus, long-term observations are needed to evaluate the environmental impacts of biochar and N fertilisers	[51]
30 days incubation experiment	Control; Biochar	Biochar amendment to saline soil decrease CH_4 uptake (8.8%), CO_2 (11.9%), and N_2O (9.8%) emissions	Biochar amendment to soils mitigates GHG emissions where CO_2 and N_2O are driven by soil rewetting events.	[63]

Table 3. *Cont.*

Experiment Type	Treatment Detail	Observation (GHG Emissions)	Key Findings and Reasoning	References
Rice experiment in irrigated saline soils of Gadakujang (a fishing hamlet) of coastal Odisha, India	Prilled urea (40 kg N ha^{-1}); Sesbania green manure (5 Mg ha^{-1}) + Prilled urea (20 kg N ha^{-1}). Ipomoea lacunose (5 Mg ha^{-1}) + Prilled urea (28 kg N ha^{-1})	Sesbania and Ipomoea lacunose green manure reduced CH_4 emission by 23.2 and 29.9%.	Locally available Ipomoea lacunose green manure ca use CH_4 mitigation and yield enhancement from the coastal saline rice ecosystems	[71]
Field experiment with rice	GM (S. Rostrata: 20 t ha^{-1}) + urea (30 kg urea ha^{-1}); GM + urea + gypsum (6.60 t ha^{-1})	Green manure addition enhances CH_4 emissions by 10 times than that of urea application alone, further gypsum addition reduced CH_4 emission by about 71.1%	Database for CH_4 emissions mitigation from rice grow on high-sulfate containing soils	[36]
Field experiment was conducted in saline sodic soils in the upper Yellow River basin, Northwest China	Organic fertiliser (CK), sheep manure (FYM), lignite bioorganic fertiliser (LBF1) (1.5 t ha^{-1}) LBF2 (3 t ha^{-1}), LBF3 (4.5 t ha^{-1}), and LBF4 (7.5 t ha^{-1})	LBF treatments decreased CH_4 and CO_2 and increasing N_2O emissions beyond 3 t ha^{-1} application rate. FYM acted as a CH_4 source, and LBF2 and LBF3 treatments acted as CH_4 sinks	The application of lignite bioorganic fertiliser at 3.0–4.5 t ha^{-1} is appropriate for GHG mitigation in saline-sodic farmlands	[27]
Microcosm experiments of 80 days incubation	Interaction of salinity (0 and 1.2% salt) with biochar	5–10 times higher N_2O emissions occurred from saline soils than that from non-saline soils. Aged biochar decreased N_2O emissions and increased CO_2 emissions in saline soils.	Aged biochar could be a better option for mitigation of N_2O emissions from saline soils	[73]
Field experiment with rice crop	Nonsaline (NS) soi; NS soil + DMPP (0.8% *w*/*w* of N); low saline (LS) soil; LS soil + DMPP; high saline (HS) soil; HS soil + DMPP	The nitrification inhibitor DMPP (3,4-dimethyl pyrazole phosphate) reduced cumulative N_2O emissions by 61% in non-saline soil and by 75% in low saline soil.	DMPP offsets low salinity-induced high N_2O emissions by inhibiting ammonia oxidation.	[19]

6. Influence of Temperature on Methane Oxidation Activity

The increase in anthropogenic greenhouse gas (GHG) emissions has led to a significant rise in air temperatures, currently increasing at a rate of 0.2 °C per decade [20]. Projections indicate that this warming trend is expected to persist, with an estimated average temperature increase of up to 4.8 °C [21]. Temperature plays a crucial role in influencing biochemical reactions, including methane oxidation. Understanding the temperature kinetics of these reactions is vital for designing systems exposed to ambient temperatures, as metabolic activities tend to decrease during colder seasons, such as winter [22].

Previous research conducted using material from a pilot biofilter plant located on the same landfill site revealed an interesting phenomenon. Methane oxidation activity in the laboratory was found to be significantly higher when the biofilter material was sampled during the winter and incubated at 10 °C compared to incubation at 17 °C [23]. This observation led to further investigations and the enrichment of a co-culture consisting of *Methylobacter* sp. and *Rhodococcus erythropolis* at the 10 °C incubation temperature [24]. This highlights the importance of considering temperature effects when studying methane oxidation and its microbial communities in different environmental contexts. Methane oxidation in the biofilter material exhibited typical mesophilic behavior, with the optimum methane consumption rate occurring at 38 °C [25]. This process displayed a broad temperature range, with methane oxidation still detectable at temperatures as low as 3 °C and as high as 45 °C [26]. An activation energy of 74.5 kJ mol^{-1} was calculated for a temperature increase from 10 to 20 °C [27].

Interestingly, the co-culture of *Methylobacter* sp. and *Rhodococcus erythropolis* had a different temperature response profile, with the optimum methane oxidation rate observed at 22 °C. When the incubation temperature was raised to 28 °C, methane uptake rates dropped below those observed at 4 °C. At 37 °C, which is close to the optimum temperature for the biofilter material, virtually no methane oxidation could be detected in the enrichment culture [28]. An activation energy of 97.7 kJ mol^{-1} was calculated for a temperature increase from 10 to 22 °C in this culture.

Comparing these findings with other studies, temperature optima for methane oxidation have been reported in the range of 20–31 °C for landfill covers, soils, and peatlands [29], and a temperature optimum of 35 °C was found for paddy soils [30]. Notably, the temperature optimum observed for the biofilter material falls slightly on the higher side of this range, while the *Methylobacter*-containing culture optimum is in the lower range of reported values [31]. These temperature responses highlight the variability in methane oxidation kinetics among different microbial communities and environmental conditions.

Exposure to low temperatures during the winter can indeed lead to shifts in methanotrophic temperature optima [32]. For example, enrichment and isolation conducted at 28 °C resulted in a *Methylosinus* sp. culture, while performing the same procedure at a 10 °C incubation temperature yielded a culture containing *Methylobacter* sp. as the sole methanotroph [33]. This suggests that temperature changes can lead to species shifts within the methanotrophic population rather than the mere adaptation of the same species to temperature variations [34].

For biofilter operation at ambient temperatures, these findings suggest better performance during the winter than previously assumed. Reduced methane emissions during colder periods might be explained by increased sulfate availability due to higher salinity [35]. Methanogens are the least competitive among heterotrophic microorganisms in soils, and the presence of major electron acceptors, including sulfate (SO_4^{2-}), can push methanogens out of the competition for substrates, leading to a decrease in methanogenic activity [36]. Sulfate-reducing bacteria and methanogens compete for acetate and hydrogen, which are primary substrates for methanogenesis. Therefore, an increase in sulfate reduction activity due to elevated sulfate availability can significantly reduce methanogenic activity, resulting in decreased soil methane emissions [37].

Rates of microbial CH_4 oxidation are indeed influenced by a range of environmental factors, and numerous studies have demonstrated the impact of these factors on changes in methanotrophic community structure and diversity. Factors such as soil texture, pH, gas concentration, and moisture content play crucial roles in shaping community structure in landfills [38]. However, it is worth noting that there have been relatively few studies that have investigated the effects of temperature on microbial diversity using molecular techniques across various ecosystems [39] (Table 4).

Methanotrophs are typically mesophilic microorganisms that thrive at moderate temperatures, typically in the range of 25–35 °C [40]. Various laboratory incubation studies across different ecosystems have reported peak CH_4 oxidation rates at temperatures ranging from 20 to 31 °C in environments like landfill cover soil, peat soil, wetlands, forests, and boreal soils [41]. There is research on temperature effects and CH_4 oxidation potential in landfill cover soil by subjecting soil cores to temperatures ranging from 4 to 46 °C and moisture contents ranging from 5 to 71% [42].

The optimal conditions for CH_4 oxidation were 31 °C and 11% moisture content [43]. When the moisture content was held constant at 11%, increasing CH_4 oxidation rates were observed as temperatures rose from 4 to 36 °C, but a decline in oxidation rates was noted at temperatures exceeding 46 °C [44]. It is important to note that CH_4 oxidation rates also decreased significantly when moisture content was at 11% [45]. In contrast, previous studies suggested that moisture content had a more dominant influence on CH_4 oxidation rates compared to temperature, with optimal moisture content ranging from 15.6 to 18.8% and an ideal temperature range of 20–30 °C [46]. Their study indicated a decrease in the optimal temperature as moisture content increased, suggesting that temperature had minimal effects on CH_4 oxidation [47]. Previous research explored various factors affecting CH_4 oxidation in landfill cover soil and concluded that moisture content, temperature, and gas concentration were the most critical factors influencing CH_4 oxidation [48]. The optimum conditions were identified as 25% moisture content, which facilitated gas transport for microbial activity, and a temperature of around 30 °C [49].

Indeed, temperature plays a crucial role in influencing the composition of microbial communities, including methanotrophs. Previous researchers [50,51] conducted a study using phospholipid fatty acids (PLFAs) as biomarkers in landfill cover soil and found temperature to be a significant factor affecting community composition. They observed the growth of Type-I methanotrophs at lower temperatures (5–10 °C) and Type-II methanotrophs at higher temperatures (20 °C) [52]. This temperature-dependent division of methanotroph types has been supported by other studies as well [53].

However, there can be variations in the relative abundance of methanotrophs in different environments [54]. The differences in the relative abundance of methanotrophs in two distinct soils (rice field and forest soil) by analysing terminal restriction fragment length polymorphism (T-RFLP) of particulate methane monooxygenase genes (*pmoA*) were described previously [55]. Their findings suggest that environmental factors beyond temperature can also impact methanotroph community composition. Furthermore, the temperature dependence of methanotrophs may vary in different contexts. Temperature dependence and the coexistence of both Type-I and Type-II methanotrophs across a wide temperature range (5–45 °C) in soils were described in previous research [56,57]. This suggests that the response of methanotrophs to temperature can be complex and context-specific, influenced by various environmental factors.

While previous studies have primarily focused on abiotic parameters like pH, temperature, and pressure in the context of CH_4 biofiltration, it is crucial to also consider the role of methanotrophs and their diversity in these systems. Methanotrophs are the key drivers of CH_4 oxidation, and understanding how changes in abiotic parameters affect their community dynamics can provide valuable insights into system performance. Nitrogen cycling, in particular, has a significant influence on methanotrophic communities and CH_4 abatement potential. Additionally, it is important to consider the potential for the emission of more potent greenhouse gases (GHG_s) in these systems.

Table 4. Studies showing genus- or species-level methanotrophs/methylotrophs identified in ecosystems at varied temperatures.

Temperature (°C)	Specific temperature (°C)	CH_4 Concentration (%)	Ecosystem	Molecular Biomarker	Genus/Species/Type of Methanotroph	References
6–70	6	5	Landfill cover soil	Shotgun sequencing, 16S rRNA	*Methylobacter luteus*, *Methylobacter tundripaludum*, *Methylotenera*	[38]
6–70	23				*Methylobacter luteus*, *Methylocystis*	
6–70	30				*Methylobacter luteus*, *Methylovorus glucosetrophus*	
6–70	40				*Methylocaldum* sp. *SAD2*, *Methylocaldum* sp.*14B*	
6–70	50				*Methylocaldum Szegediense*	
5–45	5, 10, 15, 25, 35	4	Rice field and forest soil	TRFLP-pmoA gene	*Methylobacter Methylococcus*/ *Methylocaldum Methylocystis*/ *Methylosinus Methylomonas Methanica*	[41]
3–20	5, 10	5	Landfill cover soil	PLFA	*Type-I methanotrophs*	[75]
3–20	20				*Type-II methanotrophs*	
4–21	4	10	Arctic lake	DNA-SIP	*Methylophilus*, *Methylobacter*	[32]
4–21	10				*Methylobacter*, *Methylomonas*, *Methylosoma*	
4–21	21				*Methylocystis*, *Methylophilus*, *Methylobacter*, *Methylomonas*	
5–40	5	5–50	Landfill cover soil	16S rRNA gene analysis (DGGE)	*Methylotenera versatilis*	[63]
5–40	10				*Methylobacter tundripaludum*, *Methylovorus glucosetrophus* *Methylocella tundrae*, *Methylobacter marinus*, *Methylosinus Sporium*	

Table 4. *Cont.*

Temperature	Specific temperature	CH_4 Concentration	Ecosystem	Molecular Biomarker	Genus/Species/Type of Methanotroph	References
5–40	20				*Methylobacter marinus*, *Methylobacter luteus*, *Methylobacter tundripaludum*, *Methylosinus trichosporium*, *Methylosinus Sporium*	
5–40	40				*Methylocaldum Gracile*	
4–20	4	-	Hydrocarbon contaminated aquifer	FISH, TRFLP-pmoA gene	*Methylococcaceae*, *Methylobacteriaceae* sp., *Methylomonas* sp.	[51]
4–20	12				*Methylococcaceae*, *Methylobacteraceae* sp.	
4–20	20				*Methylocystis* sp., *Methylococcaceae*, *Methylobacteraceae* sp.	
7.5–9.5	-	-	Tundra bog soil	Immunofuorescence	*Methylomonas*, *Methylobacter*, *Methylococcus*, *Methylocystis*, *Methylosinus*	[70]

Future research efforts should focus on developing easily measurable, site-specific parameters that can provide a more comprehensive understanding of methane emissions and soil carbon storage estimates. Depending on the specific context, detailed field investigations and direct methane monitoring may be necessary to verify the radiative forcing effects of created or restored wetlands, especially in tidal fresh, oligohaline, and mesohaline environments. By integrating both abiotic and biotic factors, researchers can gain a more holistic understanding of CH_4 biofiltration systems and their environmental impact, ultimately contributing to more effective mitigation strategies for reducing methane emissions.

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