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Review

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Advances in high-value resource recovery of greenhouse gases driven by methanotrophic communities

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Abstract

Amid rising global temperatures and accelerating carbon-neutral initiatives, the efficient valorization of greenhouse gases has emerged as a central focus of contemporary research. Microbial metabolism enables the low-cost transformation of methane, which has evolved into a strategic technological reserve for a green and low-carbon future. Methanotrophs, widely distributed across diverse habitats, utilize methane as both a carbon and an energy source. Through key enzymes in their central metabolic pathways, these microorganisms sequentially oxidize CH_4 into methanol, formaldehyde, formate, and ultimately to CO_2. In synthetic microbial consortia comprising methanotrophs and methylotrophs, inter-species cross-feeding effectively alleviates the accumulation of inhibitory metabolites, improving overall methane conversion efficiency. Beyond regulating the source-sink balance of atmospheric greenhouse gases, methanotrophic consortia also drive the high-value resource utilization of high-concentration CH_4 and CO_2. Type I, II, and X methanotrophs possess distinct carbon fixation pathways and are capable of synthesizing high-value products such as methanol, single-cell protein (SCP), and polyhydroxyalkanoate (PHA). Investigating their mechanisms and efficient cultivation strategies is conducive to further exploring the potential of methanotrophs in carbon cycling and biomanufacturing. However, the practical application of methanotrophs still faces several challenges, including difficulties in process control, ineffective suppression of byproduct formation, and potential safety concerns associated with the synthesized products. Addressing these bottlenecks is imperative to unlock their full potential for large-scale industrial applications in greenhouse gas mitigation and sustainable biomanufacturing.

Keywords: Greenhouse gases, Methanotrophs, High-value resource utilization, Cross-feeding, Metabolic regulation

Highlights

- Methanotrophs with unique functional traits are summarized.
- Divergent metabolic and electron transfer mechanisms are deciphered.
- The dual role of methanotrophs in climate change is evaluated.
- Species-specific yields of high-value products are benchmarked.
- Metabolic regulation underlying efficient PHA biosynthesis is unveiled.

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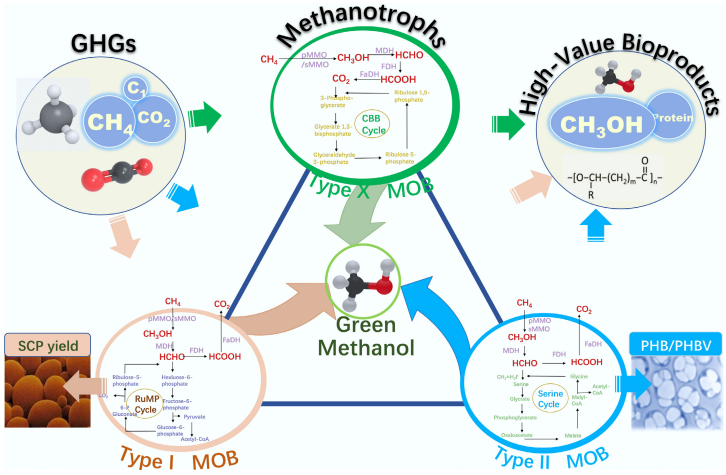
Graphical abstract



Introduction

Methane is a potent greenhouse gas capable of absorbing long-wave radiation and driving the greenhouse effect[1]. On a mass basis, CH_4 shows a significantly higher global warming potential (GWP) than CO_2, approximately 28 times higher over a 100-year horizon[2]. Methane originates from both geochemical and biochemical processes, and biogenic methane is predominantly generated by methanogens[3]. The establishment of anaerobic conditions is a critical factor enabling biogenic methane production, as observed in environments such as anaerobic wastewater treatment[4], solid waste digestion[5], flooded rice paddies[6], and anoxic zones of river and lake ecosystems[7]. Globally, methane emissions are estimated at 500–600 Tg/year, with roughly 70% originating from biogenic sources, whereby aerobic methanotrophs play a critical role in the atmospheric source-sink balance by oxidizing approximately 60% of this biogenic fraction[8].

Aerobic methanotrophs (methane-oxidizing bacteria, MOB) represent a group of microorganisms that utilize methane as their carbon and energy source. They are widely distributed in natural environments and can be found in mineral springs[9], lakes[10], wetlands[11], forests[12], and grasslands[13], where they frequently thrive through syntrophic associations with other microorganisms[14]. Since their initial discovery in 1906, advances in molecular phylogenetics and high-throughput omics have progressively refined the taxonomic framework of methanotrophs and deepened the understanding of their global biogeography, metabolic versatility, and ecological significance[15]. Beyond their ecological roles, methanotrophs possess unique biocatalytic machinery that oxidizes methane under ambient conditions. This process mitigates atmospheric emissions while concurrently generating a spectrum of value-added bioproducts, serving a dual functionality that underpins their emerging relevance in industrial and biotechnological applications[16]. Furthermore, the methane monooxygenase (MMO) expressed by methanotrophs exhibits relatively broad substrate promiscuity, which enables the co-metabolic degradation of a wide array of emerging contaminants[17,18], including alkylmercury[19], halogenated hydrocarbons[20], microplastics[21], and certain antibiotics[22]. This trait not only highlights their potential in bioremediation but also implies an adaptive advantage that sustains metabolic robustness under the stress of emerging contaminants.

Methanotrophs exhibit significant advantages in methane removal and resource utilization. Current chemical conversion strategies, such as thermal, photocatalytic, and electrocatalytic processes, aim to transform CH_4 into chemicals like methanol and formaldehyde[23,24]. However, the high C-H bond energy and chemical inertness of CH_4 necessitate severe reaction conditions, which often result in considerable CO_2 emissions and exacerbate greenhouse gas effects[25]. Although carbon capture, utilization, and storage (CCUS) technologies offer an effective means of carbon sequestration, their widespread implementation remains constrained by high costs of operation and maintenance[26]. In contrast, methanotroph-based biological systems operate under mild conditions with low energy input, offering a viable and sustainable alternative for efficient methane removal and conversion. Consequently, the valorization of methane through biological pathways has attracted growing research interest. Nevertheless, the metabolic network of methanotrophs is highly complex, and their interactions with other microorganisms, as well as their responsiveness to environmental factors such as nitrogen sources, are not yet fully elucidated. These knowledge gaps currently hinder the engineered application of methanotrophs at scale.

This review systematically summarizes research advances in methanotrophs over the past decade, emphasizing that overcoming bottlenecks in reaction efficiency, product selectivity, and process stability through multi-level metabolic engineering strategies is crucial for transitioning these systems from laboratory-scale studies to industrial applications. We elucidate how the diversity of methanotrophic metabolic pathways underpins their functional versatility, evaluate and summarize their potential for greenhouse gas mitigation and synthesis of high-value products, and discuss the key regulatory mechanisms of carbon flux, along with analytical approaches and underlying principles for improving microbial product yields. Finally, the future development direction for integrating high-value resource utilization technology of methanotrophs with cutting-edge interdisciplinary fields is prospected.

Ecophysiology and distribution of methanotrophs

Phylogeny and core metabolism

Methanotrophic microorganisms are broadly categorized into two functional groups: aerobic methanotrophs and anaerobic methanotrophs. The latter group includes NC10 bacteria[27] and anaerobic

methanotrophic archaea (ANME)[28], which utilize substances such as nitrate and nitrite as electron acceptors[11] and are generally unable to grow in oxygen-rich environments. In contrast, aerobic methanotrophs employ O_2 as their terminal electron acceptor, exhibit considerable phylogenetic and metabolic diversity, and demonstrate remarkable functional versatility with some strains retaining activity even under hypoxic conditions[10]. Owing to these traits, aerobic methanotrophs play a significant role in both ecological remediation and contribute substantially to the biogeochemical regulation of carbon flux.

Based on phylogenetic divergence and distinct carbon assimilation pathways, aerobic methanotrophs are primarily classified into Type I (Gammaproteobacteria), Type II (Alphaproteobacteria), and Type X (primarily belonging to Verrucomicrobia)[29,30]. Type I methanotrophs, characterized by intracellular membrane systems arranged as vesicular disks or bundles, predominantly drive methane oxidation in high-methane environments such as wetlands, hot springs, and marine ecosystems; in contrast, Type II methanotrophs possess layered intracytoplasmic membranes and demonstrate higher adaptability to low-methane environments, including acidic soils, wetlands, and plant-associated niches; additionally, Type X methanotrophs represent extremophilic lineages with relatively simplified membrane structures, enabling them to thrive under highly acidic and elevated temperature conditions[29,31].

A suite of unique enzyme systems employed by methanotrophs catalyze methane oxidation, primarily including methane monooxygenase (MMO), methanol dehydrogenase (MDH), formaldehyde dehydrogenase (FDH), and formate dehydrogenase (FaDH)[32]. Among these enzymes, MMO is classified into two types: particulate methane monooxygenase (pMMO) and soluble methane monooxygenase (sMMO). Specifically, pMMO is bound to the intracellular membrane and exists in nearly all methanotrophs, while sMMO is only present in a few methanotrophic groups and distributed in the cytoplasm[32]. In addition, there are some methylotrophs lacking MMO in the methane oxidation system, which cannot directly utilize methane but fix carbon using the metabolic products of methane[33]. pMMO and sMMO are structurally and evolutionarily unrelated enzymes, differing fundamentally in their molecular architecture and catalytic mechanisms, and their expression is regulated by distinct trace metal ions: pMMO activity is strictly copper-dependent, whereas sMMO expression requires sufficient iron availability[34]. Moreover, copper concentration acts as a key metabolic switch: elevated copper levels promote pMMO expression, while copper limitation induces sMMO expression[35]. In summary, methanotrophs exhibit considerable diversity in their carbon fixation pathways, which involve markedly distinct intermediate metabolites. Notably, the *pmoA* gene, encoding a critical subunit of pMMO, is conserved across the majority of methanotrophs and has been established as a key molecular marker for assessing their ecological distribution and abundance in diverse environments[36].

The central metabolic pathway of methanotrophs involves the sequential oxidation of CH_4 to methanol, formaldehyde, formate, and ultimately CO_2, catalyzed by the key enzymes mentioned above[37]. During this process, pivotal intermediate metabolites can be channeled into different carbon assimilation routes to support either cellular growth or the synthesis of specific bioproducts. Type I methanotrophs predominantly employ the ribulose monophosphate (RuMP) pathway for carbon fixation, with 3-hexulose-6-phosphate synthase acting as a key enzymatic step; whereas Type II methanotrophs utilize the serine pathway, relying on hydroxypyruvate reductase as a critical catalyst; and Type X methanotrophs primarily fix carbon via the Calvin-Benson-Bassham (CBB) cycle[4]. The diversity in phylogeny and metabolic pathways directly determines their diverse resource utilization potential. Methanotrophs employ three principal electron transfer mechanisms. Type I methanotrophs primarily utilize a direct coupling mechanism for methane oxidation, while Type II methanotrophs predominantly rely on a redox arm mechanism[38]. Under specific physiological or environmental conditions, certain methanotrophs may also engage in an uphill electron transfer mechanism[39]. This metabolic versatility not only expands their potential for applications in biomanufacturing and environmental remediation but also provides a robust physiological foundation for their industrial deployment across diverse scenarios. Metabolic pathways of methanotrophs are demonstrated in Fig. 1, while the representative genera and characteristics of methanotrophic communities are shown in Table 1.

Habitats and global prevalence

On a global scale, distinct methanotroph species possess specific habitat preferences. While the majority thrive under mesophilic and neutral pH conditions, certain methanotrophic lineages have adapted to extreme environments, displaying thermophilic, acidophilic, or alkaliphilic characteristics[70,71]. A recent study in 2025 revealed that *Mycobacterium* (Actinobacteria) also possesses methane-oxidizing capabilities, and strain MM-1 shows significant NH_3 tolerance and pH tolerance, maintaining activity even at an NH_4^+ concentration of 143 mM and pH = 4[72]. This finding has significantly expanded the known physiological boundaries of methanotrophs and provides a new microbial resource for methane emission reduction in high-ammonia environments such as livestock and poultry farms, and landfills.

In terms of specific sites, the community structure and spatial distribution of methanotrophs are co-regulated by climatic and edaphic factors. Methanotroph abundance is generally elevated in regions with favorable hydrothermal conditions[36], showing a positive correlation with pH and a negative correlation with concentrations of ammonium and nitrate nitrogen[73]. Significant functional differentiation is observed across distinct habitats, and aside from spatial heterogeneity, methanotroph populations also display marked seasonal fluctuations. For instance, their abundance in aquatic ecosystems is influenced by hydrological characteristics and seasonal variations in dissolved constituents[74]. Although summer typically offers richer nutrient availability and higher overall bacterial abundance, the relative abundance of methanotrophs in certain rivers and lakes has been reported to peak during winter[74], which may be attributed to a combination of factors such as elevated dissolved oxygen levels, reduced solar radiation, and higher organic carbon content during the colder months[75].

Cultivation and separation methods

The optimal growth temperature for most methanotrophs is approximately 30 °C, with a preferred pH near neutral (around 7.0)[76]. Nevertheless, some acidophilic and thermophilic methanotrophs have been successfully cultivated and isolated under high temperatures and low pH. For example, Verrucomicrobia bacteria can be cultivated at 55 °C and pH = 3[77]. In terms of carbon sources, methanotrophs typically use methane as a growth substrate, but they differ in substrate affinity. Low-affinity methanotrophs typically require high methane concentrations for cultivation, whereas high-affinity methanotrophs are capable of metabolizing atmospheric trace methane[78]. Commonly, standard cultivation media include nitrate mineral salts (NMS) and ammonium mineral salts (AMS)[79]. Notably, certain methanotrophic strains can fix atmospheric nitrogen, enabling growth in

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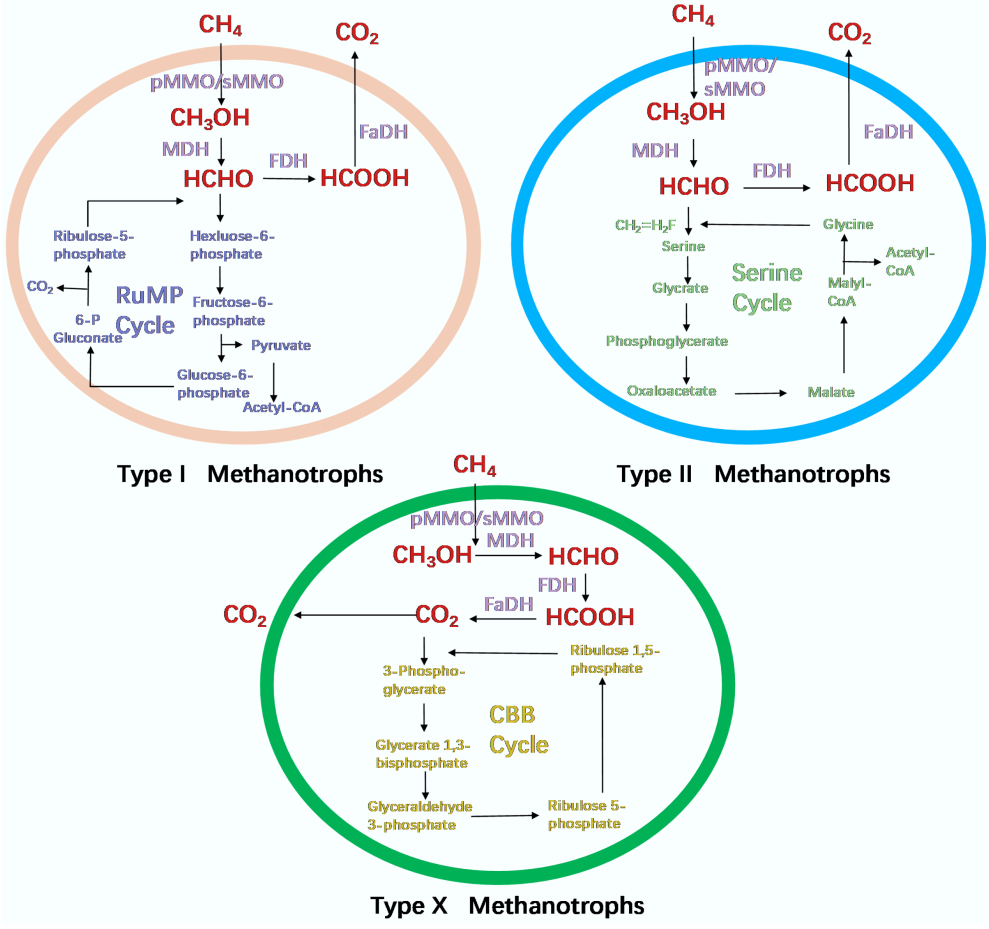

Fig. 1 Metabolic pathways of methanotrophs (adapted from Park & Kim[32]).

media devoid of exogenous nitrogen sources[80]. Beyond nitrogen, essential mineral salts must be supplemented, as several metal ions act as cofactors of key enzymes in methane oxidation. As mentioned above, MMO activity depends on Cu or Fe[35]. Similarly, the XoxF-type MDH requires lanthanide elements such as Ce, Eu, or Yb to function[81]. In addition, methanotrophs display considerable divergence in salt tolerance, because of which medium composition can be directionally optimized according to the ecological origin and physiological type of the strain. For example, dilute nitrate mineral salt (DNMS) medium may be employed for strains inhabiting low-salt environments[82]; whereas ammonium-nitrate mineral salt (ANMS) medium with 3% NaCl may be utilized for marine strains[83].

Conventional procedures for obtaining methanotrophs typically involve environmental sampling, microscopic examination, and enrichment culture[16]. Common inoculum sources include paddy soils[14,84], marine sediments[83], and biodesulfurization filter beds[85]. However, due to the propensity of methanotrophs to form microbial aggregates with heterotrophic bacteria, obtaining axenic colonies remains challenging[86]. Traditional isolation methods such as the 'dilution to extinction' technique, consume a large amount of time and effort[86]. It has been reported that increasing the dilution rate gradually can improve specific growth rate to 0.40 h^{-1}, yet this approach is generally effective only for fast-growing species[87]. In recent years, several novel separation strategies have been developed to improve the isolation efficiency of methanotrophs[16]. For instance, a label-free, high-throughput Raman-activated cell sorting platform (pDEP-DLD-RACS), pioneered by Qingdao Single-Cell Biotechnology Co., Ltd, enables rapid screening of target live cells based on metabolic function[88]. Raman flow cytometry can achieve a 58% yield improvement of docosahexaenoic acid (DHA) over wild-type strains by sorting DHA-overproducing mutants within two days[88]. This advanced methodology provides a powerful tool for the efficient and precise acquisition of functional methanotrophic strains.

Biotechnological applications of methanotrophs

Carbon mitigation and ecosystem restoration

Conventional approaches to mitigating methane emissions from various sources (such as fugitive releases during biogas utilization) often focus on suppressing methanogenesis at the source, such as adding chemical inhibitors to suppress methanogenic activity[89]. As a complementary strategy, the use of methanotrophs for methane removal offers distinct advantages, including applicability across diverse locations and emission modes[90]. For example, in mining operations, the application of ultrafine water mists containing methanotrophs has been shown to reduce methane concentrations in ambient air, lowering the risk of gas explosions[91]. Currently, a range of methanotroph-based engineering solutions has been developed, such as bio-cover systems, biofiltration units, and bacterial suspension injection, enabling efficient methane removal tailored to different operational scenarios[92]. Representative applications include exhaust

Table 1 Representative genera and characteristics of methanotrophic communities

Type	Genera	Species	Representative strains	Separation source	Characteristics	Ref.
Type I	*Methylococcus*	*Methylococcus geothermalis*	IM1	A geothermal spring	Thermophilic (48 °C)	[40]
	Methylomonas	*Methylomonas methanica*	MC09	Coastal seawater	Halotolerant (seawater)	[41]
		Methylomonas koyamae	Fw12E-Y	A rice paddy field	Methanol-utilizing	[42]
	Methylobacter	*Methylobacter tundripaludum*	SV96	Arctic wetland soil	Nitrogen-fixing (*nifH*)	[43]
	Methylovulum	*Methylovulum miyakonense*	HT12	Forest soil	Formaldehyde-assimilating	[44]
		Methylovulum psychrotolerans	Sph1	Low-temperature terrestrial environments	Psychrotolerant (2 °C)	[45]
	Methylosoma	*Methylosoma difficile*	Lc 2	Lake sediment	Nitrogen-fixing (*nifH*)	[46]
	Methylothermus	*Methylothermus thermalis*	MYHT	A hot spring	Thermophilic (67 °C)	[47]
		Methylothermus subterraneus	HTM55	Subsurface hot aquifer	Thermophilic (65 °C)	[48]
	Methylogaea	*Methylogaea oryzae*	E10	A rice paddy field	Nitrogen-fixing (*nifH*)	[49]
	Methylohalobius	*Methylohalobius crimeensis*	10Ki	Hypersaline lakes	Extremely halophilic (15% NaCl)	[50]
	Methylomarinum	*Methylomarinum vadi*	IT-4	Marine environment	Obligate marine	[51]
	Methyloprofundus	*Methyloprofundus sedimenti*	WF1	Marine sediment	Nitrogen-fixing (*nifH*)	[52]
	Methylotenera	*Methylotenera versatilis*	301	Lake sediment	Multiple substrate utilization	[53]
Type II	*Methylocystis*	*Methylocystis hirsuta*	CSC1	A groundwater aquifer	Special surface structure	[54]
	Methylocella	*Methylocella silvestris*	BL2	An acidic forest cambisol	Multiple substrate utilization	[55]
	Methylocapsa	*Methylocapsa aurea*	KYG	A forest soil	Multiple substrate utilization	[56]
	Methyloferula	*Methyloferula stellata*	AR4	Acidic *Sphagnum* peat bogst	Acidophilia (pH = 3.5)	[57]
	Methylorubrum	*Methylorubrum rhodesianum*	MB200	A household biodigester	Multiple substrate utilization	[58]
	Methylobrevis	*Methylobrevis albus*	L22	Freshwater lake sediment	Oxidase and catalase production	[59]
Type X	*Methylacidiphilum*	*Methylacidiphilum fumariolicum*	SolV	Volcanic region	Hydrogenase-possessing	[60]
		Methylacidiphilum infernorum	V4	A geothermal field	Hyperthermophilic (60 °C)	[61]
	Methylacidimicrobium	*Methylacidimicrobium fagopyrum*	3C	Volcanic soil	Acidophilia (pH = 0.6)	[62]
		Methylacidimicrobium tartarophylax	4AC	Volcanic soil	Acidophilia (pH = 0.5)	
		Methylacidimicrobium cyclopophantes	3B	Volcanic soil	Acidophilia (pH = 3.6)	
	Candidatus Methylacidithermus	*Candidatus Methylacidithermus pantelleriae*	PQ17	Volcanic environments	Sulfur-fixing (*cysD/C/H*)	[63]
Methylotrophs	*Methylophaga*	*Methylophaga marina*	ATCC 35842	Sea water	Fructose and methylamine utilization	[64]
		Methylophaga thalassica	ATCC 33146	Sea water	Fructose and methylamine utilization	
	Methylotenera	*Methylotenera mobilis*	JLW8	Lake sediment	Methylamine-utilizing	[65]
	Hyphomicrobium	*Hyphomicrobium denitrificans*	TK 0415	–	Anaerobic denitrification	[66]
	Paracoccus	*Paracoccus denitrificans*	Stanier 381	Garden soil	Hydrogen-utilizing	[67]
	Methyloversatilis	*Methyloversatilis universalis*	FAM5	Freshwater wetlands	Multiple substrate utilization	[68]
	Methylopila	*Methylopila capsulata*	IM1	Soil	Multiple substrate utilization	[69]

treatment in biogas upgrading facilities[93], rhizoremediation of diesel-contaminated soils[94], and mitigation of methane and odorous compounds in landfill sites[95]. Furthermore, during wastewater treatment, methanotrophs can simultaneously remove dissolved methane and nitrite, achieving synergistic reduction of greenhouse gases and pollutants[96].

However, the regulatory role of methanotrophs in greenhouse gas dynamics is bidirectional: while oxidizing CH_4, they may inadvertently trigger the emission of other greenhouse gases. For instance, aerobic methanotrophs can compete with denitrifying bacteria for Cu^{2+}, potentially suppressing denitrification activity and leading to N_2O release[97]. Similarly, certain anaerobic methanotrophs have been reported to generate N_2O via NO dismutation during denitrification[98]. Given that the GWP of N_2O is approximately 10 times that of CH_4 over 100 years, even minor N_2O emissions can substantially offset the climate benefits gained from CH_4 oxidation[90]. Therefore, controlling concomitant N_2O emissions is critical for maximizing net greenhouse gas mitigation. Notably, some methanotrophs possess N_2O reductase genes, enabling them to concurrently remove both CH_4 and N_2O[98]. Certain aerobic methanotrophs, such as *Methylocella tundrae* and *Methylacidiphilum caldifontis,* can grow under anaerobic conditions, using methanol or C-C substrates (such as pyruvate) as electron donors to respire N_2O, and they can also adapt to suboxic environments[99]. Anaerobic oxidation of CH_4 by aerobic methanotrophs can be coupled with denitrification, utilizing N_2O produced during denitrification as an electron acceptor, significantly reducing emissions of both CH_4 and N_2O and influencing the net greenhouse effect of the ecosystem[100]. Furthermore, the newly identified anaerobic methanotroph *Candidatus Methylomirabilis sinica* has been shown to completely reduce nitrate to N_2 via a methane-dependent denitrification pathway without N_2O production and accumulation, preventing the generation of N_2O at the source[101]. This unique metabolic capability offers a promising route for the synergistic mitigation of multiple greenhouse gases.

In addition, microorganisms, including methanotrophs, can act as effective bioindicators for oil and gas resource exploration[102]. In petroleum reservoir areas, the upward seepage of light hydrocarbons causes an increase in surface methane, which in turn induces specific changes in the abundance and community structure of methanotrophs, and a significant positive correlation has been observed between their population density and the intensity of

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hydrocarbon seepage[103]. Compared to traditional exploration techniques, which are often characterized by high costs and long operational cycles[104], microbial prospecting of oil and gas offers considerable advantages, including lower expense and higher sensitivity[105].

Synthesis of high-value products

Methanotrophs not only contribute to greenhouse gas mitigation but also synthesize a range of value-added products through carbon assimilation pathways. Currently, methanotrophs are capable of synthesizing high-value resources such as methanol[77], single-cell protein (SCP)[14], polyhydroxyalkanoate (PHA)[106], ectoine[107], fatty acids and lipids[108], succinate[109], carotenoids[82], and so on. Additionally, methanotrophs can be co-cultured with other microorganisms to produce new products such as mevalonate[110]. As shown in Fig. 2, pyruvate and acetyl-CoA play pivotal roles in the high-value product production of methanotrophs. Overall, Type I methanotrophs are suited to producing pyruvate-related products, while Type II methanotrophs are suited for products originating from acetyl-CoA. Due to the anaplerotic role of the RuMP cycle towards the tricarboxylic acid (TCA) cycle, Type I methanotrophs are more capable of producing certain products related to the TCA cycle.

However, the primary products that have reached scale-up production include methanol, SCP, and PHA[111]. Although challenges remain in regulating carbon flux and optimizing the expression of key enzymes during large-scale production[111], their application potential in sectors including food and pharmaceuticals is considerable. A systematic comparison of the production status for three major value-added products is summarized in Table 2. The cases of methanol, SCP, and PHA production by methanotrophs are shown in Tables 3, 4, and 5, respectively.

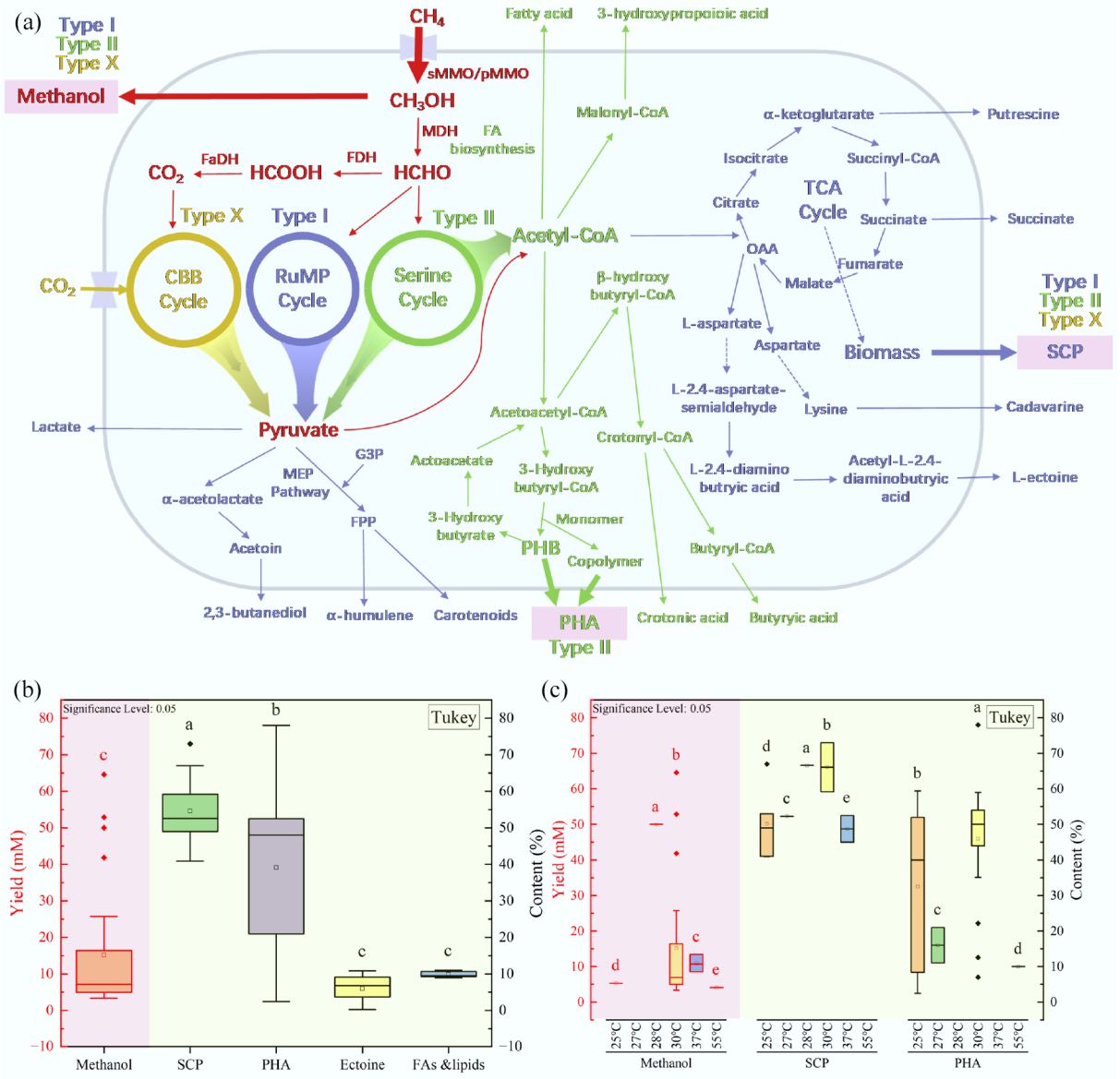

Fig. 2 Pathways for high-value product production by (**a**) methanotrophs, (**b**) yields of primary high-value products, and (**c**) yields of key high-value products with large-scale production potential at common reaction temperatures (G3P: Glyceraldehyde 3-phosphate; MEP: Methyl-erythritol Phosphate; FPP: Farnesyl Pyrophosphate; PHB: Poly-3-hydroxybutyrate; OAA: Oxaloacetate, FA: Fatty acid. Data are sourced from the literature[111], and Tables 3[112–119], 4[85,120–124], and 5[106,125–131]).

Methanol production

Methanol serves as a crucial industrial feedstock and clean fuel, valued for its high energy density and ease of storage and transportation[132], with broad applications across the energy and chemical sectors. Compared with conventional catalytic synthesis processes, which are typically energy-intensive, methanotroph-based conversion of CH_4 to methanol operates under mild conditions and offers distinct advantages such as minimal byproduct formation and reduced process carbon emissions[133]. In practical applications, the immobilization of methanotrophic cells has been shown to improve both the efficiency and operational stability of methanol production, and various materials such as coconut shell biochar, ion-exchange resins, and chemically modified chitosan have been employed as effective immobilization carriers, some of which can achieve a maximum yield increase of more than 20 times[112–114]. However, these supports differ significantly in mass transfer efficiency and operational costs, necessitating careful selection based on the specific production system. Interestingly, it has been reported that a thermophilic methanotroph species can reduce CO_2 to methanol via the CBB cycle[115], providing promising prospects for the synergistic resource utilization of greenhouse gases.

It has been indicated that the methanol production yield by methanotrophs ranges between 5.34 and 64.6 mM (Table 3)[115,116]. The production efficiency is influenced by multiple factors including strain type, gas composition, immobilization carrier, and cultivation conditions. Among the investigated species, *Methylocystis bryophila* has demonstrated robust methanol synthesis capability in several studies[113,116], and is often applied in combination with other methanotrophs such as *Methyloferula stellata*[112,114,117]. Culturing with 20%–30% CH_4 or a CH_4 : CO_2 ratio of 2:1 to 4:1 can improve the output of methanol[112–114], and coupling with 15% H_2 can attain a methanol yield of up to 64.6 mM[116]. In addition, certain methanotrophs, including *Methylocaldum* sp., exhibit notable tolerance to sulfur impurities (500 ppm H_2S), highlighting their potential applicability in the treatment of real industrial off-gases[118].

SCP production

SCP, also referred to as microbial protein, represents a resource-efficient alternative protein source[134,135]. It is characterized by rapid growth rates and high spatial productivity[136], offering a sustainable pathway to alleviate the environmental pressures associated with conventional protein production. Methanotrophs possess strong protein biosynthesis capacity and can utilize methane-containing waste gases like biogas as substrates to enable the valorization of pollutants[137]. These microorganisms can be cultivated either in pure culture or in co-culture systems with other functional bacteria, such as sulfur-oxidizing bacteria (SOB), to optimize both protein yield and amino acid profile[14,85,120]. It has been shown that methanotroph-derived SCP is rich in diverse amino acids, including essential amino acids[14], and sulfur-containing amino acids[85,120], meeting the nutritional standards for feed applications, whereas its potential use in the food industry still entails certain safety and regulatory considerations[4].

It has been indicated that SCP synthesized by methanotroph generally possesses high protein content, with reported values ranging from 41% to 73% of cell dry weight (Table 4)[85,121]. Representative methanotrophic genera employed in SCP production include *Methylococcus*[122], *Methylosinus*[123], and *Methylomonas*[121], and non-methanotrophs such as *Terrimonas*[14] and *Chryseobacterium*[85,120] are also frequently present in production consortia. In current practice, optimal SCP content is typically achieved using a CH_4 : O_2 ratio between 1:4 and 2:3[85,124], supplemented with controlled amounts of CO_2[138], and a cultivation temperature maintained within 25–37 °C[121,122].

PHA production

PHA represents a class of biodegradable polyesters that serve as environmentally friendly alternatives to conventional petroleum-based plastics[139]. To achieve cost-effective production, C1 gases such as CH_4 from biogas or industrial off-gases can be utilized as economical carbon sources for large-scale PHA synthesis by methanotrophs[140]. Within the PHA family, poly-3-hydroxybutyrate (PHB) is the most

Table 2 Comparison of high-value resource products of methanotrophs[4,15,111]

Production	Methanol	SCP	PHA
Biosynthesis pathway	Central metabolic pathway	Multiple carbon assimilation pathways	Serine carbon assimilation pathway
Producers	Type I, II, and X capable	Type I dominant, Type II, and X applicable	Primarily type II
Product value	Moderate	Relatively low	Relatively high
Commercialisation status	Not yet commercialised	Large-scale commercialisation	Small-scale commercialisation
Carbon conversion challenges	Methanol is a metabolic intermediate that is readily oxidized, leading to low accumulation.	The production requires maximized carbon flux toward biomass and suppression of complete oxidation.	The production is typically induced under nutrient imbalance, creating a growth-synthesis trade-off.
Applications	Chemical feedstocks, fuel, bioplastic precursors	Animal feed, food additives, nutrient supplements	Biodegradable plastics, biomedical materials

Table 3 Cases of methanol production by methanotrophs

Production	Output	Production condition	Corresponding producer	Ref.
Methanol	52.9 mM	30% CH_4, 30 °C, NMS medium, immobilized on coconut coir, eight repeated batch conditions	*Methylocystis bryophila*, *Methyloferula stellata*, *Methylocella tundrae*	[112]
Methanol	25.75 mM	CH_4 : CO_2 = 2:1, 30 °C, NMS medium, immobilized on chitosan, eight repeated batch conditions	*Methylocystis bryophilla*	[113]
Methanol	24.36 mM	CH_4 : CO_2 = 4:1, 30% CH_4, 30 °C, NMS medium, immobilized on chemically modified chitosan, eight repeated batch conditions	*Methylomicrobium album*, *Methylocystis bryophila*, *Methyloferula stellata*	[114]
Methanol	5.34 mM	Cultivation in biogas containing CH_4, 25 °C, AMS medium, six repeated batch conditions	Primarily *Methylobacter* and *Methylosarcina*	[115]
Methanol	64.6 mM	30% CH_4, 15% H_2, 30 °C, NMS medium, six repeated batch conditions	*Metholosinus sporium*, *Methylocystis bryophila*	[116]
Methanol	16.4 mM	30% CH_4, 15% CO_2, 30 °C, NMS medium, immobilized on synthetic precursor solution, ten repeated batch conditions	*Methyloferula stellata*, *Methylocystis bryophila*	[117]
Methanol	8.59 mM	CH_4 : air = 1:4, 37 °C, NMS medium, 500 ppm H_2S	*Methylocaldum* sp.	[118]
Methanol	5.37 mM	30% CH_4, 30 °C, NMS medium, immobilized on polyvinyl alcohol, five repeated batch conditions	*Methylocystis bryophila*, *Methyloferula stellata*	[119]

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Table 4 Cases of SCP production by methanotrophs

Production	Content	Production condition	Corresponding producer	Ref.
SCP	56.10% ± 10.99%	CH_4 : O_2 = 1:2, NMS medium, 2,973 ppm H_2S	Primarily *Methylocystis* and *Terrimonas*	[14]
SCP	73% ± 5%	CH_4 : O_2 = 2:3, 30 °C, NMS medium, 1,500 ppm H_2S	Primarily *Methylocystis* spp. and *Chryseobacterium* spp.	[85]
SCP	59.2% ± 3.6%	CH_4 : CO_2 = 70:30 or 50:50, CH_4 : O_2 = 2:3, 30 °C, AMS medium, 4,000 ppm H_2S	Primarily *Methylocystis* spp. and *Chryseobacterium* spp.	[120]
SCP	41% ± 2.0%	CH_4 : O_2 = 1:2, 25 °C, dAMS medium	Primarily *Methylophilus* sp.1 and *Methylomonas* sp.1	[121]
SCP	45%	60% CH_4, 30% O_2, 10% CO_2, 37 °C, cultivation in wastewater containing NH_4^+	*Methylococcus capsulatus*	[122]
SCP	52.3%	60% CH_4, 40% CO_2, 27 °C, AMS medium	Primarily *Methylosinus* and *Methylococcus*	[123]
SCP	67%	CH_4 : O_2 = 1:4, 25 °C, AMS medium	Primarily *Methylomonadaceae* and *Methylococcaceae*	[124]
SCP	50.2%	Primarily CH_4 : O_2 : CO_2 = 1:2:0.05, NMS medium	Primarily *Methylococcus* and *Methylotenera*	[138]

dAMS: dilute ammonium mineral salt.

prevalent homopolymer[141], exhibiting mechanical properties comparable to those of traditional polyolefins[111]. Methanotrophs possess the capacity to accumulate intracellular carbon reserves, with PHA primarily synthesized by Type II strains, whereas Type I strains tend to produce extracellular polysaccharides[125].

It has been indicated that the methanotroph-derived poly-3-hydroxybutyrate (PHB) content can reach up to 59.4% (Table 5)[126]. The polymer composition can be modulated by supplementing specific co-substrates. For instance, the addition of valerate promotes the incorporation of 3-hydroxyvalerate monomers, leading to the formation of poly(3-hydroxybutyrate-co-3-hydroxyvalerate) (PHBV) copolymers with improved mechanical properties[127]. *Methylocystis sp.* MJC1 has been reported to synthesize PHBV copolymers with a content of 41.9%. In an optimized medium, *Methylocystis parvus* OBBP reached a PHA content of approximately 54%[128]. Under specific recovery strategies, genera such as *Methylocystis* and *Pseudomonas* can reach PHB content approaching 60%[126]. Optimal production conditions, typically involving a CH_4 : O_2 ratio between 1:1 and 2:3[128,129] and a temperature range of 25–30 °C[126,128], are critical for achieving high PHA accumulation.

Metabolic regulation for resource valorization

In the high-value resource valorization of methanotrophs, precise metabolic regulation is key to enhancing the synthesis efficiency of target products. Depending on the characteristics of the desired metabolites, mixed-culture strategies are often employed to optimize system performance through microbial synergies (cross-feeding)[142]. For instance, co-culturing methanotrophs with SOB enables the removal of H_2S from biogas, alleviating its inhibitory effect on methanotrophic activity[120]. Similarly, the presence of methylotrophs facilitates the timely consumption of metabolic intermediates such as methanol generated during methane oxidation, preventing feedback inhibition and improving the overall methane oxidation rate[33]. By sharing metabolic byproducts, different microbial species form complementary and symbiotic relationships that help overcome inherent limitations of methanotrophs, including slow growth and sensitivity to accumulated metabolites[33]. Beyond microbial interactions, the modulation of environmental and nutritional factors can effectively direct carbon flux toward target product synthesis. Optimizing the CH_4 : O_2 ratio, adjusting temperature, selecting appropriate nitrogen sources, and regulating the concentrations of trace elements such as Cu and Fe have all been demonstrated to improve the efficiency of methane-based bioconversion.

Reprogramming central metabolism for methanol yield

The high-yield accumulation of methanol relies on the precise regulation of central carbon metabolism—facilitating the conversion of CH_4 to methanol while moderately suppressing its downstream oxidation. As the first intermediate in the methanotrophic pathway, methanol contains C–H bonds that are more readily cleaved than those of CH_4, rendering it prone to further oxidation[143]. Since methanotrophs constitutively express MDH, which continuously catalyzes methanol oxidation, effective production strategies require targeted inhibition of MDH activity to facilitate methanol accumulation[32]. However, such metabolic interventions must account for cellular energy balance. The oxidation of CH_4 to methanol is an energy-consuming process that relies on reducing equivalents such as nicotinamide adenine dinucleotide (NADH), whereas subsequent methanol oxidation helps regenerate NADH, thereby forming a cyclic energy supply[144]. Complete inhibition of MDH would lead to NADH depletion, which in turn hinders the initial oxidation step of CH_4. Therefore, the ideal strategy is to partially inhibit MDH, enabling net methanol accumulation while maintaining sufficient NADH regeneration[144]. In practice, the extracellular hyperaccumulation of

Table 5 Cases of PHA production by methanotrophs

Production	Content	Production condition	Corresponding producer	Ref.
PHA	12.6% ± 2.4%	20% CH_4, 30 °C, AMS medium	Primarily *Methylocystis*	[106]
PHB	48.7% ± 1.2%	CH_4 : O_2 = 1:1, 30 °C, NFMS medium	Primarily *Methylophilus* and *Methylocella*	[125]
PHB	59.4% ± 4.5%	CH_4 : O_2 = 1:1, 25 °C, AMS medium, recycle PHB producers after accumulation	Primarily *Methylocystis* and *Pseudomonas*	[126]
PHBV	41.9%	30% CH_4, 30 °C, NMS medium	*Methylocystis* sp. MJC1	[127]
Mutiple PHA	50% ± 4% to 56% ± 4%	CH_4 : O_2 = 2:3, 30 °C, JM2 medium (modified AMS medium)	*Methylocystis parvus* OBBP	[128]
PHB	22.20%	CH_4 : O_2 = 1:1, 30 °C, NMS medium	Primarily *Methylocystis*	[129]
PHBV	35%	0.5 atm CH_4, 0.33 atm O_2, 38 °C, AMS medium	*Methylosinus thricosporum* OB3b	[130]
PHB	52.9% ± 4%	CH_4 : O_2 = 1:1, 25 °C, AMS medium	Mutiple methanotrophs	[131]

NFMS: nitrate free mineral salt.

methanol can be achieved by reducing the concentration of lanthanides in the medium to inhibit MDH activity[77] or by adding specific enzyme inhibitors such as cyclopropanol[143]. The intracellular NADH/NAD^+ ratio serves as a key indicator of the cellular redox state, providing a basis for the dynamic regulation of inhibitor dosage[144]. In summary, by finely balancing MDH activity with energy metabolism, it is possible to significantly increase methanol yield under mild reaction conditions and overcome the long-standing challenge of its rapid over-oxidation.

Enhancing carbon assimilation for protein synthesis

In SCP production, the core objective of metabolic regulation is to maximize biomass yield by directing carbon and energy fluxes toward cellular biosynthesis. Type I methanotrophs are considered preferred candidates for SCP production owing to their rapid growth rates. However, under nitrogen-limited conditions, these microorganisms tend to redirect carbon flux toward the synthesis of storage compounds such as extracellular polysaccharides[125], which can reduce protein yield. Therefore, maintaining an appropriate C/N ratio and ensuring sufficient nitrogen supply are critical to sustaining efficient protein synthesis. It has been shown that the $CH_4 : O_2$ ratio significantly influences nitrogen assimilation efficiency. For instance, at a $CH_4 : O_2$ ratio of 2:3, nitrogen assimilation approaches completion[85], improving protein synthesis efficiency. Moreover, precise editing of metabolic pathways via synthetic biology, such as the knockout of glycogen synthase or glucokinase genes, can effectively suppress carbon storage formation[145], redirecting more carbon toward protein accumulation. In summary, systematically optimizing cultivation conditions and gas composition, combined with genetic engineering to fine-tune metabolic flux, provides a dual strategy for improving the conversion efficiency of carbon and nitrogen and maximizing protein yield.

Metabolic regulation for PHA hyperconcentration

In the production of PHA, the central aim of metabolic regulation is to leverage the synthetic capacity of Type II methanotrophs by redirecting carbon flux toward storage polymer synthesis under specific nutrient-limiting conditions. Type II methanotrophs act as the primary microbial workhorses of PHA synthesis, and their pure culture system is more conducive to the efficient accumulation of PHA[130]. However, in industrial settings, inocula often consist of mixed communities of Type I and Type II methanotrophs, where interspecific competition can compromise the stability of PHA production. NH_3, due to its structural similarity to CH_4, acts as a competitive inhibitor of MMO activity, and this inhibition is more pronounced in Type I methanotrophs, thereby providing a selective advantage to Type II strains and helping them dominate the microbial community[126]. Nevertheless, if the sludge retention time (SRT) is excessively prolonged, Type I methanotrophs may adapt to the NH_3 stress and re-establish dominance, ultimately reducing PHA synthesis efficiency[131]. In addition, the capacity for PHA accumulation varies across growth phases, with higher synthesis rates typically observed during the lag and exponential phases compared to the stationary phase[79]. Therefore, appropriately optimizing operational conditions to extend the duration of these two phases may represent a viable strategy for improving overall PHA productivity.

The synthesis efficiency of PHA is regulated by multiple environmental parameters, including carbon source availability, temperature, pH, and the type of nitrogen source. Appropriately increasing the partial pressure of CH_4 can improve O_2 utilization and promote PHA accumulation[130]. Certain non-growth co-substrates such as ethane may inhibit methane oxidation, yet their metabolic derivative acetate can act as a precursor of PHA biosynthesis, indirectly facilitating polymer formation[146]. Temperature and pH exert selective influences on community structure. When strains with strong PHA production capabilities become dominant, the yield is improved. For instance, the higher abundance of *Methylocystis* facilitates PHA production at 25–30 °C, while deviations from this range can significantly impair metabolic activity[147]. Similarly, while genera of high-yield PHA, such as *Methylocystis*, exhibit a competitive advantage within pH 5.5–7.0, which is conducive to PHA production[148]. There remains considerable controversy regarding nitrogen source selection: some studies suggest nitrate is preferable due to its minimal inhibitory effect on MMO activity[149], whereas others report that ammonium exerts weaker inhibition on Type II methanotrophs harboring ammonium tolerance genes, which facilitates their enrichment[126]. No-nitrogen (NoN) conditions can trigger PHA accumulation as a carbon reserve[79], but they also retard biomass growth. Therefore, future research may need to tailor nitrogen source strategies according to the genetic background of specific strains and process objectives rather than seeking a universal solution.

To achieve high-efficiency synthesis of PHA, a variety of strategic approaches have been developed. The selection of inoculum sources selection is fundamental, with priority given to environmental samples enriched with Type II methanotrophs. For example, methanotrophs derived from *Sphagnum* moss can raise the baseline potential of the production system[150]. At the process level, biomass recycling after the PHA accumulation phase can help reduce the proportion of Type I methanotrophs, while alternating nitrogen supply regimes can optimize resource allocation between growth and synthesis phases[126]. It has been indicated that nitrogen-feeding and starvation cycles of 8 h:16 h or 24 h:24 h yield the best results, whereas excessively long nitrogen starvation (2-fold higher than the feeding duration) inhibits PHA production[151]. Furthermore, the construction of co-culture systems coupling methanotrophs with heterotrophic bacteria such as *Methylocystis sp.* OK1 with *Escherichia coli* BL21 (DE3) enables multi-directional cross-feeding[152]. In such systems, intermediates like acetone generated by *Methylocystis* can be utilized by *E. coli* for heterologous PHA synthesis, extending carbon flux and doubling overall productivity[152]. Looking forward, metabolic regulation in PHA production should evolve from single-factor optimization toward multi-scale metabolic network engineering. Integrating strain selection, process control, and system coupling will pave the way for comprehensive efficiency enhancement.

Conclusions and outlook

Methanotrophs play a pivotal role in the global carbon cycle and hold significant potential for sustainable biomanufacturing. They demonstrate considerable promise in methane emission mitigation, ecological restoration, and the synthesis of high-value products such as green methanol, SCP, and PHA. The discovery of novel species with unique traits like ammonium tolerance and pH tolerance, as well as direct denitrification, further expands their application scope. However, challenges in cultivation, metabolic complexity, and process stability hinder their large-scale deployment. Future efforts should leverage synthetic biology to construct high-capacity microbiological strains and synthetic consortia and even engineer strains with enhanced product yields, develop advanced bioreactors for optimized operation, and establish robust life-cycle assessments to evaluate sustainability. The integrated application of multiple technologies enables the full

exploitation of methanotrophs' metabolic potential, which plays a crucial role in driving the large-scale application of negative carbon biotechnology, facilitating carbon neutrality goals, and accomplishing the synergistic control of environmental pollution.

Author contributions

The authors confirm their contributions to the paper as follows: conceptualization: Qigui Niu; investigation: Jingrui Deng, Qigui Niu; writing–Original draft: Jingrui Deng, Junpeng Qiao; writing–review and editing: Qigui Niu, Siyuan Ye, Feiyang Lin, Yu-You Li; visualization: Jingrui Deng; supervision: Qigui Niu. All authors reviewed the results and approved the final version of the manuscript.

Data availability

All data generated or analyzed during this study are included in this published article.

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Declarations

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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