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Converting methane into electricity and higher-value chemicals at scale via anaerobic microbial fuel cells

Thomas K. Wood [a], [**], Ilke Gurgan [a], Ethan T. Howley [b], Ingmar H. Riedel-Kruse [b], [c], [*]

[a] Department of Chemical Engineering, Pennsylvania State University, University Park, PA, 16802, USA
[b] Department of Molecular and Cellular Biology, University of Arizona, Tucson, AZ, 85721, USA
[c] Departments of Applied Mathematics, Physics and Biomedical Engineering, University of Arizona, Tucson, AZ, 85721, USA

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ABSTRACT

Methane (CH_4) is the second most damaging greenhouse gas by absolute amounts released. Many globally distributed methane sources are of human origin, representing a significant untapped potential for capture and on-site conversion into electricity or 'higher value' chemicals. This study systematically and quantitatively analyzes the anaerobic oxidation of methane (AOM) in microbial fuel cells (MFCs) for generating electric power as well as analyzes AOM in bioreactors for producing value-added chemicals. The maximum performance of such systems is currently unknown. Based on biophysical arguments, power densities of 10 kW/m^3 and more should be achievable, and Coulombic, carbon conversion, and energy conversion efficiency could reach 90%. Such performance is much higher than what is usually predicted. This AOM MFC approach promises higher efficiency, scalability, cost-effectiveness, and easier distribution compared to existing chemical plants or aerobic biological approaches. Yet achieving this requires significant and integrated advancement of different technologies. This analysis provides an accessible primer for the necessary interdisciplinary research effort, and discusses recent enabling biotechnological advancements, open research questions and corresponding R&D pathways, where enzyme and synthetic microbial consortia engineering, microfluidic technologies, membrane and electrode materials, modular system integration, and power optimization technology will likely be critical. In conclusion, AOM MFC is a very promising technology as the performance limits estimated here show, and if realized at scale, a significant impact on green-house gas reduction and sustainable, on-demand electricity and chemical (fuel) production could be achieved; this analysis could also aid the rational MFC design for other chemical reactions.

1. Introduction

Methane (CH_4) is both a potent greenhouse gas (GHG) and a key energy source. Compared to CO_2, methane is 28 times more damaging per molecule over a 100-year period, and it is the second-most damaging GHG by absolute amounts released [1–3]. It represents 20% of anthropogenic GHG emissions, and it is released through a variety of sources, such as enteric, hydroelectric dams, oil and gas drilling sites, rice farming, landfills, permafrost thaw, coal mines, biomass burning, domestic and industrial wastewater, and livestock manure – with the first three contributing over 50% [4]. These sources are globally distributed, often localized at remote locations, and they occur at various sizes. Through advances in hydraulic fracturing, remote sources of methane may now be mined economically, and recoverable methane shale reserves are vast (7,200 trillion cubic feet) [5]. The latest IPCC (Intergovernmental Panel on Climate Change) report particularly highlighted atmospheric methane reduction as an urgent need and opportunity to combat climate change [2].

Conventional approaches of methane capture and conversion require large capital outlays, which are not practical for the many smaller methane source sites. Specifically, chemical plants to produce liquid fuels often utilize Fischer-Tropsch processes [6], and their construction requires investment up to $20 billion per facility [7]. There is also 8% methane release at the start of this process due to leaking at the fracturing sites [8], which can lead to greenhouse gas equivalents that exceed those of CO_2 released from methane combustion. For generating electricity, methane is converted via classic combustion approaches or in a non-biological fuel cells [9]. Combustion machines in general often have low energy conversion efficiency of about 35% due to operational

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[*] Corresponding author. Department of Molecular and Cellular Biology, University of Arizona, Tucson, AZ, 85721, USA.

[**] Corresponding author. Department of Chemical Engineering, the Pennsylvania State University, University Park, PA, 16802, USA.

E-mail addresses: twood@engr.psu.edu (T.K. Wood), ingmar@arizona.edu (I.H. Riedel-Kruse).

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Nomenclature

Abbreviations

AOM	anaerobic oxidation of methane
MFC	microbial fuel cell
GHG	greenhouse gas
ANME	anaerobic methanotroph
MBfR	membrane-biofilm reactor
PBS	phosphate-buffered saline
R&D	research and development
IPCC	intergovernmental panel on climate change
PVS	photovoltaic system

Chemical Formulas

CH_4	methane
CO_2	carbon dioxide
O_2	oxygen
H^+	hydrogen ion
OH^-	hydroxide
HCO_3^-	bicarbonate
H_2O	water
CH_3COO^-	acetate
$[Fe(CN)_6]^{3-}$	ferricyanide
$[Fe(CN)_6]^{4-}$	ferrocyanide
CoP	cobalt (III) phosphide
MnO_2	manganese (IV) oxide
$Fe–N_4$	iron based catalytic material with nitrogen at 1:4 composition
MgO	magnesium oxide

Notations

CoM	coenzyme M
CoMS-SCoB	heterodisulfide of coenzyme M and coenzyme B
Mcr	methyl-coenzyme M reductase
MtaABC	methanol:coenzyme M methyltransferase
Car	carboxylic acid reductase
Adh	alcohol dehydrogenase
MA	acetyl-CoA acetyltransferase
Hbd	3-hydroxybutyryl-CoA dehydrogenase
Crt	crotonase
Ter	*trans*-enoyl-CoA reductase
AdhE2	aldehyde/alcohol dehydrogenase
pH	potential hydrogen
T	time
e^-	electron
ΔG	change in Gibbs free energy
E	energy
n	number of moles
F	Faraday constant
P_V	power density per volume
P_A	power density per area
I_A	current density per area
L	length
k_La	volumetric mass transfer coefficient
σ	conductivity
R	flow rate of gas molecules
R_Ω	electric resistance
A	area
(g)	gas phase
(l)	liquid phase
ρ	enzyme packing density
f	mass flux
k	enzymatic rate constant
d	cell diameter
L_S	system overall thickness
L_B	biofilm thickness
L_N	Membrane thickness
L_{ES}	electrode separation
L_M	MFC reactor thickness
c	concentration

Units

m	meter
mm	millimeter
μm	micrometer
m^2, m^3	squared, cubed meter
s	second
h	hour
g	gram
Tg	teragram
l	liter
ml	milliliter
M	mole per liter
mM	millimole per liter
mol	mole
J	joule
kJ	kilojoule
A	ampere
V	volt
W	watt
kW	kilowatt
mW	milliwatt
C	coulomb
S	siemens
K	kelvin

Symbol

$	United States dollar

constraints [10], while industrial gas turbines meanwhile reach 64% [11]. Using the ‘waste heat’ for other purposes like heating homes or driving thermoelectric generators can of course increase the overall economic and ecological utility of combustion approaches [12–14]. Long-distance transport of methane from many field sites to such facilities is often challenging and not considered economical, leading to burning or even uncontrolled atmospheric release of the methane [8, 15]. Hence there is a significant environmental need and economic opportunity for flexible, low-cost, small-scale systems to be deployed at various field sites that convert methane into electricity or value-added chemicals while preventing the methane from escaping into the atmosphere.

Emerging technologies based on the anaerobic oxidation of methane (AOM) [3] for generating electricity in microbial fuel cells (MFCs) [16] and value chemicals in bioreactors more generally [17] provide exciting alternatives for methane capture as illustrated in Fig. 1A. A microbial fuel cell is a bio-electrochemical system that uses microbes to convert chemical energy into electric current; Fig. 1B provides typical components and potential reactions inside such AOM MFC [16]. Biological methane conversion is expected to be more economical and environmentally sustainable and less-technologically-complex while having a smaller footprint than the above-mentioned existing technologies, and high-temperature heat loss and corrosive media are avoided [18]. One can distinguish between aerobic and anaerobic methane oxidation, where the latter is generally preferable as it has significantly higher turnover efficiency, at the expense of slower microbial growth [7]. Such

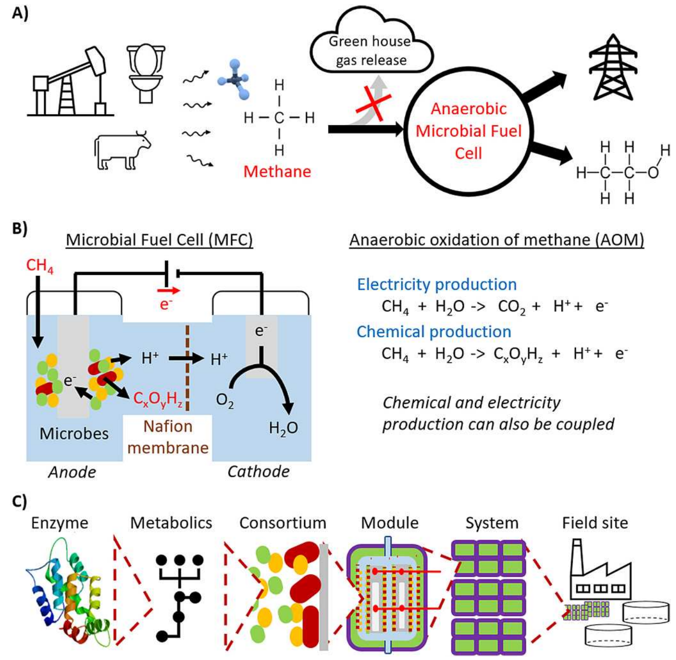

Fig. 1. Anaerobic oxidation of methane in microbial fuel cells (AOM MFC) provides new opportunities for green-house gas (GHG) reduction while generating electricity and value-added chemicals. A) Methane source-to-product flow chart. **B)** Illustration of AOM to generate electricity or chemicals or both. Note: stoichiometry is simplified. The reactions shown correspond to the reactions at the anode and happen without oxygen; ultimately, secondary oxidizing reactions are required at the cathode to capture H^+ and e^- (here illustrated with ferricyanide, but other options exist including oxygen). **C)** Multi-scale systems engineering approach for designing efficient AOM MFCs.

anaerobic cells for electricity generation are termed AOM MFCs [1,16,19]. The number of publications on MFCs have been (exponentially) increasing over the past 15+ years – and a number of excellent reviews exist that cover these and related concepts, and multiple primary studies address the conversion of methane to electricity (and also value chemicals) [18,20–32]. These studies describe a variety of successful explorations and options for this technology, yet systematic optimization on all levels as illustrated in Fig. 1C, i.e., from enzyme engineering to field-site integration, is in its infancy, and the highly interdisciplinary aspects of this field appear to make coherent development challenging.

Therefore, this work now provides an analysis focusing on the opportunities and challenges of AOM MFCs. First, the key advances for the bioconversion of methane into electricity and chemicals are reviewed. Then the biophysical performance limits of such systems are derived, and key components and their optimization potential, especially regarding ‘flux optimization,’ are quantitatively discussed. Key aspects of multiscale bioengineering and optimization from enzymes to microbial consortia are highlighted. The analysis also briefly touches on aspects relevant for practical deployment. Finally, key open questions for future R&D are provided. This work primarily focuses on electricity generation from methane, but much of the analysis applies to the production of chemicals from methane, or even other bioelectrochemical conversions [20] not involving methane.

2. Background: genetic engineering of microbes to convert methane into value-added chemicals and electricity

To bio-capture methane and to convert it into electricity or chemicals is to mimic nature. Up to 300 Tg of methane per year are captured by the anaerobic oxidation of methane (AOM) by microorganisms in ocean sediments as part of the global flux of methane in the carbon cycle [19]; this prevents 88% of the leaking methane from the ocean floor from reaching the atmosphere [33]. However, AOM in nature is achieved via poorly-characterized natural consortia of an anaerobic methanotrophic archaeal population (ANME - anaerobic methanotroph) and syntrophic bacteria. The enzyme to achieve this conversion is methyl-coenzyme M reductase (Mcr) [34]. The bacteria and archaea of these consortia have never been grown as pure cultures due to their long lag phase (~60 years) [35] and doubling times (~7 months) [36]. Hence direct use or genetic modification of these species for biological methane capture and conversion applications is very challenging.

A significant step forward was the insertion of Mcr from ANME-1 (population from a Black Sea mat [34,37]) into the culturable archaeal strain *Methanosarcina acetivorans* [38] and the subsequent reversal of methanogenesis in order to synthesize chemicals, i.e., acetate [39] and later lactate [17]. *M. acetivorans* was chosen [39,38] as it is genetically tractable and usually produces methane and therefore naturally has already many of the relevant co-factors [40]. *M. acetivorans* has its own Mcr version, but the ANME-1 was much more efficient as it has evolved for methane conversion rather than genesis. Various electron acceptors were tested and 10 mM $FeCl_3$ was found to be optimal [39]. The cells grew into a biofilm on solid $FeCl_3$ and increases in cell density and total protein as well as acetate production were observed [39]. Subsequently, this strain was further modified to produce the 3-hydroxybutyryl-CoA dehydrogenase (Hbd) from *Clostridium acetobutylicum,* which led to the conversion of methane to optically pure L-lactate, a pre-cursor of biodegradable plastic [17]. This anaerobic approach also showed a 10-fold greater yield than aerobic methane to lactate conversion [41], representing the first metabolic engineering of a methanogen with a synthetic pathway. Hence, methanogenesis was reversed for the first time [39] as shown in Fig. 2A–C, and this approach can now be adapted and optimized to many other value chemicals including fuels, such as butanol [42], methanol, and ethanol as illustrated in Fig. 2D, and which are often easier and more cost-effective to transport than methane [8].

The second successful application of the reversal of methanogenesis was the generation of electricity via a three-species synthetic consortium inside an MFC [16] and the subsequent systematic performance improvement [1] as illustrated in Fig. 2. In this consortium, the ANME Mcr-producing *M. acetivorans* (as before) consumed methane to produce oxidized intermediates (including acetate and electrons), which were then consumed by the bacterium *Geobacter sulfurreducens* [16] to produce additional electrons to facilitate electron transport to the anode. *M. acetivorans* also donated electrons to *G. sulfurreducens*, which used multi-heme cytochromes to rapidly transfer electrons to shuttles produced by the bacterium *Paracoccus denitrificans* [16] (*P. denitrificans* had been identified before as a key component in a less specific sludge). The electrons were consumed by converting ferricyanide to ferrocyanide at the cathode to complete the circuit for the generation of electricity [16] as ferricyanide leads to greater power densities [45,46]. This ultimately created an MFC that converted methane directly into significant electrical current. This MFC as shown in Fig. 2A consisted of two 155 ml bottle chambers separated by a treated Nafion 117 proton exchange membrane. The anode and cathode consisted of a carbon fiber brush electrode and a carbon cloth circle, respectively. A maximum power density of 0.17 W/m^2 and 90% Coulomb efficiency was reported [16].

Subsequent work systematically and significantly increased this electric power output to $I_A = 5.2\ W/m^2$ with a high current density of $I_A = 7.3\ A/m^2$ by adding electron carriers (humic acids) [1], which provided 100 times more current and 25 times more power than the best aerobic methanotrophic MFCs achieved very recently [28]. Various groups have generated electricity from methane anaerobically with different approaches and MFC designs [26,29], and methane has been aerobically converted using methanotrophs to methanol, which was converted into electricity [101] and Coulomb efficiencies of 8%–90% and maximum power densities of $I_A = 0.6\ mW/m^2$-$5.2\ W/m^2$ were reported. Note that most environmental processes occur within microbial consortia [47], and the natural process for oxidizing methane occurs in a

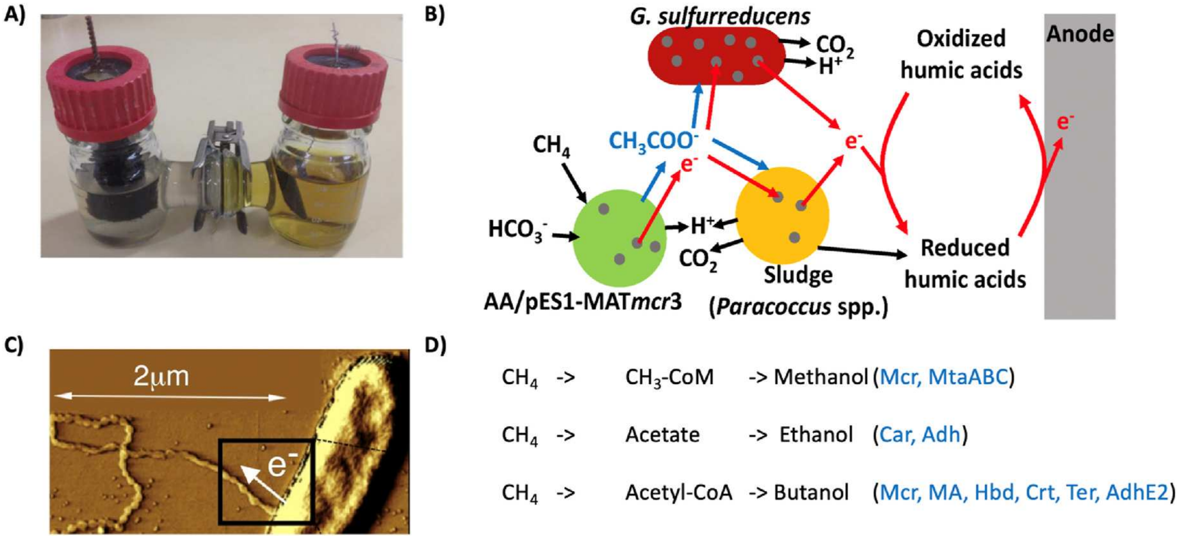

Fig. 2. AOM MFCs for converting methane into electricity and value-added chemicals have recently been demonstrated. A) Example of an MFC for methane to electricity and chemical conversion utilizing a microbial consortium engineered to reverse methanogenesis [1,16]. **B)** Anode compartment from (A) under methane headspace with *M. acetivorans* (MAT*mcr*3 enzyme), *G. sulfurreducens*, and sludge [1,16]. **C)** Electron pili for electron conductance [43,44].). **D)** Future options for converting methane into value chemicals; key enzymes in blue [17,39] (Mcr: methyl-coenzyme M reductase, MtaABC: methanol:coenzyme M methyltransferase, Car: carboxylic acid reductase, Adh: alcohol dehydrogenase, MA: acetyl-CoA acetyltransferase, Hbd: 3-hydroxybutyryl-CoA dehydrogenase, Crt: crotonase, Ter: *trans*-enoyl-CoA reductase, AdhE2: aldehyde/alcohol dehydrogenase). (Images adapted from A, B [16]; C [44].).

consortium as well [48], essentially enabling a division of labor. Hence electricity was produced from methane anaerobically, and a deliberate synthetic consortium (rather than unspecific sludge or just a single species) also significantly improved performance [16], which should be a focus when engineering future MFCs and which is discussed in the following sections.

3. Theoretical and practical performance limits for AOM MFC methane to electricity conversion

Motivated by these in-lab proof of concept MFCs, this work now systematically analyzes the theoretical and practical performance limits when generating electricity from methane, and how various system parameters can then be tuned to optimize overall performance. Here anaerobic conditions are considered, with acetate as a possible intermediate, and eventual turnover into oxygen and water. Other reactions and final products could be considered, but the following analysis illustrates the key points and quantitative analysis approach. More details on fuel cell thermodynamics can be found in Ref. [49].

Many performance parameters should be considered, such as voltage, power output, power density (per system volume or electrode area), current density, heat loss, and overall system size; downstream application aspects like production cost or maintenance are not considered here. Comparing published MFCs can be challenging as definitions and measurement procedures for these parameters sometimes vary, and since often only a subset of parameters is reported [20,21,50,51].

As an example, the following sub-reactions inside the MFC are assumed. At the anode:

$$4CH_4 + 2HCO_3^- \rightarrow 3CH_3COO^- + 9H^+ + 8e^- \quad \text{(R1)}$$

$$3CH_3COO^- + 6H_2O \rightarrow 6CO_2 + 21H^+ + 24e^- \quad \text{(R2)}$$

This combines to:

$$CH_4 + 2H_2O \rightarrow CO_2 + 8H^+ + 8e^-$$

here $2HCO_3^-$ are replenished by $2CO_2 + 2H_2O \rightarrow 2HCO_3^- + 2H^+$. R_1 and R_2 were realized in Ref. [1,16]. For the cathode reaction and for maintaining the pH [52] it is assumed:

$$8e^- + 2O_2 + 4H_2O \rightarrow 8OH^- \quad \text{(R3)}$$

$$8OH^- + 8H^+ \rightarrow 8H_2O \quad \text{(R4)}$$

This then leads to the complete 'combustion',

$$CH_4\ (g) + 2O_2\ (g) \rightarrow CO_2\ (g) + 2H_2O\ (l) \Delta G_{Methane} = -891\ \text{kJ/mol} \quad \text{(Rtotal)}$$

Complete conversion of chemical into electric energy determines the maximal possible cell voltage $E = -\Delta G_{Methane}/n/F = 1.15$ V, with $F = 96{,}485$ C/mol being the Faraday constant and $n = 8$ the number of electrons donated per methane molecule to oxygen, and assuming standard conditions of 300 K and 100 kPa [21].

The theoretical thermodynamic efficiency of a fuel cell can get into the range of 90–100% [10,53]. To achieve these efficiencies in MFCs, the energy contained in all the reaction intermediates would have to be recovered [7]. Coulomb efficiencies above 90% in MFCs have been reported [16], where Coulomb efficiency is defined as the percentage of electrons that transfer from the reactant to the product contribute to the electrical current that runs through the external load between the anode and cathode. Practical energy conversion efficiencies of MFCs of 50% [21] and even 85% [54] have already been reported. There are practical trade-offs between efficiency vs. reaction speed and reactant conversion percentage ('carbon efficiency'). Contrary to common misconceptions, combustion engines could also reach ~100% efficiency when executing the same reaction, but it is impractical to drive these engines under the necessary extreme conditions; see Lutz [53] and others [10] for a deeper discussion. Also note that a more holistic view of 'efficiency' should include other uses for the 'lost energy', such as heating homes or green-houses, which applies to both MFCs and combustion engines [12–14].

This poses the question on what the theoretical and practical performance limits of an AOM MFC are. Based on the following back-of-the-envelope 'bottom-up' estimate as illustrated in Fig. 3 and published experimental data, power densities per system volume of about $P_V = 10$ kW/m^3 could be practically achievable in $L_B = 10$ µm thick biofilms containing (spherical) cells with an effective diameter of $d = 1$ µm diameter and that are packed with enzymes at adensity of $\rho = 8{\times}10^5$

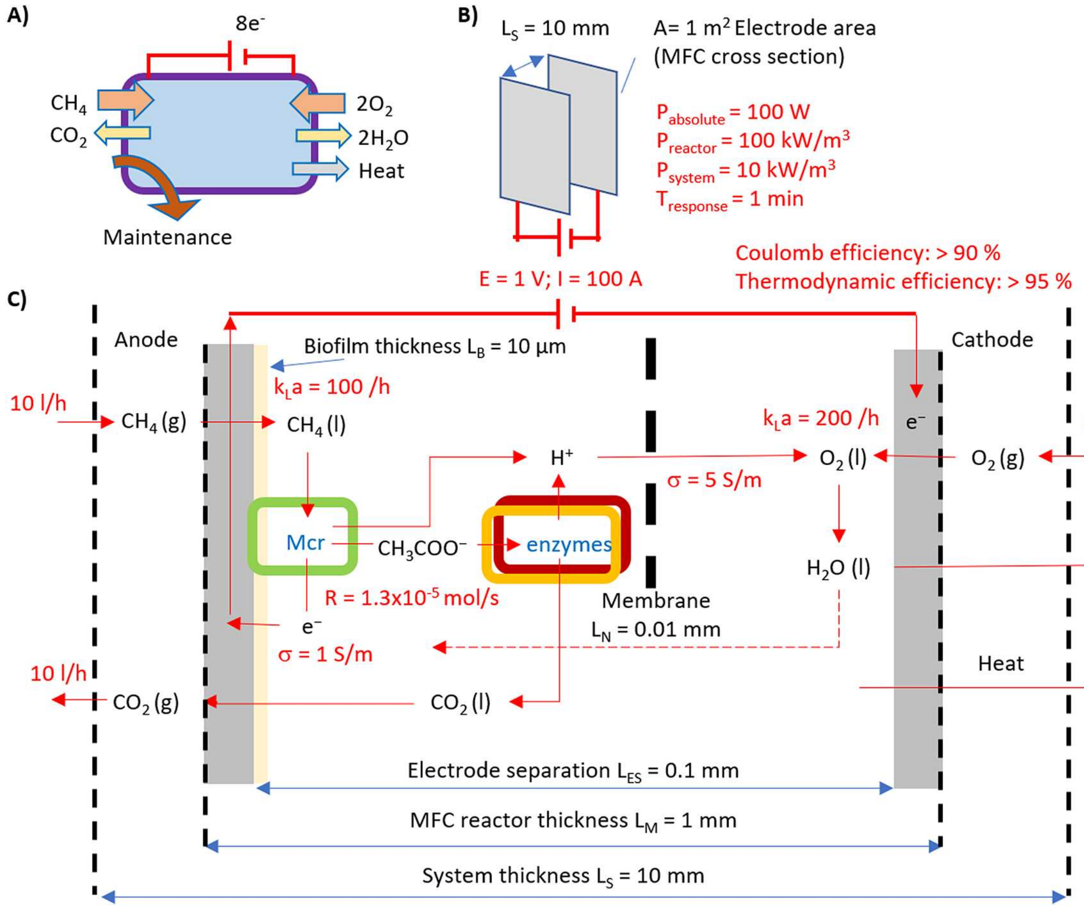

Fig. 3. A 'bottom-up' quantitative analysis of key fluxes reveals that AOM MFCs could in principle reach power densities similarly to other power conversion systems like combustion engines and photovoltaics. A) Schematic of key input and outputs of MFC module. **B)** Key performance characteristics for an MFC normalized to 1 m^2 cross section. **C)** Key fluxes and conversion rates inside the MFC; values are to be considered as typical (i.e., order of magnitude).

molecules/µm^3 inside these cells (corresponding to 8×10^{18} enzymes per m^2), furthermore enzyme rates of $k = 10$/s are assumed, which are values similar for those for muscles [55]. For comparison, a human body achieves $P_V = 3$ kW/m^3, a muscle itself achieves $P_V = 500$ kW/m^3, and mitochondria achieve $P_V = 1{,}000$ kW/m^3; the latter likely represents a general bio-physical limit, and which is not concerned with elaborate support structures for fuel and waste transport over larger length scales [56]. From a practical point of view [52], this seems also realistic given that a microfluidic MFC (not involving methane) with $P_V = 0.7$ kW/m^3 was reported (based on the anolyte chamber volume, not on overall system volume), and where transport and surface area were optimized through a porous channel and anode design [57]. If one wanted to achieve a system performance of $P_V = 10$ kW/m^3 as illustrated in Fig. 3, the cell internal performance would likely have to be about $P_V = 100$ kW/m^3 (as 90% of space is assumed due to support structure), which could be achieved with an MFC thickness of $L_M = 1$ mm (and the space between electrodes of $L_E = 0.1$ mm) and $E = 1$ V, leading to power and current density of $P_A = P_V L_M = 100$ W/m^2 and $I = P_A/E = 100$ A/m^2, respectively. With the enzyme density assumed previously, methane consumption at this power output would be $f = 1.3\times10^{-4}$ mol/s/m^2 (or 2.9 ml/m^2/s or 10.5 l/m^2/h). For comparison, power and current density per electrode area have been reported with $P_A = 5.2$ W/m^2 and $I_A = 7.3$ A/m^2 for methane conversion [1], and $P_A = 0.5$–3 W/m^2 for various other biological substrates [27], i.e., which are only one order of magnitude lower than what is proposed here. In conclusion, high power densities for MFCs appear achieve-able, and are comparable to established non-biological approaches, e.g., combustion power generators ($P_V = {\sim}50$ kW/m^3) and photovoltaic cells ($P_V = {\sim}0.3$ kW/m^3) [58].

Based on this high-level result, the following sections analyze whether such high performance for methane to electricity conversion is practical. This approach identifies and quantifies important issues at key levels that could limit overall system performance and discusses how these issues could be resolved and how system performance could be optimized. Future research may reveal additional challenges or limitations related to these systems (see also further research questions in section 7), but from an 'order of magnitude' perspective, all key items are identified and properly estimated based on available knowledge. The laws of thermodynamics (electrochemistry) should certainly be motiving to identify technological solutions to these issues.

4. Transport channels and transport losses

What MFC dimensions and fluxes are required to realize $P_V = 10$ kW/m^3, and is that physically even possible? It is key to minimize anode-cathode distance as otherwise positive charge transport can be limiting as reactants diffuse between electrodes; nevertheless, this spacing also needs to be large enough to prevent substrate bleed-through between reaction sites on both electrodes, likely also requiring selective membranes. Processes that appear particularly close to potentially become rate limiting are the dissolving of methane in water and the conduction of positive charges to the cathode. This analysis assumes an MFC with electrode separation of $L_{ES} = 0.1$ mm, inner MFC reaction chamber dimension of $L_M = 1$ mm, biofilm thickness of $L_B = 10$ µm, electrode thicknesses of $L_{ET} = 1$ mm, anode chamber thickness of $L_A = 0.01$ mm, cathode chamber thickness of $L_C = 0.01$ mm, and overall system thickness (including support structures) of $L_S = 10$ mm – see

Fig. 3 for details. For ease of unit conversion, the cross-sectional area is set at $A = 1\ m^2$; whether areas of that size could be achieved within a single MFC is of less concern here as a parallel arrangement of multiple MFCs with correspondingly smaller area each would have the same performance. Enhancement of reactant transport between electrodes with large spacing in between could be achieved with active fluid flow [21]. High current density MFCs use buffered liquid anolyte that flows or recirculates through the anode chamber to maintain a stable pH and improve proton transfer [59–61]. The anolyte flow rate and buffer concentration may be a significant factor in determining the geometry of the MFC design, and increasing the anode chamber width in calculations does not add much additional voltage loss as long as other parameters are optimized.

Apart from enzyme densities and activity, power density and conversion efficiency are ultimately limited by the available transport capacity and transport resistance losses of the relevant chemicals, charge carriers, and even heat. These limitations can be divided into multiple categories: (1) Insufficient 'conductance channels' limiting throughput; (2) 'resistance' generating heat; (3) 'leakage' where reactants spontaneously combust also generating heat; and (4) 'incomplete reaction' with unconverted reactants getting exhausted. Categories can be coupled, e.g., fluid friction leads to transport limitation as well as heat production. Overall 'conductance matching and flux optimization' should prevent a bottleneck for the whole process; ideally the rate limiting factors still enable the maximal power density determined above, and where the total system internal losses might be brought down to the 1–5%. In case of 'leakage', better insulation is required, such as selective membranes, but which could reduce conductance. For incomplete reactions, reactants should be recycled back into the system, or the system should run more slowly. Potential physical work is performed and lost, e.g., pressure build-up due to expanding gas – which is particularly the case if the number of gas molecules changes during the reaction (which is the case in reaction R_{total}). The following quantifies some of the key transport factors in more depth.

Methane (and oxygen) could be delivered to the system as gas or already dissolved in water. The system consumes 2 mol of O_2 (4 e^- per molecule) for every mole of methane (8 e^- per molecule). Many of the above-mentioned methane sources are of gaseous nature, and methane (MW: 16 g/mol) has water solubility of $c = 0.02$ g/l, but its delivery has been demonstrated through membranes with gas on one side and biofilm on the other [30,31]. These bioanodes consist of a carbon cloth directly attached to a gas permeable membrane with pores large enough to allow methane to diffuse directly into water, but small enough to prevent bubbles. In addition, hollow fiber membranes, which have suitable methane transport properties, have been made conductive by reducing graphene oxide via a methanotrophic biofilm and used to improve methane transfer and oxidation at the anode in MFCs [62]. This builds on the success of using reduced graphene oxide with silver nanoparticles to achieve the best rates at the anode (39 A/m^2), albeit it with the substrate lactate and *Shewanella oneidensis* MR-1 [63]. Typical volume mass transfer rates for CH_4 into water are 100–1000 h^{-1} [64–66], about a factor of 2 higher for oxygen [66]. Assuming a k_La of 100 h^{-1} and 200 h^{-1} for methane and oxygen [66], respectively, a sufficient gas flux is possible. Methane delivered at 100% concentration (4.46×10^{-2} mol/l) and atmospheric pressure will dissolve at a maximum rate of $f = 1.24\times10^{-3}\ mol/m^2/s$ (10 times higher than the methane consumption rate predicted to occur at 100 A/m^2). Depending on the thickness of liquid and/or membrane between the gas layer and the biofilm, diffusion rate of methane/oxygen to the reaction sites could be limiting. Conventional inorganic H_2/O_2 fuel cell technology has developed gas diffusion layer materials that can support current and power densities 10–100 times higher than what should be needed [67–69], but there may be challenges in adapting those materials to a biological system. In any case, the distance that gases need to diffuse through water should be as minimal as possible.

In most AOM MFC demonstrations, the methane was directly dissolved into the water. Recent membrane-biofilm reactors (MBfR) provide interesting approaches to deliver methane, oxygen, and other gases to a biofilm through a membrane as illustrated in Fig. 4E [70], and designs using hollow fiber membranes have been successfully tested as well [71,72]. Hence, a sufficiently high gas delivery rate should be feasible, yet this requires attention during the overall reactor design as the geometry, delivery method, and partial pressure may change maximum gas delivery rates significantly. Keeping additional components like casing and (if necessary) liquid cooling to just a few mm thick would allow the entire assembly to be around $L_S = 1$ cm thick, but as discussed earlier, the distance between anode and cathode is the main determinant of electrical efficiency. Furthermore, the potential energy expenditure required for gas delivery should be considered and quantified in the future as well, which is likely less than 5%.

There are multiple different ways to transport the electrons from the AOM reaction center inside the microbe to its surface and then ultimately to the electrode [18]: (i) Direct electron transfer – requiring bacteria electrode contact, (ii) conductive pili (nanowires) [43] and multiple heme complexes [76], and (iii) diffusible metabolites and redox mediators. For example, the estimated typical conductivity (i.e., specific conductance normalizing for cross section and distance) of nanowires based on single nanowire measurements [43] is $\sigma = 250$ S/m, which is 2.5 S/m if 1% of the biofilm volume is filled with nanowires. This is similar to pure phosphate-buffered saline (PBS) which has $\sigma = 1.45$ S/m [77], but given the crowded biofilm environment, nanowires now likely make a significant difference by better utilizing the intercellular space. This would keep the nominal anode voltage drop at or below 1 mV, i.e., being small compared to the desired overall 1 V. Note that electrode materials itself like solid copper and carbon (graphite) are typically not limiting given conductivities of $\sigma = 6\times10^7$ S/m, and $\sigma = 3\times10^2$–3×10^5 S/m (depending on the carbon structure), respectively [78]. Electrical conductance in the biofilm and close to the anode could likely be made sufficiently small. Optimizing the contact resistance to the anode itself might be more challenging [79].

Optimizing the transport of positive charge to the cathode inside the MFC likely provides a larger challenge, which is both a question of transport as well as preventing the bleed of chemicals between electrodes. Each methane molecule oxidized produces 8 protons – implying $10^{-3}\ mol/m^2/s$ of electrons to be produced in order to achieve $I_A = 100\ A/m^2$. Positive charge carriers (e.g., H^+) are generated close to the anode and then need to travel all the way to the cathode, where they get reduced, e.g., $4H^+ + 4e^- + O_2 \rightarrow 2H_2O$. The conductance of positive charges (i) is proportional to the conductivity of any species in the medium, and which is proportional to its concentration, its diffusion constant and the square of its charge, (ii) is proportional to the distance between both electrodes, and (iii) depends on the conductivity of a membrane (if present) in order to separate the reactants. In a saline solution, conductivity would be $\sigma = 5$ S/m, and for an electrode separation of $L_{ES} = 0.1$ mm, voltage loss would be around 2% ($dE/E = R_\Omega I/E = L/A/\sigma I/E = 10^{-3}\ m/(1\ m^2)/(5\ S/m) x\ 100\ A/(1\ V) = 0.02$) and proton conductance would be 5,000 S. If high salinity is detrimental to the biology, a standard PBS solution would produce a voltage drop of under 10%. Hence, sufficient conductance between electrodes is possible, but it could become rate limiting. Here it is particularly important to make the spacing between electrodes small, i.e., going into the sub-mm regime, and while many research type MFCs work with much larger spacings, microfluidic MFCs with small spacings have been reported [57]. In one example, the addition of humic acid was shown to significantly increase conductance and hence MFC power density [1]. Added charge carriers and their concentration need to be biocompatible. Active fluid flow could also be considered, such as through an external drive or by microbial flagella, or by periodically driving the charge carriers directly through high frequency acoustic wave-driven electrolyte flow thereby avoiding the diffusion limitation [80]. Membrane proton conductivity of 30 S/m and much higher have been reported [27,75], which would then not be rate limiting, and membranes can be ultrathin.

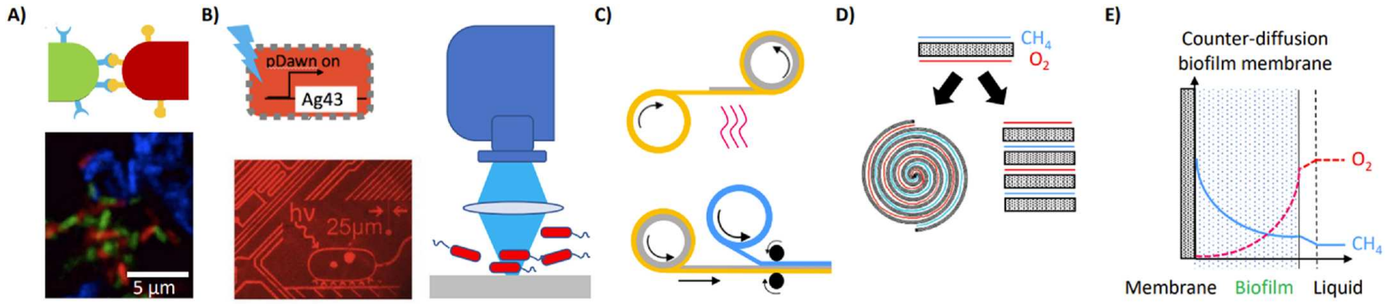

Fig. 4. Suggested key fabrication approaches. A) Synthetic adhesion based self-assembly [73] and B) Biofilm lithography [74] enable the spatial patterning of microbial consortia. **C)** Roll-to-roll processes [75] for producing thin-film MFCs at scale. **D)** Double-spiral rolling or alternate stacking should enable efficient packing of thin MFC and gas delivery. **E)** Counter-diffusion reactor design to enhance methane solubility. (Images adapted from A [73], B [74], C-D [75], E [70].).

Membranes separating the chambers are not strictly needed, and biofilm thicknesses of about 50 μm have been found to be sufficient to remove all relevant oxygen and to provide anaerobic conditions beyond that [81]. Potentially, a biofilm could even bridge between both electrodes, and even carry out the reducing and oxidizing reactions, facilitating the charge transport, and acting as a barrier for reactants (CH_4/O_2) instead of a membrane.

Direct delivery of oxygen to the cathode might be challenging as the reaction $8e^- + 2O_2 + 4H_2O \rightarrow 8OH^-$ could be too slow or potentially require expensive catalysts. Furthermore, O_2 might bleed over to the anode given limitations of the membrane or the short anode-cathode distance. It is not clear at this point how serious these issues might be, but there are multiple options to address these: (i) Capturing electrons at the cathode by some other intermediate, like converting ferricyanide to ferrocyanide [1,45], where ferricyanide then has to be replenished (with O_2 or H_2O_2) through a secondary process, e.g., by continuously circulating the liquid in the cathode chamber – but which overall complicates the system design and would take additional energy. (ii) Identify suitable cathode materials and processes that can directly run the reaction $O_2 + 4H^+ + 4e^- \rightarrow 2H_2O$. (iii) Note also that cathode current densities of $I_A = 38\ A/m^2$ and $I_A = 42\ A/m^2$ have been reported [52,63], which supports the $I_A = 100\ A/m^2$ desired here and illustrated in Fig. 3. Bicarbonate can be regenerated in the cathode by supplying CO_2 to the reactor, as CO_2 will react with OH^- ions to form HCO_3^- which has been shown to reduce overpotential related to pH [82]. Additionally, using an anion exchange membrane instead of a PEM can mitigate pH issues at the anode as OH^- ions can selectively diffuse from the cathode to the anode [60]. The cathode reaction could be a rate limiting issue and certainly deserves attention for further development.

Although this review primarily examines the anode reactions, cathode chemistry is extremely important in determining the energy output of an MFC. The benchmark cathode material for MFC air cathodes has been platinum catalyst embedded in a conductive matrix like activated carbon or carbon cloth, and while Pt is efficient at catalyzing the 4 e^- oxygen reduction reaction, it is an expensive precious metal, and it can be irreversibly poisoned [83,84]. A number of alternative cathode materials have been tested in lab-scale MFCs, for example, metal compounds such as CoP, MnO_2, Fe–N_4, and MgO have produced power densities comparable to Pt/C cathodes [84]. Cathodes can also be produced without any metal using carbon compounds or nanotubes, and while carbon materials do not have nearly the affinity for oxygen reduction that metallic catalysts do, carbon is not irreversibly poisoned by electrolyte contaminants, and it has potential sustainability benefits [83]. Microbial biocathodes have also been tested in microbial fuel cells with performance not yet matching Pt, but with further development they may be a viable option [85,86].

The MFC will produce heat, while mediators and nutrients, waste products, and products need to be transported [51]. Although the ideal goal is a near perfect chemical-electric power conversion efficiency of >90%, a conservative 50% electrical efficiency is assumed here in order to estimate the heat flux that the system potentially has to deal with. The heat produced is 5 W/m^2, which is about 10% of a human body at rest [87]. Assuming the MFC is folded up (or many are stacked together) to maximize volume to surface area, then the surface area available for radiative colling decreases to about 1%, which then potentially requires active cooling [87] but which likely does not provide a technological challenge. On the other hand, an increase in MFC temperature (‘self-heating’) to some extent might even be desirable to speed up the reactions, especially at cold field sites. If significant amounts of waste heat are generated, then secondary usage as established for conventional systems could also be considered [12–14], thereby increasing the overall efficiency. Using microbes with thermophile properties might also be beneficial [88]. This MFC will also produce 300 ml of water per hour as well as CO_2, which needs to be removed. To enable initial proliferation and later self-regeneration – at least for the enzymes – nutrients would have to be supplied, and waste products removed. C, H, O and energy are already applied. Long-term maintenance of a desired consortium configuration can likely be achieved given overall slow growth, little biofilm formation, and the option to administer suitable nutrients and other factors [39].

5. Bioengineering aspects: enzymes, co-factors, microbes, synthetic consortia, spatial structure

There is ample room for increasing enzyme efficiency, enzyme density, and necessary co-factors. Mcr expression level and activity have not been characterized previously. However, Mcr is similar to soluble methane monooxygenase in aerobic methanotrophs, which is well characterized for converting methane into methanol and where activities of $k = 0.2$–$4.4/s$ have been reported in different contexts [89], and 5% of total protein can be generally assumed. Expression levels and activity of Mcr inside *M. acetivorans* [39] can be increased using established methods such as DNA shuffling and protein engineering [90,91]. Coordinated packing and localizing enzymes in the cell, e.g., at the surface, would also be desirable. One can combine genome-wide mutations and growth selection on methane with previous assays to optimize the ratio and production of co-factors and metabolites for the cloned Mcr (e.g., CoMS-SCoB) [39]. Methane responsive gene expression can be improved at least 10 times with a previously identified MA0463 promoter [16]. In general, one can also increase relevant gene expression, such as the number of extracellular MHC complexes that transport electrons via nanowires [92] as shown in Fig. 2D. Even better-suited species (microbial ‘chassis’) should be considered, as *M. acetivorans* was chosen [39] to host the archaea Mcr enzyme as it already expressed relevant co-factors and was easy to engineer and culture [38]. ANME archaea have been studied significantly but still many key aspects are unclear [30]. And while extremophiles/archaea are currently very challenging to work with, in the long run harnessing their properties might improve reaction kinetics by utilizing more extreme conditions such as salinity, pH, or temperature [88]. One may also consider or discover other microbes that are particularly suited for anodophilic electron transfer [93].

Utilizing more than one microbial species inside a microbial consortium (biofilm) has the potential advantage for the division of labor as illustrated in Fig. 4A, especially when it comes to multi-step reactions that might require different reaction conditions, e.g., anaerobic vs. aerobic conditions [16]. Many reported MFCs rely on a single species, or on an unspecific sludge of various species that coexist in some dynamic equilibrium, which is then either spatially unstructured, or where some spatial structure with respect to the electrodes emerges [16]. Control over species presence and their spatial and stochiometric ratio can put them at the optimal distance to the electrode and provide ideal porosity of intercellular space for charge transport. For example, electron transfer can be optimized from *M. acetivorans* to other consortia members, i.e., *G. sulfurreducens* (acetate to electron conversion) and *P. denitrificans* (providing electron shuttles) [16] by expressing nanowires [92]. This also raises the question of how to achieve the desired patterning in such a consortium. The recent advancements for synthetic adhesins [73] and optogenetics [74] to control microbial self-assembly and living materials [94–96] (with examples shown in Fig. 4A and B) hold significant promise to coordinate corresponding bacterial self-assembly; metabolic dependencies might also achieve spatial cooperation and stability. In the ideal scenario, a biofilm would initially grow fast to the desired configuration (potentially due to some outside guidance due to certain nutrient stimuli, self-organizational processes, or even more direct approaches like bioprinting or biofilm lithography processes). Alternatively, it might actually be desirable to rely on a single well-defined species to reduce consortia complexity, but that likely requires sub-cellular spatial separation of different reaction steps that could interfere with each other, which is challenging in procaryotes. Another approach would start from a single cell type that then differentiates into different cell types while achieving the desired spatial order or using eukaryotes that allows for subcellular compartmentalization. Different approaches have been demonstrated to fabricate multi-layer thin films at scale [75] as illustrated in Fig. 4C, which could then be used to manufacture according MFCs as illustrated in Fig. 4D. Overall, the scientific understanding of how to actively achieve any desired consortium structure is still rather limited.

Overall, MFC design including its long-term viability and maintenance needs to be considered as well. Different reactor designs for converting methane into electricity or chemicals have been demonstrated and analysed [64,97,98]. Many lab-scale research type MFCs take weeks to mature until they reach a peak output, and long-term assessment after that is absent, yet run-times of years with minimal maintenance similarly to photovoltaic systems would be desired [22]. Note that the high methane conversion efficiency of anaerobes is directly connected to slow growth [7]. As cells might grow, divide, and die, and as enzymes denature, overall performance might drop. On the other hand, one of the major promises of 'living materials' compared to traditional inert catalysts is the feature of self-renewal [94]. Biofilms are also very challenging to remove, even more so in small spaces as desired for optimizing transport, hence maintenance of consortia might be challenging. Related considerations include the need to 'feed' the consortium with relevant nutrients.

6. Other key aspects: modularity and power optimizers; long term robustness; cost/economics; social and environment

A practical MFC system might share many features with modular photovoltaic systems (PVS) [22], and both require similar modular and dynamic electronic control with power management and inverters [54,99]. An MFC system likely consists of many MFC modules, each of which will consist of many MFCs as illustrated in Fig. 5. The many MFC modules provide small and fluctuating output voltages that need to be strung together in parallel-series combination to achieve the desired voltage and current when connected to an external load such a battery or the grid, and external load control need to ensure that the majority of the voltage drop occurs outside of each MFC. The short-term power output of the MFC can be regulated in multiple ways, e.g., methane supply, operating temperature, and external resistance. A basic calculation suggests that the CH_4 inside the proposed MFC is turned over on the time scale of 10 s, but this calculation assumes saturated methane concentration inside the anode chamber so the actual response time would be shorter since most CH_4 would be consumed at the biofilm/anode interface and not make it into the bulk liquid; hence, within a minute of starting or stopping the CH_4 delivery, the system could go from zero to full power or back, respectively. MFC operation likely also poses tradeoffs, e.g., between fastest chemical turnover vs. maximal electricity production per methane molecule. Interestingly, biofilm development and even evolution can be affected and potentially controlled through the external load or through electrical stimulation [22]. Electronic sensors regarding biological state and changes in each MFC would be desired [100].

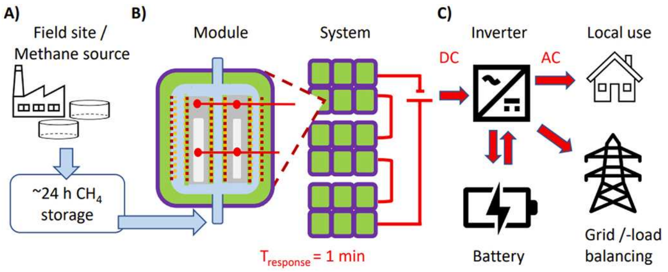

Fig. 5. Potential field-site integration. A) Generated methane can be stored for a few hours or even days or months to buffer fluctuations from other energy sources, e.g., solar or wind. **B)** Modular scalable systems with an expected on/off response time of about 1 min. **C)** Control and grid integration technology will be similar to photovoltaic systems.

Different chemical intermediates could have different overall yields and should therefore be chosen carefully, and it might even be beneficial to generate electricity and value-added chemicals in a synergistic process. An illustrative example from methane to chemical conversion (without electricity production), 1 mol n-butanol requires 4 mol CH_4 as the carbon source, yet it only contains 76% of the original energy despite 100% carbon yield [7], hence finding ways to capture part of this lost energy in electricity (or other value chemicals) could be important. Pathways with different intermediates should be considered in general, e.g., consider acetate [16] vs. methanol [101], which can provide different advantages based on specific circumstances, such as being able to control reaction rates individually, utilizing different enzymes in different bacterial strains, spatially separating reactions with anaerobic and aerobic reaction requirements within the consortium, or optimizing for 'on-demand' electricity production [7]. Electrofermention provides additional options, i.e., controlling the microbial metabolism through external voltages applied to the electrodes [102]. To avoid CO_2 release into the atmosphere, other products or coupling to CO_2 capture, sequestering, or closed-loop integration with algae photo reactors or similar could be considered [26]. MFCs could be run in reverse to turn electricity into methane, with applications for energy storage, grid load balancing, and the chemical industry [103].

MFC studies have been run for many months treating wastewater with consistent performance [104–106]. AOM MFCs have not yet been evaluated for the time scales required for long term installations. The lack of research on the long-term stability of MFC technology is currently a limitation in the field. Most studies have been at the bench scale, and for only a few weeks or months. The microbial part of the system should be self-renewing and stable once the system has equilibrated, given that the inputs remain steady and waste products are efficiently removed. Moreover, since methane is the only carbon source, these MFC systems select for methane-oxidizing microorganisms; hence, they are likely to be stable as they are the only microorganisms that can grow. Special consideration should be applied to the choice of cathode and membrane materials to ensure longevity. If methane is delivered via a membrane, the AOM MFC is semi-isolated from the environment, which should lead to longer performance compared to reactors that use liquid waste directly as a feedstock.

Rational engineering should be accompanied by quantitative modelling. Many of the key contributions can be identified and quantified with back-of-the-envelope calculation and in a linear and additive breakdown as provided in this analysis. Also, several quantitative models at different scales have been developed [51,107–109]. Enzymatic and subcellular modelling can be based on standards from systems biology [110]; individuum-based and continuum methods established [94] can model consortia, and the integrated system can be modeled analogously to photovoltaics [99].

The field site integration conditions, economics of operation as well as environmental considerations and socio-economic implications need to be considered already in the early design phases. Regulatory and safety standards need to be considered regarding combustion and electricity hazards as well as the (most likely) use of genetically modified organisms. Furthermore, education is needed for the operator and to garner acceptance by the wider public [111]. A modular approach like that of photovoltaic systems consisting of many modules consisting of many cells should allow flexible scaling and control [22]. This technology should be set on an exponential path as happened for PVS, where economics of scale and continuous advancement and replacement happens as technology improves and more use cases become economically viable [112]. Ideal field-sites for first adoption and development could involve collaborations with mid-sized methane sources like communal waste-water treatment plants or farms that are spatially close to the technology developers, and that have sufficient knowhow for operating and maintaining such systems [113,114]. Besides the obvious field sites stated above, affordability and operational simplicity for a wider user base in direct need should be considered. For example, many rural communities in developing countries or many Native Americans in the US have no direct access to an electricity grid, but available biological waste could be directly converted to methane to then supplement solar cell electricity generation at night [115]. Finally, major companies like in oil and gas should have the practical use cases, economic incentives, financial means, and social and environmental responsibility to support MFC R&D [116].

7. Conclusions and future open questions

The key contributions of this study are estimation and discussion of the theoretical and practical performance limits of AOM MFCs, which had not been established previously. In contrast to much other published work on the topic, this wholistic and systematic analysis with direct comparisons to the performance of related naturally evolved systems makes a substantial case for the feasibility of methane MFCs from a technical point of view. Effective and rapid climate demands are leading to stricter controls on methane emissions, and the technology discussed here could be one useful avenue to utilize significant amount of methane that is currently wastefully burned or even directly released into the atmosphere. Hence, if realized at scale, a significant impact on greenhouse gas reduction and sustainable, on-demand electricity and chemical (fuel) production could be achieved. The proposed technology could make a particular impact for small and medium sized, more sparsely distributed methane sources, such as found on smaller farms or smaller waste-water treatment facilities [113,114]. The presented analysis could also aid the rational MFC design for other chemical reactions. Direct collaborations between scientists and potential first adopters will be a key next step in the R&D pathway presented here.

Based on existing MFCs as well as thermodynamic and biophysical arguments, future AOM MFCs could have performance characteristics that rival and exceed traditional methane-conversion technologies and could therefore be much more effective and applicable than currently thought. The technical realization of such systems could be enabled by recent advancements in methanogen engineering [34,37] and microbial consortia engineering [73,74,94] as well as operational and technological frameworks such as for PV systems [22]. There is the promise that biological systems will eventually be more effective than inorganic catalysts, e.g., due to higher enzyme specificity, operation under standard conditions, and self-renewal properties [7]. Whether that holds true remains to be seen – and long-term stability is as of yet unproven. As a related route, future research might realize hybrid systems where functional sites of biological enzymes are incorporated into a non-living system.

In the presented analysis, several simplifications were made and a more detailed analysis of some of the underlying processes might reveal additional limitations. Key potential inaccuracies in this analysis are: (i) High performance AOM MFC should be feasible based on established biophysical laws as well as demonstrated similar performance in naturally evolved systems. Nevertheless, it is possible that some absolute biochemical, technological, or economic barriers exist for the specific reactions and systems considered here that could not be overcome but that would only reveal themselves with a more detailed analysis. (ii) The numerical values of used parameters as well as the performance of systems reported as published by others are assumed to be correct and to apply to this system; some of these values might be off by a factor of two to three, which could become a deciding factor in any economic adoption scenario.

The following lists key research areas that warrant additional investigation:

1. Increase methane conversion rates through increased enzyme density, protein engineering, and co-factor expression.
2. Optimize MFC internal transport of charges, chemicals, and heat through surface maximization yet distance minimization, e.g., through porous materials and microfluidics; assess new, inexpensive yet selective and effective materials for electrodes and membranes.
3. Engineer multispecies microbial consortia to advance division of labor in multistep reactions, to control 3D spatial arrangements stochiometric relationships between species, and to optimize MFC internal transport.
4. Understand and optimize long-term consortia management of MFCs (initial setup, longevity, self-healing); long-term AOM MFC studies have not yet been undertaken.
5. Systematically consider other enzymes and suitable reaction pathways.
6. Develop quantitative system modelling tools to support rational engineering.
7. Pursue significant research efforts on natural methanotrophs and extremophiles to discover and characterize new enzymes, cofactors, reaction pathways and resilience under extreme conditions such as high temperature or salinity.
8. Evaluate radically different design approaches to what has been described previously, i.e., whether structured microbial consortia could directly span anode to cathode while functioning as catalysts, charge carriers, and selective membranes at the same time.
9. Develop a practical and modular scale-up system to understand challenges and opportunities when combining multiple MFC for long-term operation.
10. Develop new materials (including for electrodes and membranes) and thin film MFC production approaches.
11. Adapt high flux gas diffusion layers from conventional fuel cells to MFC application or develop new technologies to deliver the gas fluxes required for highly efficient MFC operation.
12. Investigate reversible MFCs that could also turn electricity into methane without significant loss, with significant applications for energy storage, grid load balancing, and the chemical industry.

13. Identify and characterize practical use-cases and develop an R&D strategy that can put such technology onto an exponential trajectory as has happened for PVC, while also addressing a positive social and environmental impact.
14. Collaborate directly with potential first adopters of this technology, such as small-scale farms or smaller communal waste-water treatment facilities.

AOM MFCs have some advantages and disadvantages compared to the current state of the art technology: (1) Compared to conventional methane combustion for energy, AOM MFC technology should have significantly less heat loss; it should also be scalable and thus not require the initial investment of a conventional full-scale plant. (2) Existing MFCs have significant energy loss and have not yet been deployed at scale. The potential stand-out features of AOM MFCs compared to these alternative approaches then are: They could work much more efficiently compared to the existing state of the art, potentially by a factor of two to three, they could be deployable at small scale, and they could be modularly scalable to large scales. Moreover, the estimated energy conversion density (i.e., system size vs. methane converted per time) could be much higher than currently assumed in published work by others – and ultimately rival conventional approaches. The bioengineering catalysts (i.e., enzymes inside cells) could eventually be much more effective/cheaper/less reliant on expensive/rare elements compared to conventional chemistry, furthermore, could automatically renew themselves. Clearly, AOM MFCs are not yet established technology – hence many technical issues need to be solved, but they seem all solvable.

The existing published work on the topic naturally stems from a highly interdisciplinary authorship, also leading to differences in terminologies, performance metrics and methods. Many published MFC are still in the exploratory phase by combining various novel components, which often represents a good first on its own, but systematic parameter evaluation, systematic integration of all aspects, and long-term monitoring is often limited (which is naturally challenging given the long-time scales involved for such MFCs). The main performance limiting steps should always be identified as other potentially significant performance aspects remain hidden otherwise. A much more detailed analysis would be desired, such as numerical simulation of such as system with all its aspects in detail. Comparison between different published systems can be very challenging as usually only a subset of performance parameters is reported, and as any two systems differ in a great number of parameters and used materials. Given the small turnovers of many MFCs examined in research settings, great care and analytical measurements are also required to ensure that the reported performance is truly due to primarily assumed mechanism. Given the aspects involved from very different disciplines, projects should involve collaborations or focus systematically on specific sub-aspects of the MFC, e.g., enzyme engineering vs. membrane optimization. Hopefully this analysis helps to bring different disciplines together and provides an entry point into the versatile aspects and published work to bring these MFC technologies to fruition. The discussed R&D pathway including economically viable adoption illustrates the potential synergy between biotechnology and sustainable energy production – in systems design and power density similar to photovoltaic systems, and other microbial technologies would benefit from similar strategies.

Declaration of competing interest

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.

Data availability

No data was used for the research described in the article.

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