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Clearing the air: unraveling past and guiding future research in atmospheric chemosynthesis

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SUMMARY Atmospheric chemosynthesis is a recently proposed form of chemoautotrophic microbial primary production. The proposed process relies on the oxidation of trace concentrations of hydrogen (≤530 ppbv), carbon monoxide (≤90 ppbv), and methane (≤1,870 ppbv) gases using high-affinity enzymes. Atmospheric hydrogen and carbon monoxide oxidation have been primarily linked to microbial growth in desert surface soils scarce in liquid water and organic nutrients, and low in photosynthetic communities. It is well established that the oxidation of trace hydrogen and carbon monoxide gases widely supports the persistence of microbial communities in a diminished metabolic state, with the former potentially providing a reliable source of metabolic water. Microbial atmospheric methane oxidation also occurs in oligotrophic desert soils and is widespread throughout copiotrophic environments, with established links to microbial growth. Despite these findings, the direct link between trace gas oxidation and carbon fixation remains disputable. Here, we review the supporting evidence, outlining major gaps in our understanding of this phenomenon, and propose approaches to validate atmospheric chemosynthesis as a primary production process. We also explore the implications of this minimalistic survival strategy in terms of nutrient cycling, climate change, aerobiology, and astrobiology.

KEYWORDS atmospheric chemosynthesis, microbial ecology, astrobiology, nutrient cycling, climate change, aerobiology, trace gases, hydrogenase, primary production, foundational science

THE PROPOSED NICHE FOR BACTERIA THAT LIVE ON TRACE GASES

In desert soils, water and inorganic electron donors are often scarce (1–5), limiting photoautotrophs (6–10) and the chemoautotrophs that use inorganic electron donors

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present within the soil from non-atmospheric sources (11–13) to low abundances and activities. This restricts carbon and energy inputs from these well-established primary production strategies. Despite the harsh conditions, microbial communities in these arid environments are frequently abundant and diverse. In these ecosystems, alternative energy acquisition strategies supplement carbon and energy inputs and aid microbial persistence. These strategies include trace gas oxidation (14–16) and heterotrophic activities fueled by nutrient inputs from aeolian deposition (17). Until recently, an understanding of what processes support primary production in such communities was largely unknown.

Hydrogen (H_2), carbon monoxide (CO), and methane (CH_4) concentrations fluctuate within the atmosphere due to extensive biological and chemical cycling, with average global mixing ratios of 531 (18, 19), 90 (20–23), and 1,857 (24) ppbv, respectively. These gases are ubiquitously present at the interface of air and soil, diffuse readily into the soil and microbial cells, and produce electron yields upon oxidation for input into diverse biochemical reactions, including the electron transport chain (25–29). As a result, the oxidation of these gases represents the use of a highly reliable energy source, particularly for microbial communities that are starved of alternative energy sources, such as those inhabiting dry and oligotrophic desert soils.

Within terrestrial microbiomes, the activity of high-affinity hydrogenases, carbon monoxide dehydrogenases, and methane monoxygenases, capable of oxidizing trace gases, has been predominantly linked to microbial survival strategies rather than cellular growth (15, 30–33). In cultivated taxa, the link between trace gas oxidation and microbial survival has been supported by the upregulation of these enzymes during nutrient starvation, particularly in late-stage exponential and stationary growth phases (26, 30, 34–36). However, given the low abundance of well-characterized primary producers in extreme environments, particularly oligotrophic soil niches, and the prevalence of diverse microbiomes that include trace gas oxidizing bacteria, it has been hypothesized that the energy liberated from trace gas oxidation also supports microbial primary production in these environments through a process coined "atmospheric chemosynthesis" (14, 15, 31, 37).

ATMOSPHERIC CHEMOSYNTHESIS: THE PROPOSED PATHWAYS

During atmospheric chemosynthesis, high-affinity [NiFe]-hydrogenases (forms 1h, 1l, 1m, and 2a) and carbon monoxide dehydrogenases are proposed to oxidize trace H_2 and CO, respectively (Fig. 1). These [NiFe]-hyrogenases have a substantially higher affinity for H_2 [Michaelis constant (*Km*) = 30–200 nM], compared to other forms (*Km* > 500 nM) which are unable to conduct hydrogen oxidation at trace atmospheric levels (38). Similarly, a large group of microbial carbon monoxide dehydrogenases have a low affinity for CO (*Km* > 400 nM), making them unable to oxidize CO at atmospheric levels (39). Comparatively, higher affinity carbon monoxide dehydrogenases (*Km* < 400 nM) are required for this to proceed (30). The high activity of these enzymes liberates electrons for input into the electron transport chain, resulting in the production of ATP (40–42). It is hypothesized that, due to the rapid activity of the hydrogenases and carbon monoxide dehydrogenases observed during activity studies, sufficient ATP is produced to surpass cellular maintenance energy requirements, and is directed into carbon fixation pathways, allowing inorganic carbon to be fixed into microbial biomass (Fig. 1) (14, 37, 43).

The Calvin-Benson-Bassham (CBB) cycle is the microbial carbon fixation pathway most associated with atmospheric chemosynthesis. This is due to the widespread and abundant detection of CBB cycle enzyme markers alongside trace gas oxidation genes within soils (44), and derived metagenome-assembled genomes (MAGs) (31, 37, 45, 46). In particular, these genetic markers co-occur in numerous soils that rapidly oxidize trace gases and have shown significant increases in carbon fixation upon trace gas stimulation (14, 43, 47). For example, in Robinson Ridge, East Antarctica, soils oxidized H_2 at 3.49 nmol/h/g and CO at 0.42 nmol/h/g, with 1h [NiFe]-hydrogenase (*hhyL*), carbon monoxide dehydrogenase (*coxL*), and RuBisCO form IE (*rbcL1E*) gene expression

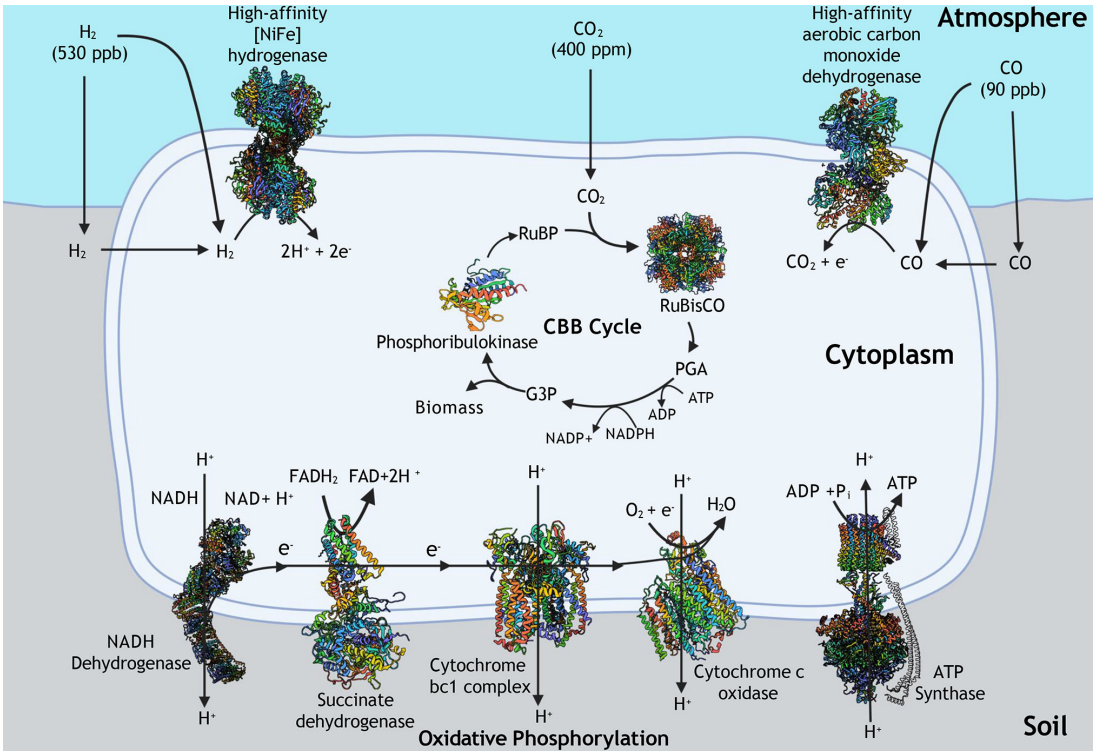

FIG 1 The proposed pathway for trace gas-driven carbon fixation. Representative protein structures used were obtained from the Research Collaboratory for Structural Bioinformatics (RCSB) Protein Data Bank (PDB); 1h [NiFe]-hydrogenase from *Cupriavidus necator* H16 (PDB ID = 5AA5), carbon monoxide dehydrogenase from *Oligotropha carboxidovorans* (PDB ID = 1N5W), RuBisCO from *C. necator* (PDB ID = 1BXN), phosphoribulokinase from *Cereibacter sphaeroides* (PDB ID = 1A7J), NADH dehydrogenase from *Thermus thermophilus* (PDB ID = 6I1P), succinate dehydrogenase with ubiquinone bound from *Escherichia coli* (PDB ID = 1NEK), cytochrome bc1 complex from *Paracoccus denitrificans* PD1222 (PDB ID = 2YIU), cytochrome c oxidase from *Rhodobacter sphaeroides* (PDB ID = 1M56), and ATP synthase from *Paracoccus denitrificans* (PDB ID = 5DN6). During atmospheric chemosynthesis, trace gases are oxidized by high-affinity hydrogenases and carbon monoxide dehydrogenases. Electrons liberated drive oxidative phosphorylation, which produces ATP, which is subsequently input into the RuBisCO form IE-driven Calvin-Benson-Bassham (CBB) cycle. The orientation and size of proteins are not to scale, and the CBB cycle displayed is simplified. *C. necator* was selected as the model organism for 1h [NiFe]-hydrogenase as although lower affinity, higher affinity variations of this enzyme have yet to be structurally modeled through pure enzyme studies. Inspired by references (14, 40).

confirmed. Furthermore, in this study, these genetic markers were detected in 43%, 13%, and 30% of the MAGs examined, respectively (14). In contrast, genetic indicators of alternative microbial carbon fixation pathways are frequently far less abundant.

Despite the dominance of CBB cycle genes widely associated with atmospheric chemosynthesis in oligotrophic desert soils, trace hydrogen oxidation has been more recently linked to microbial carbon fixation through the reverse tricarboxylic acid (rTCA) cycle (48). In this case, the metabolically flexible genus *Nitrospira* supplements nitrite-dependent growth using electrons derived from atmospheric H_2 oxidation by high-affinity group 2a [NiFe]-hydrogenase (48). In contrast to oligotrophic cold desert soils, where 2a [NiFe]-hydrogenase has a low relative prevalence (43, 47), this enzyme is widely detected in marine surface waters, with its expression linked to mixotrophic growth in the marine bacteria *Sphingopyxis alaskensis* RB2256 (49). Mixotrophy is the simultaneous usage of heterotrophic and autotrophic processes, thereby involving multiple different inorganic and organic carbon and energy sources (50).

Links between the microbial oxidation of atmospheric methane and carbon fixation offer another alternative atmospheric chemosynthetic pathway. In this case, oxygen-dependent particulate methane monooxygenase oxidizes methane to methanol, which is then oxidized to formaldehyde by periplasmic methanol dehydrogenase (51, 52). After being transported into the cell, the formaldehyde is oxidized to formate, which is then

oxidized to CO_2 or incorporated into microbial biomass through the reductive glycine pathway and the serine cycle (51, 52).

Atmospheric chemosynthesis is predicted to complement heterotrophic energy and carbon acquisition pathways. For example, bacteria within the phylum *Eremiobacterota* encode glycoside hydrolase, complete glycolysis and pentose phosphate pathways, and a complete tricarboxylic acid (TCA) cycle, while MAGs from six candidate *Eremiobacterota* genera are putatively atmospheric chemosynthetic, co-encoding a high-affinity [NiFe]-hydrogenase, RuBisCO form IE and a complete CBB cycle (53). This indicates a mixotrophic lifestyle, with the genetic potential for atmospheric chemosynthesis alongside heterotrophy (53). Indeed, the first *Eremiobacterota* isolate, *Vulcanimicrobium alpinus*, recently obtained from a dark, oligotrophic, volcanic cave ecosystem rich in CO_2, is a highly metabolically flexible aerobic anoxygenic photoheterotrophic bacterium. This strain appears to require elevated CO_2 concentrations (>5%) for growth, even when cultivated under heterotrophic conditions (54). Despite this finding, *V. alpinus* was able to grow when incubated under the light in organic carbon-rich 6 cm stab cultures, despite being sealed to surrounding air and receiving no headspace amendments throughout the 30-day incubation (54). Further characterization studies are essential to clarify the underlying growth strategies of this novel taxa, including its capacity for atmospheric chemosynthesis alongside heterotrophic and photosynthetic mechanisms, and under what environmental conditions each is activated. Moreover, the isolation and characterization of additional *Eremiobacterota* cultures are vital for fully understanding this metabolically flexible phylum, including the potential for atmospheric chemosynthesis.

GAPS IN OUR FOUNDATIONAL UNDERSTANDING OF ATMOSPHERIC CHEMOSYNTHESIS

Trace gas oxidation can now be viewed as an almost ubiquitous process in terrestrial microbiomes, with rates quantified in numerous and diverse soils (55–58), including deserts (14, 15, 30, 31, 43, 46, 47), forests (59, 60), and volcanic soils (61–63). However, trace gas oxidation is generally slower in soils from temperate desert regions compared to their colder counterparts, often requiring wetting that mimics rare rainfall events for rapid oxidation to be observed (31, 46, 47). For example, in unwetted Negev Desert soils, H_2 oxidation rates have been reported as 0.009–0.035 nmol/h/g, and in Australian dryland soil, H_2 and CO oxidation rates have been reported as 0.00064 nmol/h/g and 0.0061 nmol/h/g, respectively (31). Comparatively, 6.3–623.9 H_2 nmol/mol/h/g and 388 0–2.6 CO nmol/mol/h/g have reported in unwetted soils from the Antarctic, high Arctic, and Tibetan Plateau (43). Furthermore, few studies directly link rapid trace gas oxidation rates with significant increases in microbial carbon fixation ($p < 0.05$); such observations are restricted to cold deserts throughout the Antarctic, including the Vestfold Hills (43), the Windmill Islands (14), the McMurdo Dry Valleys (43), and high Arctic soils (43), with temperate deserts limited to Israel (47). Therefore, while trace gas oxidation has been established as a widespread mechanism for sustaining microbial survival, it remains unclear how pervasive atmospheric chemosynthesis is as a growth strategy in terrestrial ecosystems.

It is also unclear whether trace gas oxidation supports atmospheric chemosynthetic growth in other, more diverse environments. The recent identification of trace gas oxidizing microorganisms in marine ecosystems (63) demonstrates the potentially under-investigated ecological significance of these microorganisms in aquatic environments. There is a definite need to extend studies of the diversity and function of trace gas chemosynthetic microorganisms into diverse environmental reservoirs, including aquatic habitats (oceans, rivers, lakes, and wetlands), endolithic environments (inside rocks), lithic niches (the deep subterranean biosphere), and the aerosphere.

Rapid improvements in sequencing technologies over the past 5 years have expanded our understanding of atmospheric chemosynthesis. Genetic markers for trace gas oxidation, including those encoding RuBisCOs, high-affinity hydrogenases, and carbon monoxide dehydrogenases, are ubiquitous in soils globally, including

throughout the Antarctic (14, 37, 44), Arctic (44), Tibetan Plateau (44), Israel (47), Namibia (46), the Americas (55, 64–66), and Australasia (31, 32, 46). In soils, the expression of RuBisCO form IE has been detected alongside key markers for trace gas oxidation; group 1h [NiFe]-hydrogenase and aerobic carbon monoxide dehydrogenase (14). Through extensive MAG analysis, numerous bacterial phyla have been shown to have the genetic capacity for atmospheric chemosynthesis. Relevant marker genes, in particular *rbcL1E* (encoding RuBisCO Form IE), *coxL* (encoding the large subunit of carbon monoxide dehydrogenase), and *hhySL* (encoding small and large subunits of high-affinity hydrogenase) co-occur in *Actinobacteriota*, *Ca*. Dormibacterota, *Eremiobacterota*, *Chloroflexota*, *Firmicutes*, *Deinococcota*, and *Verrucomicrobiota* (14, 43).

The taxonomic diversity of microorganisms performing atmospheric chemosynthesis may extend beyond seven phyla, particularly if additional unidentified enzymes and pathways are involved. For example, RuBisCO form IE and the CBB cycle are typically linked with atmospheric chemosynthesis, as they frequently co-occur and are co-expressed alongside trace gas oxidation markers in microbiomes that demonstrate significant increases in microbial carbon fixation activity with H_2 supplementation at atmospherically relevant levels (14, 37, 43, 47). However, other yet to be identified forms of RuBisCO may also be involved in the process. RuBisCO forms IC and ID are of particular interest due to their close phylogenetic relationship with form IE, their association with light-independent primary production and their co-detection with 1h and/or 1l [NiFe]-hydrogenases within trace gas oxidizing microbiomes (67) and associated MAGs, including the uncultivated *Chloroflexota* class Ellin6529 (37). Furthermore, novel forms of high-affinity hydrogenases continue to be uncovered in diverse taxa and environments (37, 38, 43, 49, 68), suggesting that their distribution and ecological significance require further elucidation. To fully understand the atmospheric chemosynthetic pathway, RuBisCO form IE and associated trace gas oxidative proteins must be purified and structurally and enzymatically characterized so that any distinguishing features and activities can be determined. Only then can genetic marker detection be implemented to accurately assess the taxonomic distribution of microorganisms capable of atmospheric chemosynthesis.

Critically, while whole microbiome activity assays indicate the occurrence of atmospheric chemosynthesis, there is currently no unequivocal evidence linking the processes of trace gas oxidation and carbon fixation in individual microorganisms. Although MAG analysis has revealed microbial taxa that exhibit the genetic capacity for atmospheric chemosynthesis within these whole microbiomes, further studies are required to confirm that these microorganisms perform atmospheric chemosynthesis in pure culture. Furthermore, a selection of MAGs with atmospheric chemosynthetic potential have cultured representatives, which are heterotrophic or chemoautotrophic, having been isolated under conditions rich in organic carbon or inorganic electron donors (43). It is vital that these isolated microorganisms are studied under conditions conducive to atmospheric chemosynthesis, namely trace H_2 and CO exposure under dark incubation, to confirm that they conduct this growth mechanism upon nutrient starvation.

Numerous approaches to validate this process rely upon the isolation of putatively atmospheric chemosynthesis microorganisms. Alternatively, atmospheric chemosynthesis could be validated and characterized in environmental microbiomes or enrichment cultures through the application of more sophisticated techniques, including DNA stable isotope probing (SIP), metatranscriptomic or metaproteomic analysis. In the case of DNA SIP, soils or enrichments would be incubated under conditions that inhibit photoautotrophs and stimulate atmospheric chemosynthetic activity, through the inclusion of trace gases alongside $^{13}CO_2$. Following incubation, labeled and unlabeled DNA fractions would each be characterized using community profiling and metagenomic approaches. This approach would require substantial optimization, particularly regarding incubation time and soil or enrichment selection. However, if effectively implemented with appropriate controls and replication, this technique could prove invaluable for validating

atmospheric chemosynthesis, and identifying taxa that undertake this process even within difficult-to-culture "microbial dark matter". Perhaps more simply, metatranscriptomics or proteomics approaches could be applied under similar incubation conditions without radio isotopically labeling the headspace CO_2. Conducting this experiment under varying conditions (e.g., different combinations of atmospheric gases at different concentrations) and multiple timepoints could effectively identify the atmospheric chemosynthesis pathway and characterize the conditions in which this survival strategy is activated. Furthermore, with a binning approach, omics techniques could continue to identify atmospheric chemosynthetic taxa within complex microbiomes.

Applying expression-based omics strategies to soil microbiomes has traditionally been technically challenging (69) due to RNA instability (70, 71), the co-extraction of complex organics (72) which impair molecular analysis (69), and considerable community complexity (73, 74). In the case of oligotrophic desert soils, the application of RNA and protein extraction methods is additionally challenging, due to low biomass and activities yielding lower concentrations of mRNA. However, improvements in sequencing technologies and methodological approaches have improved outlooks in this area. These improvements include the snap-freezing of samples or the use of RNA preservation solutions (75–77), incorporation of humic and fulvic acid separation and mRNA enrichment steps (69), and analysis against custom reference databases obtained using metagenomic analysis of identical or highly similar samples alongside public databases (78, 79). Recent transcriptomic studies have been successfully conducted on hyper-arid soils from the Namib Desert (80, 81). Furthermore, a recent preliminary metaproteomics study conducted on low-biomass and low-activity soil from Casey station in East Antarctica identified significant expression of 295 proteins, including RuBisCO form IE and group 1h [NiFe]-hydrogenase (82). These successes encourage further application of omics techniques to hyper-arid deserts. In addition, pure culture expression-based studies are vital for directly linking trace gas oxidation and microbial carbon fixation processes in individual taxa, potentially allowing atmospheric chemosynthesis to be validated and quantified under a range of environmental conditions.

THE MULTIDISCIPLINARY IMPLICATIONS OF ATMOSPHERIC CHEMOSYNTHESIS

The survival and growth strategies of microbiomes in extreme environments could have broad-reaching implications upon nutrient cycling, the minimum requirements for life, aerobiology and aeolian dispersal, and informing microbial cultivation for biodiscovery. Therefore, it is vital that our understanding of these mechanisms is further developed.

Uncovering roles in global nutrient cycling

Microbiomes have a fundamental role in nutrient cycling (83–85). On a global scale, microbial cycling of gaseous compounds, such as carbon dioxide, hydrogen, carbon monoxide, and nitrogen is a critical element of biogeochemical cycling (86–88). It is becoming clear that bacteria performing atmospheric chemosynthesis may function as a prominent carbon sink within desert ecosystems, and there is a need to assess and quantify this metabolic functionality in more diverse and under-investigated global ecosystems.

Within desert ecosystems, atmospheric chemosynthesis is thought to provide organic carbon to higher order, heterotrophic assemblages through the trophic web (15, 16, 31). Soil heterotrophs oxidize organic carbon as a source of energy through cellular respiration, with a proportion of the resulting simpler organic compounds incorporated into new microbial biomass through biosynthesis (89). Greater proportions of organic carbon assimilated into biomass equates to a higher carbon use efficiency (CUE) (90). A study of 23 taxonomically diverse heterotrophic bacterial isolates from temperate forest soils found that 26%–81% of consumed carbon was used for growth, averaging ~60% across the conditions studied (91). This suggests that in organic carbon-rich soils, heterotrophs assimilate and release CO_2 at comparable rates (91). Comparatively,

mixotrophs that supplement their energy input through atmospheric gas oxidation theoretically require less organic carbon for energy. This allows soil mixotrophs to more efficiently allocate carbon derived from consumed organic carbon matter into new microbial biomass, as opposed to being terminally respired and released into the atmosphere (92). A mixotrophic lifestyle potentially makes them a more effective carbon sink than their heterotrophic counterparts, particularly in organic carbon-limited environments. To verify this, it would be necessary to quantify and compare rates of microbial carbon fixation and respiration in identical soil microbiomes from various environments, with and without exposure to trace atmospheric gases. This objective poses significant technical challenges, as the metabolic products of respiration (CO_2 and H_2O) are commonly consumed by autotrophic carbon assimilation processes (89, 93). Instead, activity studies that trace and quantify the incorporation of ^{13}C-labeled substrates into microbial biomass, or the incorporation of ^{18}O from labeled water into newly formed microbial DNA, alongside the release of respiratory CO_2 are most widely used to measure CUE (94–96). To determine the impact of trace gas oxidation upon CUE, this method should be applied to soil microbiomes from a range of environments, with and without trace gas exposure. We propose that metabolite-independent methods, including metatranscriptomic and metaproteomic analysis, should be implemented in conjunction with this research. These techniques could verify and quantify the expression of respiratory and carbon assimilatory pathways, alongside observed carbon and energy fluxes, for comparative analysis within whole microbiomes and isolated bacteria.

Guiding conservation frameworks to include microbes in changing environments

Terrestrial microbiomes play a substantial role in global carbon cycling, and in some cold desert environments such as the high Arctic, this role is rapidly changing due to climate change (97–99). It remains unclear how this warming will impact microbial ecology and the carbon cycle in Antarctica, particularly in under-studied regions, and in this case, in relation to photosynthetic and atmospheric chemosynthetic primary producers.

Under warming conditions, thawing events occur more frequently (100, 101), increasing microbial respiration rates, and resulting in the subsequent decomposition of ancient organic matter deposits (100–103). This process has the potential to release 92 (±17) Pg carbon into the atmosphere by 2100 (100). Rising temperatures and moisture availability are also expected to alter the carbon cycle in polar soils by increasing the biomass and activity of photosynthetic populations. Within terrestrial Antarctica, most studies on the effects of climate change have centered on the maritime regions of West Antarctica, where plant life is increasing (104–106). However, vascular plants capable of counteracting increased CO_2 release from microbial decomposition are absent from most of the ice-free areas of the continent (107), and photosynthetic microorganisms are frequently limited to localized niches (6, 10, 14, 108, 109). In remote coastal regions in eastern Antarctica, where phototroph abundances are very low, atmospheric chemosynthesis may be the dominant mode of energy acquisition (14).

A warming Antarctic environment has the potential to alter the carbon balance and deselect microorganisms performing atmospheric chemosynthesis. For example, in cold oligotrophic soils at Mitchell Peninsula in the Windmill Islands of East Antarctica, phyla linked to this process, specifically *Eremiobacterota* and *Ca*. Dormibacterota, exist in far higher abundances (8.1% and 5.1%, respectively) than in temperate copiotrophic environments (110). In the dry Windmill Island soils, these taxa have been shown to decrease significantly alongside microbial community turnover when soil moisture levels exceeded 10%–12% (111). Given the projected increases in temperature, precipitation, and meltwater events across the Antarctic continent (97, 112), particularly the peninsula (113), it is critical that long-term monitoring of these soil communities is established. Furthermore, trace gas chemosynthetic taxa should be investigated across a broader array of threatened cold desert environments before the opportunity is lost.

Investigations into the impacts of increasing temperatures on photosynthetic and atmospheric chemosynthetic primary production are severely limited, both geographically and temporally (114). Studies that expand our understanding of the distribution and functional capacity of microorganisms performing atmospheric chemosynthesis across a broader Antarctic continental scale would allow us to further understand the impacts of climate change and microbial primary production dynamics. Such knowledge will be vital in the development of long-term observation systems and conservation strategies (115).

Redefining the minimum nutritional requirements for life

In the ongoing search for extra-terrestrial life, researchers have focused on planetary bodies that demonstrate potentially habitable conditions (116). While the requirements of habitability have remained controversial (117, 118), one condition that is widely regarded as vital is the presence of bioavailable water (119, 120). Although other requirements may limit extra-terrestrial life, including the presence of inorganic sources of energy, carbon, and trace elements, these are common throughout the universe (121). Comparatively, liquid water is far rarer (116, 121), making it the first variable considered when assessing a planet's habitability. There is increasing evidence suggesting the presence of liquid water on extra-terrestrial bodies, including the interior of Enceladus (122–124), beneath the outer ice sheet of Europa (125, 126), and in the subsurface polar regions of Mars (127).

Despite a dependence upon bioavailable water, microbial life has been discovered in the most arid environments on Earth (128) with few reports of apparently abiotic habitats (13, 129). Within cold hyper-arid deserts, such as those of the McMurdo Dry Valleys and the Vestfold Hills in Antarctica, atmospheric chemosynthesis provides microbiomes with the energy required for bacterial growth and may also be a strategy for generating metabolic water (37, 130). This is because the microbial oxidation of trace hydrogen is hydrogenic ($2H_2 + O_2 = 2H_2O$) (130).

In cold deserts, microbial trace H_2 oxidation has been reported to be as rapid as 421.4 nmol/mol/h/g in unwetted soils (43), resulting in an estimated 0.2 mg of H_2O produced per day, per gram of soil (130). Trace gas-dependent hydro-genesis could, therefore, be a significant source of water for microorganisms residing in hyper-arid ecosystems. In hot deserts, estimates of maximum H_2 oxidation rates are theoretically sufficient to fulfil ecosystem water requirements (37); however, these rates have been primarily derived from wetted soils, which oxidize trace gases more rapidly than when dry. For example, wetting induces a 60-fold H_2-uptake rate increase in Australian soils (31) and a 26-fold increase in Judea Hills and Negev Desert soils (47) with these increases not reflected in heat-killed controls. However, temporal moisture content fluctuations greatly influence the microbial oxidation of H_2 in a non-linear manner (131), and the high levels of biochemical activity observed during these assays may only occur *in situ* during or after infrequent precipitation or snowmelt events. Therefore, the use of wetted soils to calculate H_2 oxidation rates and theoretical water yields does not directly substantiate the hypothesis that H_2 oxidation significantly contributes to cellular water budgets within arid and hyper-arid environments where water is naturally scarce. It is critical that the role and ecological significance of trace H_2 oxidation in metabolic water generation are verified under *in situ* conditions, particularly extending to hot desert environments.

In addition to water, sources of energy and carbon are also vital for life. Subsurface environments within "habitable zones" are widely regarded as plausible extra-terrestrial habitats, as liquid water and redox disequilibria are more likely to exist, and the impacts of strong, mutagenic solar radiation are minimized. Within these environments, solar radiation could potentially be utilized by photosynthetic organisms, as this has been observed at intensities as low as 0.01 μmol m^{-2} s^{-1}, which is ~5×10^{-6} of the direct solar flux at Earth (121). However, trace gas oxidation and atmospheric chemosynthesis offer alternative mechanisms for energy liberation and light-independent growth, potentially allowing for the adaptation of microorganisms to more diverse extra-terrestrial niches.

Available data indicate that trace gas chemosynthetic microorganisms can survive by oxidizing atmospheric gases to support their carbon, energy, and possibly water requirements (31, 47). This means that planetary bodies with atmospheric H_2 and CO or CO_2 could be capable of supporting atmospheric chemosynthetic lifeforms (132), given that other abiotic factors fell within the biological requirements (116, 121, 133). The Martian polar subsurface is a candidate extra-terrestrial environment where trace gas oxidation and atmospheric chemosynthesis may occur. Dry permafrost ground in the north polar plains of Mars exhibits temperatures warmer than −18°C, water activity values >0.6, and a lower atmosphere rich in CO_2 (95.32%), CO (0.6%), and H_2 (15 ± 5 ppmv) with low levels of O_2 (0.16%) available (134–137). Furthermore, in liquid environments across Mars, oxygen capable of driving hydrogen oxidation is dissolved at concentrations of ~2.5×10^{-6} mol m^{-3} to 2 mol m^{-3}, and is particularly concentrated within polar regions due to lower temperatures (138).

Biosignatures of trace gas oxidation and carbon fixation processes offer new targets in the search for extra-terrestrial life. Further research is necessary first to confirm whether atmospheric chemosynthesis fulfils the energy, water, and carbon requirements of microbiomes within terrestrial analogs on Earth (139), such as the Atacama Desert (140, 141) and the McMurdo Dry Valleys (142–144), where the indicator genes have already been detected (43, 145). If trace gas oxidation and atmospheric chemosynthesis are viable sources of cellular water, energy, and carbon, it will become necessary to update the known detection limits of life (146) and incorporate a broader range of environments into our search for extra-terrestrial life.

Aerobiology and aeolian dispersal

Earth's atmosphere is estimated to contain approximately 5×10^{22} microbial cells (147), and while bacteria have been detected in the mesosphere (148) and thermosphere (149), at altitudes as high as 400 km, the majority of this atmospheric biomass is within altitudes below 11 km (150, 151). Aerobiology is a relatively new discipline developed throughout the last century, historically focused on human health and food safety, particularly the airborne transmission of pollen, fungal spores, and pathogenic taxa (152). However, airborne bacteria are ecologically significant as they influence atmospheric composition (153) and climate events, including rainfall (154, 155), and are readily dispersed by wind to establish or alter microbiomes within new environments (151, 156, 157). As a result, there is a growing focus on the role of airborne microorganisms on microbial ecology and climate, with a dire need for studies generating more empirical data to support foundational science in this area.

Aeolian dispersal of microorganisms is of particular interest in the cold desert environment of Antarctica, where selection pressures faced in the atmosphere often resemble those in the terrestrial environment, and where geographical isolation and circumpolar currents limit microbial inputs from other sources (151). An important limitation on aeolian dispersal is the timeframe that microorganisms can remain dormant or metabolically active within the troposphere, although this duration is predicted to be longer over Antarctica compared to temperate environments (157). It was once believed that airborne microorganisms were inherently inert and were thus termed "spora" (148). However, studies have shown bacterial survival and growth within supercooled cloud droplets (158) and on airborne particles (159). The underlying metabolic processes that support airborne bacteria, and the proportion of airborne bacteria that remain active, are poorly understood. Organic material at oligotrophic concentrations may support heterotrophic communities (151, 160–162), and light exposure may support their photosynthetic counterparts (163–165). *Actinobacteriota*, a phylum widely linked to trace gas oxidation and atmospheric chemosynthesis, and *Firmicutes* and *Verrucomicrobiota*, which have recently been associated with these processes through metagenomic analysis (43), have been identified within outdoor aerobiomes, including above Antarctica (151, 156, 166, 167) and the high Arctic (168). However, aerobiological studies are highly limited in quantity and scope, restricting our ability to form concrete

conclusions about the extent of this activity, the source of these microorganisms, and their taxonomic distribution throughout the broader aerosphere.

It is hypothesized here that a subset of airborne microorganisms may supplement energy needs through trace gas oxidation or use the energy to drive carbon fixation in the process of atmospheric chemosynthesis, thereby fulfilling their nutritional requirements through the uptake of almost exclusively atmospheric inputs. If this is the case, these microorganisms could also make up a substantial, uncharacterized component of aerobiology. Furthermore, if trace gas chemosynthetic bacteria do make up a significant proportion of the atmospheric microbiome, then they could be substantially influencing climatic conditions, nutrient cycling, and aeolian dispersal that warrants further investigation.

To fill this gap in our understanding, it is recommended that metagenomic and transcriptomic analyses are conducted on airborne microbial communities to identify potentially atmospheric chemosynthetic taxa and characterize their underlying functionality. Low microbial biomass in airborne environments (~$1 \times 10^4/m^3$) (160, 169) has previously restricted the use of omics technologies in aerobiology. However, improved study protocols that utilize longer sampling times and carefully designed controls, thorough DNA extraction protocols and particulate removal, and repair of damaged DNA (170, 171), as well as the development of more sensitive omics technologies (172, 173), have led to more successful analysis of air samples (170, 173, 174).

We recommend that future investigations into atmospheric chemosynthesis within airborne microbiomes focus on samples obtained from the troposphere over deserts. This is because the underlying terrestrial environment is likely to contain high abundances of trace gas oxidizing microorganisms and predicted atmospheric chemosynthetic taxa (14, 43, 47). Investigation into atmospheric microbiomes over Antarctica should be prioritized, due to the well-established significance of aeolian dispersal on the ecology within this region (175–177), higher estimated airborne residence times (157), and the existence of a proposed standardized protocol for Antarctic aerobiological sampling and analysis (178).

CONCLUSION

Atmospheric chemosynthesis is a potentially important microbial primary production process that appears to be widespread in the Earth's desert soil environments. A growing body of evidence suggests that this is an ecologically significant process, with broad-reaching implications for global nutrient cycling and aerobiology, life detection limits and environmental habitability, and for the isolation of novel microorganisms. However, many issues remain unresolved: the global extent of atmospheric chemosynthesis, the true diversity of functional taxa, the validation of underlying metabolic pathways, and the time-dependent kinetics of these processes all remain as future research objectives. To fill these substantial gaps in our understanding, sophisticated methodologies should be implemented, including global phylogeographical studies in a broader array of microbiomes, DNA stable isotope probing, carbon flux experiments, expression-based "omics" surveys, and a wide array of relevant kinetic analyses, particularly targeting purified proteins linked to atmospheric chemosynthesis. The integration of such data will ultimately yield a much more complete understanding of atmospheric chemosynthetic metabolism and provide an accurate quantitative estimate of the contribution of trace gas chemotrophy to global ecosystem processes.

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