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Review Article

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Life history strategies to study the succession of H_2-oxidizing bacteria and their ecological role along H_2 concentration gradients in upland soils

Xavier Baril and Philippe Constant *

Centre Armand-Frappier Santé Biotechnologie, Institut national de la recherche scientifique, 531 boulevard des Prairies, Laval (Québec), H7V 1B7, Canada

*Corresponding author. Centre Armand-Frappier Santé Biotechnologie, Institut national de la recherche scientifique, 531 boulevard des Prairies, Laval (Québec), H7V 1B7, Canada. E-mail: philippe.constant@inrs.ca

Abstract

The recent discovery of atmospheric chemosynthesis has caused a paradigm shift in the way H_2-oxidizing bacteria (HOB) are examined. The field has transitioned from the consideration of HOB as a specialized functional group benefiting from the energy potential of H_2 for mixotrophic growth or persistence to a versatile group of bacteria using multiple trace gases. We discuss four life history strategies supported by H_2, namely chemolithoautotrophic growth, mixotrophic growth, persistence, and atmospheric chemosynthesis. There is experimental evidence supporting the role of HOB in various ecosystem services beyond the uptake of H_2 including, for instance, carbon cycling, plant growth promotion, and primary production. Decoupling between the intensity of HOB activation in soil and compositional change of microbial communities remains puzzling, highlighting our poor understanding of the ecological role of HOB. We call for new experimental approaches to delineate the interactions between HOB and the other members of the community. We propose a dedicated framework integrating life history strategies of HOB for mechanistic assessment of microbial interactions and processes supported by H_2 in soil.

Keywords: soil; hydrogen-oxidizing bacteria; life history strategies; trace gas metabolism

Glossary

Chemolithoautotrophic growth: From chemolithoautotrophy, meaning an organism that nourishes (*trophic-*) on chemical energy source (*chemo-*), inorganic electron donor (*litho-*), and inorganic carbon source (*auto-*). For example, *Cupriavidus necator* growth supported by H_2 and CO_2.

Heterotrophic growth (chemoorganoheterotrophy): Referring to an organism that feeds on chemical energy source (*chemo-*), organic electron donor (*organo-*), and organic carbon source (*hetero-*).

Facultative chemolithoautotroph: Organism exhibiting potential chemolithoautotrophic and chemoorganoheterotrophic growth.

Mixotrophic growth: Growth supported by more than one electron donor or carbon source. For example, *C. necator* exhibits mixotrophic growth combining H_2 and CO_2 (chemolithoautotroph) as well as organic compounds (chemoorganoheterotroph). If H_2 is used in conjunction of organic compounds without CO_2 fixation, chemolithoheterotrophy can occur, where organic carbon is used for anabolism and H_2 as an energy source.

Persistence: Metabolic state exhibiting low or no growth allowing the organism to survive when resources are limited.

Atmospheric chemosynthesis: Extreme chemolithoautotrophic growth based on the uptake of atmospheric gas for energy, carbon, and nitrogen needs.

Life history strategy: Patterns of resource allocation by an organism based on trade-offs between its survival, growth, and reproduction. They are associated with sets of traits that determine the fitness of the organisms in different environments.

Succession: The process by which species composition of the community change over time.

HOB activation: Increased apparent H_2 oxidation rate following H_2 supplementation based on a metabolic cascade and/or increase in HOB biomass.

Introduction

H_2-oxidizing bacteria (HOB) are thriving in aerobic and anaerobic environments. This literature review focuses on aerobic conditions, where the oxidation of H_2 is supported by [NiFe]-hydrogenase catalyzing the interconversion of H_2 into protons and electrons. The enzyme comprises two main subunits: the large subunit comprising the binuclear nickel (Ni)—iron (Fe) active site coordinated by cyanide (CN) and carbon monoxide (CO) ligands, and the small subunit acting as an electron relay to the physiological electron acceptor of the enzyme. A systematic analysis of the physiological role and gene sequences led to the definition of four different groups of [NiFe]-hydrogenases (Vignais and Billoud 2007). These groups integrate multiple subgroups defined on the basis of gene sequence homology (Søndergaard et al. 2016). Enzymes encompassing groups 1, 2, and 3 are particularly relevant in upland soil. The uptake [NiFe]-hydrogenase subgroups 1d, 1h, and 2a preferentially catalyze the oxidation reaction supplying electrons to the respiratory chain for ATP

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generation (Fig. 1; Vignais and Billoud 2007, Pandelia et al. 2012, Greening et al. 2014, Grinter et al. 2023). The regulatory [NiFe]-hydrogenase included in subgroup 2b acts as H_2 sensor for the gene transcription regulation of the oxygen-tolerant membrane-bound [NiFe]-hydrogenases 1d (Fig. 1), also referred to as 6C [NiFe]-hydrogenase (Pandelia et al. 2012). [NiFe]-hydrogenases belonging to subgroups 3b and 3d include soluble bidirectional hydrogenases combining the oxidation of H_2 and the reduction of NAD(P) into NAD(P)H or the reverse reaction to lower reductant level in the cell (Fig. 1).

The energy potential of H_2 oxidation reaction is determined by the local concentration of H_2 and the kinetic parameters governing the catalytic activity of [NiFe]-hydrogenase. The seminal work of Schuler and Conrad (1990) has demonstrated the occurrence of two contrasting subpopulations of HOB in soil, namely high- and low-affinity HOB. The architecture of the active site of [NiFe]-hydrogenase and their physiological electron acceptor define their affinity for H_2 (Grinter et al. 2023). HOB displaying a low affinity for H_2 are involved in a rapid uptake of elevated concentrations of H_2, whereas HOB displaying a high affinity for H_2 have the capacity to consume sub-atmospheric H_2 concentrations (0.53 ppmv; Schuler and Conrad 1990, Häring and Conrad 1994, Constant et al. 2010). It is now accepted that HOB do not form two distinct groups, but rather a continuum according to the affinity spectrum of their [NiFe]-hydrogenase towards H_2 (Constant et al. 2010).

Atmospheric H_2-oxidizing bacteria (atmHOB) are expected to display high affinity for H_2 with an apparent K_M, lower than 800 nM H_2 (Conrad 1996). [NiFe]-hydrogenases in these bacteria are more efficient to scavenge trace levels of H_2 than low-affinity HOB. AtmHOB are responsible for 80% of the global sink of the atmospheric H_2 (Constant et al. 2009). Few [NiFe]-hydrogenase subgroups have a high enough affinity to enable the bacterial uptake of atmospheric H_2. The activity was demonstrated for group 1 h (also named group 5) and the group 2a, by hydrogenase gene knockouts in *Mycobacterium smegmatis* (Greening et al. 2014) and *Streptomyces avermitilis* (Liot and Constant 2016). The examination of H_2-oxidation activity in multiple bacterial isolates further corroborated the ability of these enzymes to oxidize atmospheric H_2 concentrations, as discussed in Greening and Grinter (2022). Bacteria possessing the group 1 h, Hhy type, have the highest affinity for H_2 and use the energy potential of H_2 to supply their survival and persistence. The group 2a, Huc type, displays higher expression and activity during growth on organic carbon, suggesting a role in mixotrophic growth (Cordero et al. 2019, Islam et al. 2020). There is evidence that other subgroups of [NiFe]-hydrogenases may be involved in the oxidation of atmospheric H_2. Isolates possessing only a group 1f (Hyo type; Myers and King 2016) or 1l (Hyl type; Ortiz et al. 2021) [NiFe]-hydrogenases have shown the ability to oxidize H_2 at sub-atmospheric concentrations. The group 1 h is recognized as more abundant and likely more important for the biological sink of H_2 (Bay et al. 2021). This supposition still needs to be validated considering that biogeochemical processes are generally decoupled from the abundance of functional genes in soil (Rocca et al. 2015).

The purpose of this review is to propose a theoretical framework to study the **life history strategies** of HOB in upland soil. We first introduce four life history strategies based on bacterial isolates exhibiting a range of metabolic responses to H_2 concentrations and the availability of organic substrates. We then explore an important ecological niche supporting HOB: the rhizosphere of legume plants. H_2 released as obligate by-product of nitrogen fixation likely acts as biostimulant through enigmatic mechanisms reviewed in the text. A particular emphasis is put on the enrichment of HOB in the rhizosphere and the **succession** of sub-populations encompassing the four life history strategies. Methods to study the life history strategies of HOB in the environment are put forward with consideration with the idiosyncratic nature of HOB responses to H_2 exposure. Our inability to predict the fate of HOB subpopulations and their interactions with the other members of soil microbial communities in different soil and ecosystem types is highlighted with a few case studies. We conclude the review with prospective research directions integrating life history strategies in lab-scale and field-scale experimental designs.

Life history strategies of HOB

HOB encompass four different life history strategies, namely (i) obligate **chemolithoautotrophic growth**, (ii) **mixotrophic growth**, (iii) **persistence**, and (iv) **atmospheric chemosynthesis** supported by H_2. These four life history strategies are put forward as a model of microbial succession in the environment (Fig. 2a). Chemolithoautotrophic growth strategy is the hallmark of the first HOB isolates, exhibiting growth supported by carbon dioxide (CO_2) and H_2 as carbon and energy sources, respectively (Repaske 1966). Obligate chemolithoautotrophic growth strategy (Fig. 2a) is particularly well suited to extreme environments such as burning coal piles from which *Streptomyces thermoautotrophicus* was isolated (Gadkari et al. 1990) and hot springs where the thermophilic *Hydrogenobacter thermophilus* originated (Kawasumi et al. 1984). Most low-affinity HOB display facultative chemolithoautotrophic or mixotrophic growth in upland soil (Fig. 2a). They include symbiotic or free-living nitrogen-fixing alpha-proteobacteria (Schwartz et al. 2013). The bacterium *Cupriavidus necator* (formerly *Ralstonia eutropha*) has been utilized as a model to study H_2 metabolism and the biochemical basis of [NiFe]-hydrogenase maturation, activation, and catalysis (Friedrich et al. 2005, Fritsch et al. 2011). Cultivation of *C. necator* in the presence of CO_2 and organic carbon shed light on the mixotrophic growth of HOB (Schwartz et al. 2013). The expression of group 1d [NiFe]-hydrogenase in *C. necator* is derepressed when local H_2 concentrations are high enough to be detected by the two-component H_2 sensor and gene activator system or under nutrient deprivation conditions. In contrast, high nutrient availability induces a catabolic repression of hydrogenase gene expression, supporting a transition to **heterotrophic growth** (Friedrich et al. 1981). The combination of inorganic and organic substrates for mixotrophic growth is beneficial to occupy ecological niches, including the soil in the surroundings of H_2-emitting nodules, where the enrichment of HOB leads to net CO_2 fixation (Dong and Layzell 2001, Stein et al. 2005). Mixotrophic growth thus supports well-adapted metabolic versatility for HOB to thrive under nutrient starvation and hypoxia stress (Berney and Cook 2010), in extreme environments (Ortiz et al. 2021), and environments facing feast and famine nutrient regimes (Berney et al. 2014). The local concentration of H_2 and affinity of HOB to H_2 lead to a transition between mixotrophic growth and persistence un-

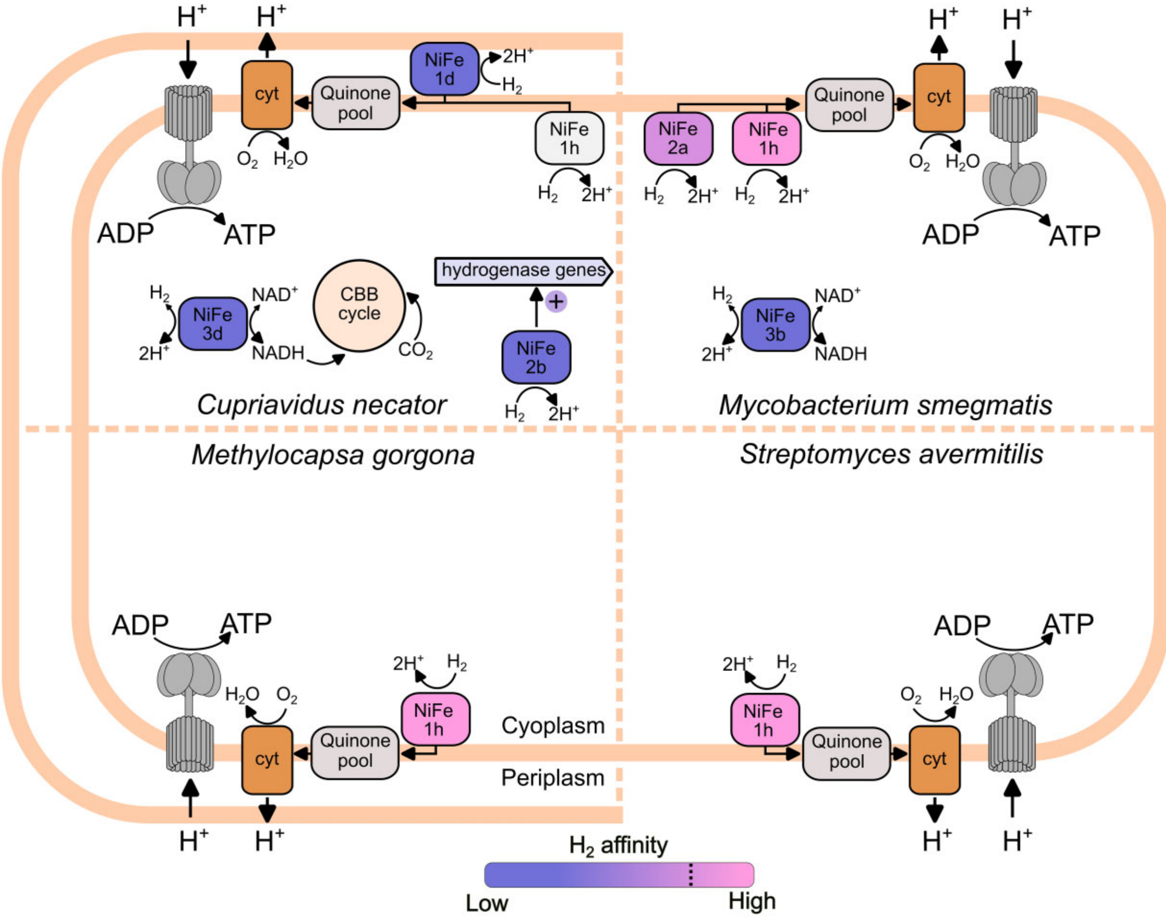

Figure 1. Conceptual metabolic implications of [NiFe]-hydrogenases in four model HOB. The hydrogenase affinity continuum for H_2 is represented with a color gradient, where the dash line represents the affinity threshold for the oxidation of atmospheric concentrations. The 1 h [NiFe]-hydrogenase in *Cupriavidu necator* is weakly expressed and does not exhibit a high affinity for H_2. Reversible reactions are represented with double-sided arrow, and the size of arrowhead reflects what is believed to be the usual direction of catalysis. More comprehensive assessments are available for *Cupriavidus necator* (Friedrich et al. 2005, Schäfer et al. 2013), *Methylocapsa gorgona* (Schmider et al. 2024), *Mycobacterium smegmatis* (Cordero et al. 2019, Greening and Grinter 2022, Grinter et al. 2023), and *Streptomyces avermitilis* (Liot and Constant 2016).

der nutrient-exhausted conditions (Fig. 2a). The first experimental evidence of such bacterial persistence was reported in *Streptomyces* sp. PCB7 displaying H_2 oxidation activity during the sporulation stage (Constant et al. 2008). The persistence of the *Streptomyces avermitilis* spore population relies on the energy potential of atmospheric H_2, as supported by the drastic reduction of spore viability in a hydrogenase knockout strain (Liot and Constant 2016). Similar contributions of H_2 to bacterial persistence under energy-limited condition was also noticed in other Actinomycetota isolates such as *Rhodococcus equi* (Meredith et al. 2014) and *Mycobacterium smegmatis* (Berney and Cook 2010, Cordero et al. 2019), as well as within two Chloroflexota strains (Islam et al. 2019) and numerous of Acidobacteriota isolates (Greening et al. 2015, Myers and King 2016, Giguere et al. 2021). Distinction between persistence and slow mixotrophic growth can be challenging in certain cases due to the absence of sporulation in the dormant state. The oxidation of atmH_2 supplies just enough energy, in theory, to support the vital needs of dormant cells (Conrad 1999). However, more cells of *Streptomyces* spp. are present in soil than the theoretical population number based on their activity, supporting the hypothesis of persistence mixotrophy (Constant et al. 2010). The regulation of metabolic network supporting mixotrophic persistence is mostly driven by nutrient availability. In *S. avermitilis*, saturating high-affinity [NiFe]-hydrogenase under elevated H_2 exposure changed gene expression profiles towards a preferential utilization of H_2 instead of organic carbon for minimal energy requirement supply (Liot and Constant 2016). The combination of atmospheric H_2 with other trace gases can, however, lead to growth through atmospheric chemosynthesis (Tveit et al. 2021). *Methylocapsa gorgona* MG08 was the first isolate demonstrating growth on air at atmospheric gas concentrations. Atmospheric chemosynthesis of the strain is supported by the energy and carbon from H_2, CO, CO_2, and CH_4, and the nitrogen obtained from N_2 fixation (Tveit et al. 2019, Tveit et al. 2021). Uneven distribution of [NiFe]-hydrogenase among different taxonomic groups, combined with the metabolic flexibility of HOB make the distinction of the four life history strategies difficult. Life history strategies likely encompass a continuum rather than discrete classes. Pure culture studies suggest that HOB possessing multiple [NiFe]-hydrogenases exhibiting different catalytic properties may switch along this continuum according to environmental constraints shaped by H_2 concentration gradients (Schwartz et al. 2009, Berney et al. 2014).

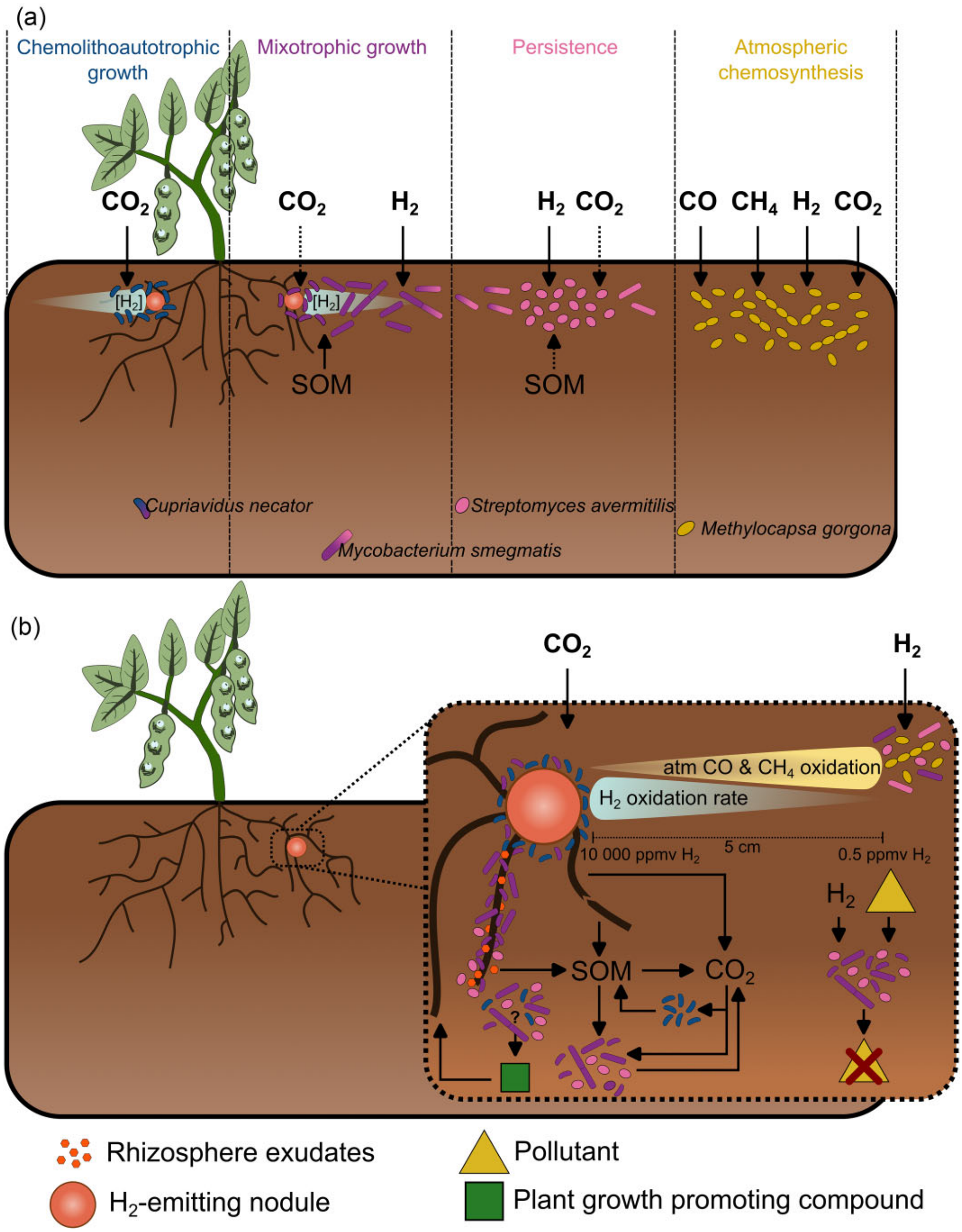

Figure 2. (a) Different life history strategies of HOB and (b) microbial mediated processes influenced by H_2 gradient in the rhizosphere of H_2-emitting legume. The response of HOB within the H_2 gradient varies according to their history strategy. A color code is used to position the life history strategies along the gradient, along with four representative bacterial isolates. Facultative chemolithoautotrophs are active member of the Hup^- legume rhizosphere. The high level of H_2 in legume rhizosphere niche modulate the metabolism toward H_2 leading to net CO_2 fixation associated to chemolithoautotrophic and mixotrophic growth. The rhizosphere is a well-suited environment for mixotrophic growth. Root exudates sustain more abundant and active microbial communities according to the so-called rhizosphere effect. The combination of high H_2 concentration and carbon gradients in the rhizosphere favors the mixotrophy growth strategy. The abundance of chemolithoautotroph is expected to decrease along the H_2 concentration gradient. This is accompanied by a rise of high-affinity HOB displaying mixotrophy growth and persistence. Soil H_2 exposure is linked with higher rate of pollutant degradation (b). The combination of H_2 with polychlorinated biphenyls (PCB) is suggested to support mixotrophic growth. Some HOB isolates exhibiting chemiolithoautotrophic growth were associated with production of plant growth-promoting compound (b), but the actual life history strategies of potential plant growth-promoting HOB are unknown.

Is H_2 exerting a biostimulant effect?

H_2 is an obligatory byproduct of N_2 fixation occurring in legume nodules (Hunt and Layzell 1993). This reaction, mediated by symbiotic N_2-fixing bacteria (NFB), accounts for an investment of ~20% of net photosynthesis energy (Layzell et al. 1979). H_2 leak alone represents ~35% of this energy loss (Hunt and Layzell 1993). To compensate for this loss of energy, NFB can be equipped with "recycling" hydrogenases (Hup^+). The fact that Hup^+ symbiosis is more energy efficient was considered to explain higher plant biomass in Hup^+ vetch than their Hup^- counterparts (Sotelo et al. 2021). Counter-intuitively, the *hup*$^-$ genotype is more abundant in nature and tends to be associated to larger root biomass (Annan et al. 2012). Thus, H_2 production from nodules usually escapes N_2-fixing bacteria to diffuse in soil. There is likely an evolutionary advantage for plants to release H_2 in the rhizosphere to recruit HOB. H_2 is entirely consumed in the first centimeters surrounding N_2-fixing nodules inducing a H_2 concentration gradient ranging from over 10 000 ppmv to sub-atmospheric levels (La Favre and Focht 1983, Piché-Choquette et al. 2018).

Two hypotheses were proposed to explain the so-called H_2 fertilization effect: one plant-centric and the other microbe-centric. The first hypothesis posits that H_2 antioxidant potential triggers a pleiotropic action culminating in interference with phytohormones controlling growth under stress conditions in plants. Alwazeer et al. (2024) published a review exploring the use of H_2 in agriculture and the possible mechanism linked with this hypothesis. However, there is a lack of experimental evidence to support the proposed mechanism (Alwazeer et al. 2024).

The microbe-centric hypothesis is based on direct and indirect effect of HOB on plants. Direct effect is founded on the recruitment of plant growth-promoting HOB in the rhizosphere of N_2-fixing legume plants. This is supported by the isolation of HOB strains promoting root growth by 1-aminocyclopropane-1-carboxylate (ACC) deaminase enzyme activity (Maimaiti et al. 2007). This evidence is indirect because the exposure to H_2 was not associated with higher ACC deaminase activity in soil, thus the impact of H_2-emitting nodules on microorganisms and plants may also be attributed to a more general mechanism involving non-HOB. It was first proposed by La Favre and Focht (1983), who considered the leakage of H_2 not as an energy loss for the soil-plant ecosystem but as a transfer to HOB as an integral part of this system. As HOB encompass broad taxonomic and functional diversity, their activation through H_2 supply is expected to activate biogeochemical processes in soil. This mechanism is analogous to the soil carbon priming effect, whereby the energy derived from H_2 in the community initiates a cascade of biochemical reactions, leading to the secretion of enzymes and secondary metabolites. This ultimately mobilizes and enhances the availability of nutrients for plants and other microorganisms. This vision is rooted by the observed impact of H_2 on a range of microbial processes, including some that are relevant to the carbon cycle (Fig. 2b). For instance, HOB can contribute to soil organic carbon degradation through their production of a wide spectrum of extracellular enzymes, including cellulase, laccases, and peroxidases (Piché-Choquette and Constant 2019). Soil exposure to elevated H_2 concentration also led to a diversification in carbon degradation profile of the soil community (Khdhiri et al. 2017) and an increase in overall microbial activity (Stein et al. 2005). The distance at which H_2 diffuses is one order of magnitude higher than the rhizosphere exudate (de la Porte et al. 2020). The exact contribution of H_2 to the rhizosphere effect is unknown, but Islam et al. (2023) have proposed a framework for investigating the contribution of hydrogen to agricultural soils and, conversely, the effect of agricultural practices on HOB.

The biostimulation effect of H_2 is not universal, likely requiring a combination of multiple factors. The complexity of biogeochemical feedback loops activated by H_2 can explain contradicting reports on plant growth promotion supported by the gas. Enhanced plant biomass yield upon soil H_2 supplementation varied from 15% to 48% for wheat, canola, barley, and non-symbiotic soybean (Dong et al. 2003) to no significant gain on maize (Peoples et al. 2008) and wheat (de la Porte et al. 2024). Mechanistic assessment of plant and microbiological processes contributing to the H_2 biostimulation effect is necessary to achieve benefits in the agricultural sector. Whether beneficial HOB for plants are restricted to specific life history traits also remains to be elucidated.

How to determine HOB life history strategies in the environment

The life history strategies of HOB can be determined in isolates (Fig. 2a), but extrapolations in environmental samples are a challenging task. Two main methods can be used to infer life history strategies in HOB populations, namely (i) measurement of potential H_2 oxidation activity and (ii) genomic approaches. Potential H_2 oxidation activity measurement is a proxy for HOB cell density (Conrad 1999). The energy potential of H_2 oxidation reaction, the minimal energy requirement to support cellular maintenance, and H_2 oxidation rates can be integrated to predict the population size of HOB relying only on H_2. Application of this principle to bacterial isolates and soil samples led to the conclusion that population density is higher than expected, suggesting that mixotrophic life history strategy dominates (Constant et al. 2010). Distinction between mixotrophic persistence, mixotrophic growth, or atmospheric chemosynthesis is not resolved by that approach.

A second level of resolution can be achieved by integrating genomic techniques. For instance, potential HOB were identified with DNA stable isotope probing (SIP) following the incorporation of $^{13}CO_2$ in presence of elevated H_2 concentration (Pumphrey et al. 2011). The method is efficient to identify HOB fixing CO_2, without distinguishing chemolithoautotrophy or mixotrophy growth strategies. For atmospheric chemosynthesis, the use of $^{13}CO_2$ DNA SIP under atmospheric conditions with trace gas levels and in which photoautotrophs are inhibited is proposed to identify this strategy in environmental samples (Ray et al. 2023). The potential metabolic features of metagenome-assembled genomes (MAGs) led to the identification of potential HOB fixing CO_2 and utilizing multiple trace gases (Lynch et al. 2014, Ortiz et al. 2021, Xu et al. 2021). Genomic techniques when used in conjunction with environmental gradients can link HOB succession to their life history strategies (Li et al. 2023, Garvin et al. 2024). However, assessing the life history strategies of HOB in the environment is complicated by a decoupling between **HOB activation** intensity and response at the microbial community level.

Intensity of HOB activation is idiosyncratic and decoupled from compositional change of microbial communities

H_2 leakages from Hup^- symbiosis in legume nodules are expected to exert a beneficial impact on soil microbial communities through microbial growth or activation. Bacterial proliferation promoted by H_2 was supported by culture-dependent methods showing an enrichment of chemolithoautotrophic

HOB along H_2 gradients (La Favre and Focht 1983). Enrichment of mixotrophic HOB, chemolithoautotrophic HOB, and promotion of mixotrophic persistence were not distinguishable, impairing an assessment on the importance of root exudates to shape the succession of HOB across the H_2 concentration gradient. The potential benefit of HOB activation on growth performance of non-HOB was not assessed.

Isolation of the H_2 effect was made in soil microcosms, where stimulation of HOB activity was achieved by H_2-supplemented atmosphere (525–50 000 ppmv). However, research conducted from the two last decades leads to the observation that H_2 exerts a modest impact on microbial community (Piché-Choquette et al. 2016, Khdhiri et al. 2017, Khdhiri et al. 2018, Piché-Choquette et al. 2018, Xu et al. 2021, de la Porte et al. 2024). That was first noticed by Osborne et al. (2010) identifying a single bacterial ribotype responding to H_2 supplementation. Deeper characterization of microbial communities through high-throughput PCR amplicon sequencing techniques first suggested a more important impact on microbial communities than expected (Piché-Choquette et al. 2016), but that finding was inflated by elevated false discovery rates of earliest gene abundance comparison techniques (de la Porte et al. 2024). These results indicate that there is no major shift in the microbial community associated with the modest effect of H_2 supplementation on microbial communities, suggesting that endogenous carbon sources in soil are insufficient to support growth of HOB. This is supported by careful examinations of the plateau reached in HOB activation after a few days of exposure to H_2 at the time scale utilized for microcosm experiments (Dip and Constant 2025).

The silent effect of H_2 supplementation on the composition of soil microbial communities occurs with the activation of a series of biogeochemical feedback loops, including positive and negative effects on soil ecosystem services. For instance, the rhizosphere of N_2-fixing legumes is associated with higher degradation rate of persistent organic pollutants such as PCB (Xu et al. 2023). The contribution of rhizospheric HOB in this process was evaluated through the utilization of H_2 supplementation treatment (Xu et al. 2023). In addition to facilitating enhanced pollutant degradation, DNA-SIP following ^{13}C-labeled PCB77 incorporation revealed that H_2 sustains mixotrophic growth of HOB that degrade PCB77 (Xu et al. 2023). In contrast, potential negative effects can emerge from H_2 supplementation. The increase in H_2 oxidation rate caused by exposure to high concentrations leads to a decrease in oxidation activity potential of CO and CH_4 (Piché-Choquette et al. 2018). Metabolic flexibility of HOB toward multiple trace gases is a plausible explanation for such H_2 interference on CH_4 and CO oxidation. Different isolates encode more than one enzyme for the oxidation of trace gases such as H_2, CO, and CH_4, reflecting their metabolic flexibility (King 2003, Schmider et al. 2024). A preferential utilization of H_2 rather than CO and CH_4 is expected in soil exposed to elevated H_2 concentration. The ability to consume multiple trace gases is therefore frequent in soil HOB. By inhibiting the microbial oxidation of CO and CH_4, H_2 leakages from N_2-fixing nodules of legume plants could be detrimental to the biological sinks of atmospheric CH_4 and CO. H_2 interference, however, relies on soil microcosms. Experimental evidence from the field or contrasting Hup$^-$ and Hup$^+$ symbiosis is awaiting to evaluate the contribution of crop rotation practice to the global budget of atmospheric CO and CH_4. Given the rather small contribution of CO and CH_4 biological sinks the global budget of these gases (Bartholomew and Alexander 1981, Khalil and Rasmussen 1990, Conrad 2009), it is unlikely that H_2 supplementation will have a significant impact on these budgets. The metabolic flexibility of HOB towards multiple trace gases should be integrated into the study of HOB across the continuum of life history traits.

Proposition for future research

A better understanding of the succession of HOB in the environment will shed light on their ecological roles. Here we proposed four relevant life history strategies to predict the distribution and activity of HOB in upland soil (Wood et al. 2023). To validate the proposed model, we call for hypothesis-driven research against the theoretical framework (Fig. 3). Examining the response of communities to environmental change will improve prediction of ecosystem functioning in response to disturbances (Fig. 3a). In that sense we propose to simulate H_2 concentrations gradient in soils with contrasting biological and physicochemical properties to induce microbial successions that are relevant to life history strategies of HOB (Fig. 3b). Synthetic gas supplementation or Hup$^-$ legume-rhizobium symbiosis (Xu et al. 2023) utilized alone or in combination are efficient approaches to recreate relevant H_2 concentration gradients found in agroecosystems integrating legume crops. Assays using Hup$^+$ and Hup$^-$ symbiosis offer the possibility to delineate mixotrophic growth of HOB triggered by H_2 and root exudates, whereas H_2 supplementation alone is expected to promote persistence mixotrophy. These concentration gradients of H_2 superimposed to various soil abiotic features, including CO_2, CH_4, CO, and soil organic matter, can facilitate the validation of the role of each substrate in shaping succession of life history strategies (Fig. 3b). Investigation of the incidence of abiotic determinants on HOB activity can be conducted in controlled microcosms (Baril and Constant 2023) and by exploiting the variation in naturally contrasting soils (Khdhiri et al. 2015). Biotic interactions, including plant cover diversity and density in shaping HOB community and activity (Baril et al. 2022), diversity erosion experiments (Saavedra-Lavoie et al. 2020), and synthetic communities integrating wild-type and hydrogenase knockout HOB strains would be relevant to decipher the ecological role of HOB and their interaction with plant and other microbes in soil (Fig. 3c). The utilization of synthetic communities was proven efficient to identify microbial interactions supporting the activity of methane-oxidizing bacteria (Ho et al. 2014). Application of similar approaches integrating HOB representative of selected life history strategies will delineate beneficial, neutral, and deleterious interactions for their proliferation and activity. Together, biotic and abiotic determinants of HOB ecological niches are expected to select traits relevant to life history strategies, including stress tolerance, growth rate, and versatility (Fig. 3d). Manipulation of biotic and abiotic determinants will allow to validate the proposed life history strategies of HOB, while assessing shared sets of ecological traits that dominate in certain niches.

Conclusion

HOB are supporting diverse ecosystem services, but the intensity of their activation upon exposure to elevated H_2 is idiosyncratic. This variable response is likely linked to environmental and intrinsic determinants of the HOB life his-

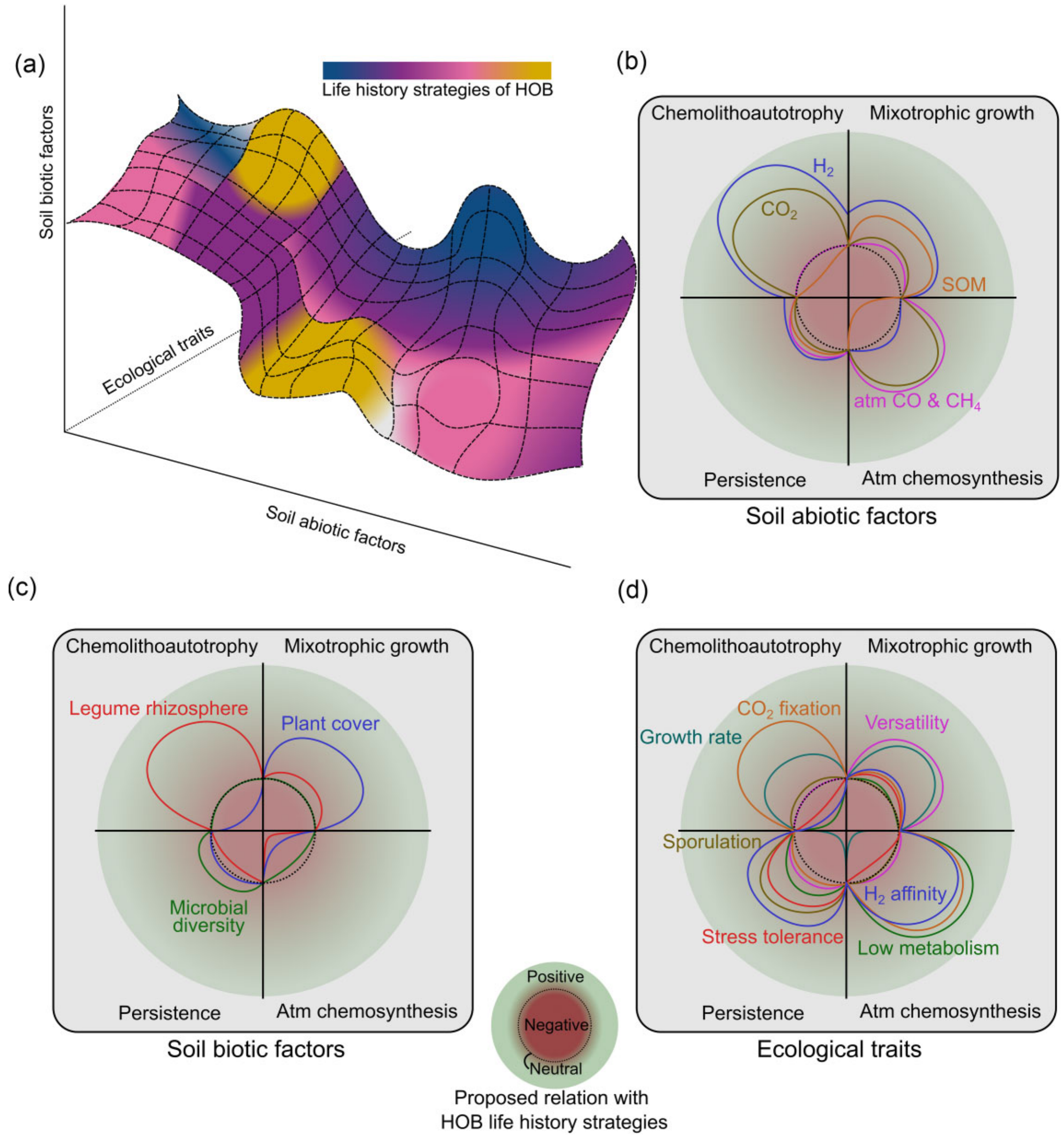

Figure 3. Theoretical framework to be tested with hypothesis-driven studies. (a) Life history strategies of HOB are determined by their ecological traits and the environmental abiotic and biotic factors. The colors represent the conceptual sequence of HOB's four life history strategies according to the three main axes. (b and c) Examples of soil abiotic and biotics determinants link to the axis in (a) and their significance for life history strategies of HOB. (d) The proposed pertinence of ecological traits for the four strategies of HOB. The colored lines in b, c, and d represent the proposed relationships between environmental factors or ecological traits and HOB life history strategies. Thus, lines associated with a factor or trait that covers a larger area of a life history strategy quadrant are expected to be positively associated with that strategy.

tory strategies. Here we propose to manipulate H_2 gradients to trigger succession of HOB encompassing the four life history strategies: chemolithoautotrophy, mixotrophic growth, persistence, and atmospheric chemosynthesis. We call for research focusing on environmental conditions and their interactions with H_2 supplementation regarding the effects on microbial community structure and functioning. In addition to a better understanding of HOB response to environmental conditions according to their traits. Ultimately, mechanistic approaches to HOB succession along H_2 gradients may also guide the choice of *hup* genotype of commercial N_2-fixing rhizobial inoculum in agriculture and improve predictions of the fate of the biological sink of atmospheric H_2 as well as other processes supported by HOB to a future H_2-based economy.

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Author contributions

Xavier Baril (Conceptualization [equal], Funding acquisition [supporting], Writing – original draft [equal], Writing – review

& editing [equal]), and Philippe Constant (Conceptualization [equal], Funding acquisition [lead], Writing – original draft [equal], Writing – review & editing [equal]).

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Data availability

No new data were generated or analysed in support of this research.

References

Alwazeer D, Hancock J, Russell G *et al*. Molecular hydrogen: a sustainable strategy for agricultural and food production challenges. *Front Food Sci Technol* 2024;**4**:1448148. https://doi.org/10.3389/frfst.2024.1448148

Annan H, Golding AL, Zhao Y *et al*. Choice of hydrogen uptake (Hup) status in legume-rhizobia symbioses. *Ecol Evol* 2012;**2**:2285–90. https://doi.org/10.1002/ece3.325

Baril X, Constant P. Carbon amendments in soil microcosms induce uneven response on H2 oxidation activity and microbial community composition. *FEMS Microbiol Ecol* 2023;**99**:fiad159. https://doi.org/10.1093/femsec/fiad159

Baril X, Durand A-A, Srei N *et al*. The biological sink of atmospheric H_2 is more sensitive to spatial variation of microbial diversity than N_2O and CO_2 emissions in a winter cover crop field trial. *Sci Total Environ* 2022;**821**:153420. https://doi.org/10.1016/j.scitotenv.2022.153420

Bartholomew GW, Alexander M. Soil as a sink for atmospheric carbon monoxide. *Science* 1981;**212**:1389–91. https://doi.org/10.1126/science.212.4501.1389

Bay SK, Dong X, Bradley JA *et al*. Trace gas oxidizers are widespread and active members of soil microbial communities. *Nat Microbiol* 2021;**6**:246–56. https://doi.org/10.1038/s41564-020-00811-w

Berney M, Cook GM. Unique flexibility in energy metabolism allows mycobacteria to combat starvation and hypoxia. *PLoS One* 2010;**5**:e8614. https://doi.org/10.1371/journal.pone.0008614

Berney M, Greening C, Hards K *et al*. Three different [NiFe] hydrogenases confer metabolic flexibility in the obligate aerobe *Mycobacterium smegmatis*. *Environ Microbiol* 2014;**16**:318–30. https://doi.org/10.1111/1462-2920.12320

Conrad R. Soil microorganisms as controllers of atmospheric trace gases (H_2, CO, CH4, OCS, N2O, and NO). *Microbiol Rev* 1996;**60**:609–40. https://doi.org/10.1128/mr.60.4.609-640.1996

Conrad R. Soil microorganisms oxidizing atmospheric trace gases (CH4, CO, H_2, NO). *Indian J Microbiol* 1999;**39**:193–204.

Conrad R. The global methane cycle: recent advances in understanding the microbial processes involved. *Environ Microbiol Rep* 2009;**1**:285–92. https://doi.org/10.1111/j.1758-2229.2009.00038.x

Constant P, Chowdhury SP, Pratscher J *et al*. Streptomycetes contributing to atmospheric molecular hydrogen soil uptake are widespread and encode a putative high-affinity [NiFe]-hydrogenase. *Environ Microbiol* 2010;**12**:821–9. https://doi.org/10.1111/j.1462-2920.2009.02130.x

Constant P, Poissant L, Villemur R. Isolation of *Streptomyces* sp. PCB7, the first microorganism demonstrating high-affinity uptake of tropospheric H2. *ISME J* 2008;**2**:1066–76. https://doi.org/10.1038/ismej.2008.59

Constant P, Poissant L, Villemur R. Tropospheric H2 budget and the response of its soil uptake under the changing environment. *Sci Total Environ* 2009;**407**:1809–23. https://doi.org/10.1016/j.scitotenv.2008.10.064

Cordero PR, Grinter R, Hards K *et al*. Two uptake hydrogenases differentially interact with the aerobic respiratory chain during mycobacterial growth and persistence. *J Biol Chem* 2019;**294**:18980–91. https://doi.org/10.1074/jbc.RA119.011076

de la Porte A, Durand A-A, Whalen J *et al*. A rhizosphere effect promotes the persistence of gas oxidization activity in soil. *Soil Biol Biochem* 2024;**199**:109599. https://doi.org/10.1016/j.soilbio.2024.109599

de la Porte A, Schmidt R, Yergeau É *et al*. A gaseous milieu: extending the boundaries of the rhizosphere. *Trends Microbiol* 2020;**28**:536–42. https://doi.org/10.1016/j.tim.2020.02.016

Dip D , Constant P The potential biofertilization effect of H2 is accompanied by a modest impact on the composition of microbial communities in the rhizosphere of common vetch. *Biorxiv* 2025. 2025.02.12.637852. https://doi.org/10.1101/2025.02.12.637852 bioRxiv (28 April 2025, date last accessed) .

Dong Z, Layzell D. H_2 oxidation, O_2 uptake and CO_2 fixation in hydrogen treated soils. *Plant Soil* 2001;**229**:1–12. https://doi.org/10.1023/A:1004810017490

Dong Z, Wu L, Kettlewell B *et al*. Hydrogen fertilization of soils–is this a benefit of legumes in rotation? *Plant Cell Environ* 2003;**26**:1875–9. https://doi.org/10.1046/j.1365-3040.2003.01103.x

La Favre JS, Focht D. Conservation in soil of H2 liberated from N2 fixation by hup-nodules. *Appl Environ Microbiol* 1983;**46**:304–11. https://doi.org/10.1128/aem.46.2.304-311.1983

Friedrich B, Buhrke T, Burgdorf T *et al*. A hydrogen-sensing multiprotein complex controls aerobic hydrogen metabolism in *Ralstonia eutropha*. *Biochemical Society Transactions* 2005;**33**;97–101. https://doi.org/10.1042/BST0330097

Friedrich CG, Friedrich B, Bowien B. Formation of enzymes of autotrophic metabolism during heterotrophic growth of *Alcaligenes eutrophus*. *Microbiology* 1981;**122**:69–78. https://doi.org/10.1099/00221287-122-1-69

Fritsch J, Lenz O, Friedrich B. the maturation factors HoxR and HoxT contribute to oxygen tolerance of membrane-bound [NiFe] hydrogenase in *Ralstonia eutropha* H16. *J Bacteriol* 2011;**193**:2487–97. https://doi.org/10.1128/jb.01427-10

Gadkari D, Schricker K, Acker G *et al*. *Streptomyces thermoautotrophicus* sp. nov., a thermophilic CO-and H_2-oxidizing obligate chemolithoautotroph. *Appl Environ Microbiol* 1990;**56**:3727–34. https://doi.org/10.1128/aem.56.12.3727-3734.1990

Garvin ZK, Abades SR, Trefault N *et al*. Prevalence of trace gas-oxidizing soil bacteria increases with radial distance from Polloquere hot spring within a high-elevation Andean cold desert. *ISME J* 2024;**18**:wrae062. https://doi.org/10.1093/ismejo/wrae062

Giguere AT, Eichorst SA, Meier DV *et al*. Acidobacteria are active and abundant members of diverse atmospheric H_2-oxidizing communities detected in temperate soils. *ISME J* 2021;**15**:363–76. https://doi.org/10.1038/s41396-020-00750-8

Greening C, Berney M, Hards K *et al*. A soil actinobacterium scavenges atmospheric H2 using two membrane-associated, oxygen-dependent [NiFe] hydrogenases. *Proc Natl Acad Sci* 2014;**111**:4257–61. https://doi.org/10.1073/pnas.1320586111

Greening C, Carere CR, Rushton-Green R *et al*. Persistence of the dominant soil phylum acidobacteria by trace gas scavenging. *Proc Natl Acad Sci* 2015;**112**:10497–502. https://doi.org/10.1073/pnas.1508385112

Greening C, Grinter R. Microbial oxidation of atmospheric trace gases. *Nat Rev Micro* 2022;**20**:1–16. https://doi.org/10.1038/s41579-022-00724-x

Grinter R, Kropp A, Venugopal H *et al*. Structural basis for bacterial energy extraction from atmospheric hydrogen. *Nature* 2023;**615**:1–7. https://doi.org/10.1038/s41586-023-05781-7

Häring V, Conrad R. Demonstration of two different H_2-oxidizing activities in soil using an H2 consumption and a tritium exchange assay. *Biol Fertil Soils* 1994;**17**:125–8. https://doi.org/10.1007/BF00337744

Ho A, De Roy K, Thas O *et al*. The more, the merrier: heterotroph richness stimulates methanotrophic activity. *ISME J* 2014;**8**:1945–8. https://doi.org/10.1038/ismej.2014.74

Hunt S, Layzell DB. Gas exchange of legume nodules and the regulation of nitrogenase activity. *Annu Rev Plant Biol* 1993;**44**:483–511. https://doi.org/10.1146/annurev.pp.44.060193.002411

Islam ZF, Cordero PR, Feng J *et al*. Two Chloroflexi classes independently evolved the ability to persist on atmospheric hydrogen and carbon monoxide. *ISME J* 2019;**13**:1801–13. https://doi.org/10.1038/s41396-019-0393-0

Islam ZF, Greening C, Hu HW. Microbial hydrogen cycling in agricultural systems–plant beneficial or detrimental? *Microb Biotechnol* 2023;**16**:1623–8. https://doi.org/10.1111/1751-7915.14300

Islam ZF, Welsh C, Bayly K *et al*. A widely distributed hydrogenase oxidises atmospheric H_2 during bacterial growth. *ISME J* 2020;**14**:2649–58. https://doi.org/10.1038/s41396-020-0713-4

Kawasumi T, Igarashi Y, Kodama T *et al*. *Hydrogenobacter thermophilus* gen. nov., sp. nov., an extremely thermophilic, aerobic, hydrogen-oxidizing bacterium. *Int J Syst Evol Microbiol* 1984;**34**:5–10. https://doi.org/10.1099/00207713-34-1-5

Khalil M, Rasmussen R. The global cycle of carbon monoxide: trends and mass balance. *Chemosphere* 1990;**20**:227–42. https://doi.org/10.1016/0045-6535(90)90098-E

Khdhiri M, Hesse L, Popa ME *et al*. Soil carbon content and relative abundance of high affinity H2-oxidizing bacteria predict atmospheric H2 soil uptake activity better than soil microbial community composition. *Soil Biol Biochem* 2015;**85**:1–9. https://doi.org/10.1016/j.soilbio.2015.02.030

Khdhiri M, Piché-Choquette S, Tremblay J *et al*. The tale of a neglected energy source: elevated hydrogen exposure affects both microbial diversity and function in soil. *Appl Environ Microbiol* 2017;**83**;e00275–17. https://doi.org/10.1128/AEM.00275-17

Khdhiri M, Piché-Choquette S, Tremblay J *et al*. Meta-omics survey of [NiFe]-hydrogenase genes fails to capture drastic variations in H2-oxidation activity measured in three soils exposed to H_2. *Soil Biol Biochem* 2018;**125**:239–43. https://doi.org/10.1016/j.soilbio.2018.07.020

King GM. Uptake of carbon monoxide and hydrogen at environmentally relevant concentrations by mycobacteria. *Appl Environ Microbiol* 2003;**69**:7266–72. https://doi.org/10.1128/AEM.69.12.7266-7272.2003

Layzell DB, Rainbird RM, Atkins CA *et al*. Economy of photosynthate use in nitrogen-fixing legume nodules: observations on two contrasting symbioses. *Plant Physiol* 1979;**64**:888–91. https://doi.org/10.1104/pp.64.5.888

Li S, Yang S, Wei X *et al*. Reduced trace gas oxidizers as a response to organic carbon availability linked to oligotrophs in desert fertile islands. *ISME J* 2023;**17**:1–10. https://doi.org/10.1038/s41396-023-01437-6

Liot Q, Constant P. Breathing air to save energy–new insights into the ecophysiological role of high-affinity [NiFe]-hydrogenase in *Streptomyces avermitilis*. *Microbiologyopen* 2016;**5**:47–59. https://doi.org/10.1002/mbo3.310

Lynch RC, Darcy JL, Kane NC *et al*. Metagenomic evidence for metabolism of trace atmospheric gases by high-elevation desert actinobacteria. *Front Microbiol* 2014;**5**:698. https://doi.org/10.3389/fmicb.2014.00698

Maimaiti J, Zhang Y, Yang J *et al*. Isolation and characterization of hydrogen-oxidizing bacteria induced following exposure of soil to hydrogen gas and their impact on plant growth. *Environ Microbiol* 2007;**9**:435–44. https://doi.org/10.1111/j.1462-2920.2006.01155.x

Meredith LK, Rao D, Bosak T *et al*. Consumption of atmospheric hydrogen during the life cycle of soil-dwelling actinobacteria. *Environ Microbiol Rep* 2014;**6**:226–38. https://doi.org/10.1111/1758-2229.12116

Myers MR, King G. Isolation and characterization of *Acidobacterium ailaaui* sp. nov., a novel member of acidobacteria subdivision 1, from a geothermally heated Hawaiian microbial mat. *Int J Syst Evol Microbiol* 2016;**66**:5328–35. https://doi.org/10.1099/ijsem.0.001516

Ortiz M, Leung PM, Shelley G *et al*. Multiple energy sources and metabolic strategies sustain microbial diversity in Antarctic desert soils. *Proc Natl Acad Sci* 2021;**118**:e2025322118. https://doi.org/10.1073/pnas.2025322118

Osborne CA, Peoples MB, Janssen PH. Detection of a reproducible, single-member shift in soil bacterial communities exposed to low levels of hydrogen. *Appl Environ Microbiol* 2010;**76**:1471–9. https://doi.org/10.1128/AEM.02072-09

Pandelia M-E, Lubitz W, Nitschke W. Evolution and diversification of group 1 [NiFe] hydrogenases. Is there a phylogenetic marker for O2-tolerance? *Biochim Biophys Acta* 2012;**1817**:1565–75. https://doi.org/10.1016/j.bbabio.2012.04.012

Peoples MB, McLennan PD, Brockwell J. Hydrogen emission from nodulated soybeans [*Glycine max* (L.) Merr.] and consequences for the productivity of a subsequent maize (*Zea mays* L.) crop. *Plant Soil* 2008;**307**:67–82. https://www.jstor.org/stable/42951861

Piché-Choquette S, Constant P. Molecular hydrogen, a neglected key driver of soil biogeochemical processes. *Appl Environ Microbiol* 2019;**85**:e02418–18. https://doi.org/10.1128/AEM.02418-18

Piché-Choquette S, Khdhiri M, Constant P. Dose-response relationships between environmentally-relevant H_2 concentrations and the biological sinks of H_2, CH_4 and CO in soil. *Soil Biol Biochem* 2018;**123**:190–9. https://doi.org/10.1016/j.soilbio.2018.05.008

Piché-Choquette S, Tremblay J, Tringe SG *et al*. H_2-saturation of high affinity H_2-oxidizing bacteria alters the ecological niche of soil microorganisms unevenly among taxonomic groups. *PeerJ* 2016;**4**:e1782. https://doi.org/10.7717/peerj.1782

Pumphrey GM, Ranchou-Peyruse A, Spain JC. Cultivation-independent detection of autotrophic hydrogen-oxidizing bacteria by DNA stable-isotope probing. *Appl Environ Microbiol* 2011;**77**:4931–8. https://doi.org/10.1128/AEM.00285-11

Ray AE, Tribbia DZ, Cowan DA *et al*. Clearing the air: unraveling past and guiding future research in atmospheric chemosynthesis. *Microbiol Mol Biol Rev* 2023;**87**:e00048–23. https://doi.org/10.1128/mmbr.00048-23

Repaske R. Characteristics of hydrogen bacteria. *Biotechnol Bioeng* 1966;**8**:217–35. https://doi.org/10.1002/bit.260080204

Rocca JD, Hall EK, Lennon JT *et al*. Relationships between protein-encoding gene abundance and corresponding process are commonly assumed yet rarely observed. *ISME J* 2015;**9**:1693–9. https://doi.org/10.1038/ismej.2014.252

Saavedra-Lavoie J, de la Porte A, Piché-Choquette S *et al*. Biological H_2 and CO oxidation activities are sensitive to compositional change of soil microbial communities. *Can J Microbiol* 2020;**66**:263–73. https://doi.org/10.1139/cjm-2019-0412

Schäfer C, Friedrich B, Lenz O. Novel, oxygen-insensitive group 5 [NiFe]-hydrogenase in *Ralstonia eutropha*. *Appl Environ Microbiol* 2013;**79**:5137–45. https://doi.org/10.1128/AEM.01576-13

Schmider T, Hestnes AG, Brzykcy J *et al*. Physiological basis for atmospheric methane oxidation and methanotrophic growth on air. *Nat Commun* 2024;**15**:4151. https://doi.org/10.1038/s41467-024-48197-1

Schuler S, Conrad R. Soils contain two different activities for oxidation of hydrogen. *FEMS Microbiol Ecol* 1990;**6**:77–83. https://doi.org/10.1111/j.1574-6968.1990.tb03927.x

Schwartz E, Fritsch J, Friedrich B. The H_2-metabolizing prokaryotes. In: Heidelberg SB (ed.), *The Prokaryotes Prokaryotic Biology and Symbiotic Associations*Vol. **1**. Berlin, Heidelberg: Springer, 2013,496–563. https://doi.org/10.1007/978-3-642-30141-4_65

Schwartz E, Voigt B, Zühlke D *et al*. A proteomic view of the facultatively chemolithoautotrophic lifestyle of *Ralstonia eutropha* H16. *Proteomics* 2009;**9**:5132–42. https://doi.org/10.1002/pmic.200900333

Søndergaard D, Pedersen CN, Greening C. HydDB: a web tool for hydrogenase classification and analysis. *Sci Rep* 2016;**6**:1–8. https://doi.org/10.1038/srep34212

Sotelo M, Ureta AC, Muñoz S *et al*. Introduction of H_2-uptake hydrogenase genes into rhizobial strains improves symbiotic nitrogen fixation in *Vicia sativa* and *Lotus corniculatus* forage legumes. *Front Agronomy* 2021;**3**:661534. https://doi.org/10.3389/fagro.2021.661534

Stein S, Selesi D, Schilling R *et al*. Microbial activity and bacterial composition of H_2-treated soils with net CO_2 fixation. *Soil Biol Biochem* 2005;**37**:1938–45. https://doi.org/10.1016/j.soilbio.2005.02.035

Tveit AT, Hestnes AG, Robinson SL *et al*. Widespread soil bacterium that oxidizes atmospheric methane. *Proc Natl Acad Sci* 2019;**116**:8515–24. https://doi.org/10.1073/pnas.1817812116

Tveit AT, Schmider T, Hestnes AG *et al*. Simultaneous oxidation of atmospheric methane, carbon monoxide and hydrogen for bacterial growth. *Microorganisms* 2021;**9**:153. https://doi.org/10.3390/microorganisms9010153

Vignais PM, Billoud B. Occurrence, classification, and biological function of hydrogenases: an overview. *Chem Rev* 2007;**107**:4206–72. https://doi.org/10.1021/cr050196r

Wood J, Malik A, Greening C *et al*. Rethinking CSR theory to incorporate microbial metabolic diversity and foraging traits. *ISME J* 2023;**17**:1–5. https://doi.org/10.1038/s41396-023-01486-x

Xu Y, Teng Y, Dong X *et al*. Genome-resolved metagenomics reveals how soil bacterial communities respond to elevated H2 availability. *Soil Biol Biochem* 2021;**163**:108464. https://doi.org/10.1016/j.soilbio.2021.108464

Xu Y, Teng Y, Wang X *et al*. Endogenous biohydrogen from a rhizobium-legume association drives microbial biodegradation of polychlorinated biphenyl in contaminated soil. *Environ Int* 2023;**176**:107962. https://doi.org/10.1016/j.envint.2023.107962

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