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RESEARCH ARTICLE

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Key Points:

- We develop a framework for the dynamics of hydrogen-oxidizing bacteria (HOB) in soils
- HOB abundance varies by moisture regime, with dormancy adopted in hyper-arid conditions
- Model better aligns with field data measurements of H_2 deposition velocity

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Modeling Dynamics of Hydrogen-Oxidizing Bacteria Under Pulsing Soil Moisture Conditions

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Abstract Hydrogen-oxidizing bacteria (HOB) are responsible for the dominant soil sink of atmospheric hydrogen (H_2); however, models estimating this sink are yet to incorporate explicit representation of these biotic drivers. Here, we use a donor-consumer model to examine how HOB and carbon-decomposing bacteria (CDB) may jointly influence organic carbon decomposition and atmospheric H_2 uptake as critically driven by hydroclimatic forcings and temporally varying soil moisture. Hydroclimatic forcing was investigated through three simulation setups: constant soil moisture, drying-wetting sequences, and intermittent rainfall. Collectively, these simulations suggest the coexistence of both HOB and CDB, with each group predominantly contributing to microbial biomass in low and high soil moisture regions, respectively. Given the strong influence of soil moisture on H_2 uptake identified in this study, our results further suggest that explicit representation of biotic drivers (HOB biomass and soil carbon) amplifies the oscillatory dynamics in soil H_2 concentration, a feature not captured by the abiotic-only model. We further examined the hypothesis that dormant microbes scavenge H_2 as a survival mechanism by incorporating microbial dormancy into the HOB dynamics and showed that dormancy leads to a higher biomass contribution of HOB in arid regions (dryness index > 5). Finally, the model was applied to estimate H_2 deposition velocity, showing improved agreement with measured data from a temperate forest and validating the importance of the explicit representation of biotic drivers. Model limitations and the potential integration with land-surface models are also discussed.

Plain Language Summary As interest grows in a future H_2 energy system, it becomes increasingly important to improve our understanding of H_2 removal from the atmosphere, which is largely (>70%) mediated by bacteria in soils. To this end, we develop a dynamic model for hydrogen-oxidizing bacteria (HOB) and their activity as influenced by hydrological activity. Our results support previous observations that these bacteria are especially abundant in dry (arid) regions, where they can make up as much as 90% of the total microbial content, whereas in wetter regions, other types of microbes (carbon-decomposing bacteria) are more dominant. One reason HOB thrive in dry environments is their ability to enter a dormant state during periods of low water availability, allowing them to survive harsh conditions and maintain higher population levels compared to situations where dormancy is not considered. Our results also reveal the presence of an optimum moisture for going dormant. Finally, we show that including the amount of HOB (their biomass) in the models improves our prediction of how the soil removes atmospheric H_2 .

1. Introduction

Due to the global interest in hydrogen (H_2) energy for climate mitigation (Hydrogen Council, 2021; IEA, 2019), recent research has been exploring the environmental and climatic consequences of perturbing the H_2 cycle due to emissions to the atmosphere (Bertagni et al., 2022; Paulot et al., 2021; Warwick et al., 2023). Although not a direct greenhouse gas (GHG), H_2 is a relatively powerful indirect GHG because it has the potential to increase the lifetime of methane and produce tropospheric ozone and stratospheric water (Ouyang et al., 2025; Paulot et al., 2021, 2024; Warwick et al., 2004, 2023). The most peculiar thing about the atmospheric H_2 cycle, however, is that it is primarily regulated by hydrogen-oxidizing bacteria (HOB) in soils, which are responsible for 70%–80% of the removal of atmospheric H_2 (Bertagni et al., 2021; Greening et al., 2022; Khalil & Rasmussen, 1990; Novelli et al., 1999). Despite this importance, the H_2 sink by soil bacteria is the most uncertain term in the global H_2 budget (Ouyang et al., 2025; Paulot et al., 2021, 2024). For a better understanding of the global H_2 budget and the potential impact of its perturbation, it is essential to improve our understanding of HOB's dynamics in the complex soil environment and their expected response to environmental changes.

A diverse subset of bacteria has been identified to oxidize H_2 , mostly to support mixotrophic growth, where both organic and inorganic energy sources are oxidized (Bay et al., 2021; Conrad, 1999; Greening et al., 2014; Greening & Grinter, 2022; Hou et al., 2025). This highlights HOB as a subset of aerobic bacteria that play a role in both the H_2 and carbon cycles (contributing to the conversion of substrates into microbial biomass). Several physiological and quantitative properties of H_2 -HOB have been determined following laboratory experiments (Drewer et al., 2026; Ehhalt & Rohrer, 2011; Fan et al., 2022; Greening et al., 2016; Khdhiri et al., 2015; Ortiz et al., 2021; Reji et al., 2025; Smith-Downey et al., 2006), field studies (Baril et al., 2022; Buzzard et al., 2022; Cowan et al., 2025; Meredith et al., 2014, 2017; Nagai et al., 2024) and modeling approaches (Bertagni et al., 2021; Ehhalt & Rohrer, 2013; Paulot et al., 2021). For example, Khdhiri et al. (2015) found that soil carbon content and HOB relative abundance explain around 90% of the variance in H_2 oxidation rates in a grassland soil, and Drewer et al. (2026) reported carbon content to be the dominant factor influencing H_2 flux rates in high-labile carbon soils such as peatland. Bertagni et al. (2021) highlighted the nonlinear response of H_2 uptake to soil moisture, with diffusion limiting uptake in humid areas, whereas biological activity constrains it in arid regions. Collectively, these works highlight the response of soil H_2 uptake to both biotic and abiotic drivers. However, current models lack a dynamic representation of HOB, a critical component for estimating H_2 -related quantities (e.g., deposition velocity, H_2 oxidation rate, and H_2 fluxes) and assessing their responses to climatic changes. In this direction, a recent study reported improved model predictions when existing H_2 models were extended to include a proxy for soil microbial activity (Karbin et al. (2026)), thereby confirming the importance of a currently lacking dynamic representation of HOB dynamics.

Under sub-optimal growth and reproduction conditions, such as limited substrate availability or low moisture, microbes adopt various survival strategies, including dormancy (Allison, 2023; Blagodatskaya & Kuzyakov, 2013; He et al., 2015; Lennon & Jones, 2011; Salazar et al., 2018). Recent studies have revealed that while in a dormant state, these microbes scavenge atmospheric trace gases, including H_2 , to sustain cellular maintenance and survival (Greening et al., 2022; Greening & Grinter, 2022; Ji et al., 2017; Jordaan et al., 2020; Leung et al., 2020; Ortiz et al., 2021). Dormancy strategies may be associated with the widespread presence of HOB across ecosystems, including cold (e.g., Antarctica) and hot (e.g., Atacama) deserts (Conrad & Seiler, 1979; Ji et al., 2017; Jordaan et al., 2020; Meredith et al., 2017; Novelli et al., 1999; Simmonds et al., 2011; Smith-Downey et al., 2008). Several studies have demonstrated the effectiveness of microbial dormancy and its potential to improve predictions in microbe-mediated models (e.g., He et al., 2015; Salazar et al., 2018; Wang et al., 2014), but never in the context of H_2 oxidation and, more generally, capturing dormancy-cost tradeoffs is not trivial (Lennon & Jones, 2011).

Given that microbial biomass forms the core of microbial-explicit nutrient models (Manzoni & Schimel, 2024), this study aims to develop a framework that helps quantify the contribution of HOB to the overall soil microbial biomass as well as examine its role in the H_2 and organic carbon cycles, with the ultimate goal of integrating HOB dynamics into land surface models (e.g., Paulot et al., 2021, 2024; Warwick et al., 2023). Recognizing that microbial communities are not static (Abs et al., 2024), this approach seeks to enhance our understanding of how diverse microbial communities interact under varying climate regimes. This is particularly important as resource allocation trade-offs often emerge, given the limited availability of essential resources (Manzoni & Schimel, 2024; Weverka et al., 2023).

Adopting a parsimonious modeling approach (Figure 1), we segregate the total microbial biomass pool into two distinct classes: HOB and carbon-only decomposing bacteria (CDB), representing bacteria that possess the enzyme (hydrogenase) to oxidize H_2 (irrespective of the hydrogenase group as specified in the literature e.g., Constant et al., 2011; Greening et al., 2016) and bacteria that do not possess hydrogenases and rely solely on organic carbon, respectively. This allows us to account for the individual contribution of each microbial class to microbial biomass and directly couple microbial biomass by HOB to the soil's H_2 and carbon cycle. By explicitly incorporating microbial dormancy into the modeling framework, we then explore how this survival strategy influences the HOB-driven microbial biomass generation and nutrient cycling, especially under conditions typical of arid environments.

Given the lack of specific experimental data on the dynamics of bacterial processes in relation to hydrogen dynamics, the purpose of our model is not necessarily to quantitatively predict microbial behavior in soils, but rather to help sharpen questions that are otherwise difficult to formulate or rigorously test. Accordingly, several

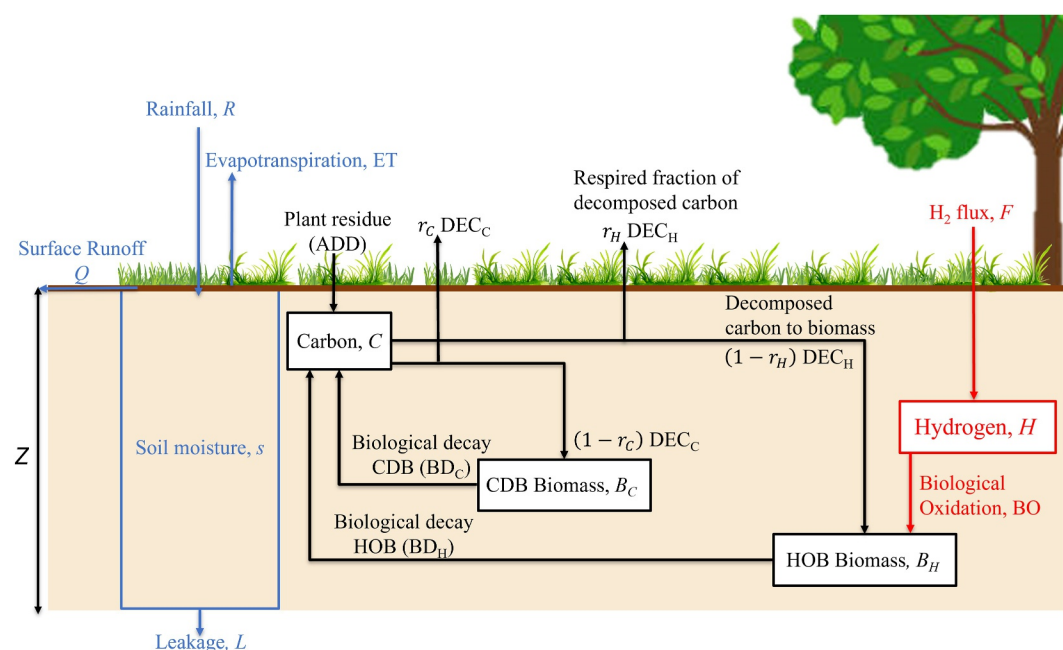


Figure 1. Schematic framework for the coupled dynamics of carbon substrate (C), hydrogen (H), and microbial biomass pools (B_C and B_H). Arrows represent fluxes for moisture (blue), hydrogen (red), and carbon and biomass (black) over depth Z . Terms description: DEC—Decomposition of carbon, BD—Biological decay of carbon, F — H_2 flux into the soil, BO—biological oxidation of H_2 within the soil, $r_{C,H}$ —respired carbon fraction, and subscripts C and H represent decomposition or biological decay by carbon-decomposing bacteria and hydrogen-oxidizing bacteria, respectively.

analyses have been specifically devoted to providing results that may be useful in planning laboratory (and possibly field) experiments to further explore the dynamics revealed by the model.

From a modeling point of view, we hence focus on the temporal evolution and dynamic behavior provided by the system of equations describing the vertically averaged dynamic behavior of HOB, CDB, hydrogen, carbon and soil moisture. The mathematical description adopts a minimalist approach, using tools from dynamical systems; for further reference, see specialized literature (e.g., Strogatz, 2024).

2. Methods

2.1. Model Structure and Philosophy

The interactions of microbial biomass and soil substrates in the decomposition process can be conceptualized as a donor-consumer relationship (Manzoni & Porporato, 2007). Originally applied to describe the interaction between carbon substrate and microbial biomass as a single pool, this is extended here to account for two substrates (H_2 and organic carbon) and two microbial biomass pools (HOB and CDB) while incorporating the effects of hydroclimatic forcing (frequency and average rainfall magnitude) and temporal variations in soil moisture. Microbial decomposition is modeled as dependent on both substrate availability and microbial biomass concentration, including a nonlinear (e.g., multiplicative) dependence, essential to capture microbial interactions and substrate decomposition in changing environmental conditions (Bertagni et al., 2021; Blagodatskaya & Kuzyakov, 2013; Bosatta & Berendse, 1984; Manzoni et al., 2004; Manzoni & Porporato, 2007; Manzoni & Schimel, 2024; Porporato et al., 2003; Salazar et al., 2018). Table 1 presents the definition of symbols and model variables, and Figure 1 presents a schematic illustration of the physical processes involved in the proposed model, with arrows representing the interactions between substrates and microbial biomass classes. While non-dormant, HOB are assumed to simultaneously decompose organic carbon and oxidize H_2 (co-metabolism, e.g., Cordero et al., 2019; Greening et al., 2014, 2019; Hou et al., 2024), only the decomposition of organic carbon contributes directly to the generation of microbial biomass. The analytical formulations of the terms depicted in the figure are detailed in the following sections.

Table 1
Definition of Symbols and Model Variables Including Their Units

Symbol	Description	Units
B_C	Biomass from carbon decomposing bacteria (CDB)	gC m^{-3}
B_H	Biomass from hydrogen oxidizing bacteria (HOB)	gC m^{-3}
BD	Biological decay of carbon	$\text{gC m}^{-3} \text{d}^{-1}$
BO	Biological oxidation of hydrogen	ppb s^{-1}
C	Organic carbon in the soil	gC m^{-3}
DEC	Decomposition of organic carbon	$\text{gC m}^{-3} \text{d}^{-1}$
ET	Evapotranspiration	cm d^{-1}
F	Flux of Hydrogen into the soil	ppb cm s^{-1}
$f_C(s), f_H(s)$	Response of CDB, HOB activity respectively, to soil moisture	—
H	Concentration of hydrogen in the soil	ppb
L	Leakage	cm d^{-1}
Q	Excess runoff	cm d^{-1}
R	Rainfall	cm d^{-1}
s	Soil moisture	—
s_w	Moisture level at which carbon decomposition by CDB ceases	—
s_{ws}	Moisture level at which HOB activity (not dormant) ceases	—
s_{dorm}	Moisture level at which HOB enters dormant state	—

2.2. Soil Moisture Dynamics

Soil moisture and its temporal fluctuations influence substrate availability, microbial activity, and overall nutrient cycling within the ecosystem. Soil moisture temporal fluctuations are driven by rainfall inputs via the soil water balance equation (e.g., Manzoni & Porporato, 2009; Porporato & Yin, 2022 etc.),

$$nZ \frac{ds}{dt} = R(t) + J(t) - I(t) - Q(t) - ET(t, s) - L(t, s) \quad (1)$$

Equation 1 represents the rate of change of the depth-averaged relative soil moisture, s [-], a dimensionless quantity obtained as m^3 water m^{-3} pore space. Therefore, s ranges between a minimum value of 0 (completely dry soil) and a maximum value of 1 (saturated soil), with the assumption that the soil is vertically homogeneous over a zone of depth Z . This zone, typically corresponding to the A horizon (Porporato & Yin, 2022), is where most plant roots and soil biological activity reside and while its depth (Z) can exceed 100 cm in some ecosystems, this study adopts an average value of $Z = 30$ cm, which is also the typical layer where key variations in atmospheric hydrogen (H) occur in the upper soil layer (e.g., Hou et al. (2025)). The soil porosity is defined as n with units of m^3 pore space m^{-3} soil, and on the right-hand side, $R(t)$ represents rainfall, $J(t)$ is irrigation, $I(t)$ is the canopy interception, $Q(t)$ is the surface runoff, $ET(t, s)$ is the evapotranspiration, and $L(t, s)$ is percolation or leakage. All terms on the right-hand side of Equation 1 have units of cm d^{-1} , and it is important to note that we consider net rainfall ($R(t) - I(t)$) as the only moisture input, and therefore, the irrigation term $J(t)$ is set to zero.

2.3. Soil Carbon and H_2 Dynamics

We consider a soil system in which compartments of carbon substrate (C) and hydrogen (H) interact with microbial biomass pools of CDB and HOB. The carbon and H_2 substrates are both assumed to be passive substrates, accessible for microbial assimilation. With reference to the block diagram of Figure 1, the balance equation for soil hydrogen can be expressed in Equation 2 as

$$nZ \frac{d[(1-s)H]}{dt} = F + Z(P - BO) \quad (2)$$

where H with units of ppb represents the concentration of H_2 in the soil-air phase, expressed in ppb. F with units of ppb cm s^{-1} represents the flux of H_2 from the atmospheric boundary layer through possible diffusive barriers (canopy, litter, snow, etc.) and the soil, P and BO (with units of ppb s^{-1}) represent the production and biological oxidation (sometimes regarded as biological sink or biological decay) of H_2 within the soil layer, respectively. The flux of H_2 (F , Equation 3) is usually modeled by adopting the discrete diffusion approximation based on the H_2 -concentration gradient between the atmosphere and the soil; that is

$$F = g_T(H_a - H), \quad (3)$$

where g_T with units of cm s^{-1} represents the total conductance between the atmosphere, the possible diffusive barriers and the soil (Bertagni et al., 2021), and H_a represents the atmospheric concentration of H_2 ($H_a \approx 540$ ppb).

Usually soils act as net sinks of H_2 from the atmosphere since H_2 production (P) by, for example, nitrogen-fixing bacteria, is largely consumed within the soil (e.g., by cyanobacteria with the group 2a [NiFe]-hydrogenase and other HOB groups immediately surrounding H_2 production hotspots) (Constant et al., 2011; Khdhiri et al., 2017; La Favre & Focht, 1983; Lenz & Friedrich, 1998; Robson & Postgate, 1980). For our simulations, we integrate the production term into BO (viz., $P = 0$) and use BO as a net sink of H_2 in the soil. The biological oxidation of H_2 (BO) is influenced by a range of factors, including the concentration of H_2 , microbial abundance and activity, temperature, and soil moisture, and potentially other unconstrained soil characteristics (Bertagni et al., 2021; Conrad & Seiler, 1981; Drewer et al., 2026; Khdhiri et al., 2017; Smith-Downey et al., 2006). Recently, experiments have shown that soil pH is not a significant driver of H_2 uptake, suggesting that soil chemistry may be less important than soil physics and biology (Drewer et al., 2026; Hou et al., 2024). Compared to previous formulations (e.g., Bertagni et al., 2021; Ehhalt & Rohrer, 2011), here we consider BO (Equation 4) to account for the dynamically variable HOB biomass (B_H) and the organic carbon (C) availability. Thus, BO is mathematically expressed in Equation 4 as

$$BO = k_H B_H C H, \quad (4)$$

where $k_H = k_H^* f_H(s) q(T)$ (Bertagni et al., 2021; Ehhalt & Rohrer, 2011; Smith-Downey et al., 2006) represents the rate of biological removal of H_2 from the soil by HOB, k_H^* with units of $\text{s}^{-1}(\text{m}^3 \text{gC}^{-1})^2$ is the maximum potential decomposition rate of H_2 substrate, while $f_H(s)$ and $q(T)$ are dimensionless reduction functions that account for the response of HOB to moisture (s) and temperature (T), respectively. To focus on the impact of hydrologic fluctuations, all simulations in this study were conducted assuming constant temperature conditions, fixed at 25°C. To account for the observed dependence of the effects of soil moisture on H_2 fluxes, $f_H(s)$ is modeled as a modified beta distribution characterized by a lower threshold (s_{ws}) and an optimum (s_{opt}) for HOB activity (Bertagni et al., 2021), see Appendix for mathematical description.

Multiple experimental studies have confirmed the existence of an optimal soil moisture (s_{opt}) that maximizes the activity of HOB and a minimum soil moisture (s_{ws}) necessary for HOB activity (Drewer et al., 2026; Ehhalt & Rohrer, 2011; Reji et al., 2025; Smith-Downey et al., 2006). Recently, tailored laboratory experiments across soil types (Reji et al., 2025) found that s_{opt} and s_{ws} correspond to correspond to soil water potentials of approximately -0.3 MPa and -100 MPa, respectively. This extremely low value of water potential (-100 MPa corresponds to a depression of around 1,000 times the atmospheric pressure) confirms the ability of HOB to survive in unfavorable conditions. These water potential values can be converted to equivalent soil moisture levels using soil-specific water retention curves (e.g., Porporato & Yin, 2022).

The rate of change of carbon substrate (C) in the soil (expressed in units of $\text{gC m}^{-3} \text{d}^{-1}$) is given by Equation 5

$$\frac{dC}{dt} = \text{ADD}(s) - \text{DEC}_C - \text{DEC}_H + \text{BD}_C + \text{BD}_H \quad (5)$$

Here, ADD denotes the input of carbon (e.g., plant residues) into the soil, DEC refers to the microbial decomposition of organic carbon, and BD represents the biological decay of microbial biomass, which subsequently contributes to the pool of available carbon. The subscripts C and H indicate that the corresponding processes are

mediated by CDB and HOB, respectively. ADD with units of $\text{gC m}^{-3} \text{d}^{-1}$ is assumed to depend on the long-term average soil moisture (see Appendix A), which is considered a proxy of ecosystem productivity (Manzoni & Porporato, 2007).

DEC represents the decomposition of the carbon substrate by microbes, where subscripts C and H represent decomposition by CDB and HOB respectively. DEC_C is expressed in Equation 6 as

$$\text{DEC}_C = k_C C B_C \quad (6)$$

where $k_C = k_C^* f_C(s)$ (Manzoni & Porporato, 2007; Rodrigo et al., 1997) represents the rate of biological decomposition of organic carbon in the soil by CDB. k_C^* with units of $\text{m}^3 \text{d}^{-1} (\text{gC})^{-1}$ is the potential decomposition rate of the C substrate, $f_C(s)$ is a dimensionless reduction function that accounts for the response of CDB to s. DEC_H , namely the carbon decomposition by HOB bacteria, is linked to the hydrogen consumption (BO) by the expression

$$\text{DEC}_H = \chi \Pi \text{BO} = \chi \Pi k_H B_H C \quad (7)$$

where Π with units gC gH^{-1} is defined the carbon-to-hydrogen ratio of HOB nutrient requirements, which we have assumed a 1 to 1 atomic consumption of C and H, resulting in a value of 12, based on the atomic weights of C and H (we note that our simulation results were consistent when we tried a value of $\Pi = 6$ (based on the atomic weights of C (12) and H_2 (2)), which technically halves the original decomposition of carbon by HOB). We intend to clarify that Π currently serves as an assumed model parameter, rather than an established HOB nutrient requirement. χ is a factor that represents the transition to and out of the dormant state ($\chi = 1$ when non-dormant and $\chi = 0$ when dormant), which is discussed in Section 2.5.

The biological decay BD is modeled following first-order kinetics and expressed in Equations 8 and 9

$$\text{BD}_C = m_C B_C \quad (8)$$

$$\text{BD}_H = m_H B_H \quad (9)$$

as in most biogeochemical models (e.g., Brangarí et al., 2020; Manzoni & Porporato, 2007; Resat et al., 2012), where m_C and m_H with units d^{-1} represents the mortality rate of B_C and B_H respectively.

2.4. Microbial Biomass Dynamics

The segregated microbial biomass pools are B_C and B_H , representing the contributions of CDB and HOB to the total biomass. The total amount of decomposing organic carbon (DEC) is partially allocated to meet the heterotrophic respiration needs of soil microbes, denoted as $r\text{DEC}$ (represented by the upward arrows in Figure 1), while the remaining portion, $(1 - r)\text{DEC}$, is used for microbial biomass generation. Here, $r_{C,H}$ is dimensionless and refers to the fraction of carbon respired by CDB and HOB, respectively. For simplicity, we assume that both microbial classes have equal carbon respiration fractions (i.e., $r_C = r_H$). The values for $r_{C,H}$ typically range between 0.5 and 0.6 (Manzoni et al., 2014; Manzoni & Porporato, 2007; McGill et al., 1981; Schimel, 2003). The balance equations for the rate of change of B_C and B_H are presented in Equations 10 and 11 respectively

$$\frac{dB_C}{dt} = (1 - r_C) \text{DEC}_C - \text{BD}_C \quad (10)$$

$$\frac{dB_H}{dt} = (1 - r_H) \text{DEC}_H - \text{BD}_H \quad (11)$$

where $(1 - r_{C,H})$ are the carbon utilization efficiency of CDB and HOB, respectively (Manzoni & Porporato, 2007).

2.5. Microbial Dormancy

When encountering unfavorable conditions, microorganisms may enter a reversible state of low metabolic activity, known as microbial dormancy, and exit when favorable conditions occur. The transition to a dormant state can be triggered by various stressing factors (Allison, 2023; Chandel et al., 2023; He et al., 2015; Lennon & Jones, 2011; Manzoni et al., 2014); however, for our analysis, we will focus exclusively on soil moisture. Modeling microbial dormancy in a way that realistically incorporates microbial survival strategies is quite complex and not fully established in the literature. Here, to incorporate microbial dormancy into the model, particularly on the dynamics of HOB, we consider the following modeling assumptions:

1. Dormancy results in H_2 uptake, albeit at low rates sufficient only to meet the energy requirements for metabolic maintenance. Mathematically, $f_H(s)$ is modified to allow an uptake of H_2 at moisture values lower than s_{ws} (see Appendix A).
2. We define s_{dorm} as the threshold below which microbes transition into a dormant state as soil moisture decreases, assuming that s_{dorm} falls within the range of s_{ws} (e.g., -100 MPa) at which point, HOB activity ceases (Reji et al., 2025), and s_w (e.g., -3 MPa), at which point CDB activity ceases (Porporato & Yin, 2022).
3. While dormant, HOB ceases decomposition of organic carbon, namely $\chi = 0$ in Equation 7, while $\chi = 1$ otherwise.
4. Lennon and Jones (2011) reported that microbes exhibit a reduced mortality rate when dormant relative to their active state. Accordingly, we assumed the mortality rate of HOB to decrease by two orders of magnitude under dormancy. Thus, m_H in Equation 9, becomes $m_{H,dorm} = m_H/100$. As the true magnitude of this reduction remains unknown, we additionally explored $m_{H,dorm} = m_H/10$ (not explicitly reported), and simulation results remained consistent.

Such dormancy assumptions will be applied when moisture levels drop below the defined threshold (s_{dorm}). Upon rewetting, as rainfall increases the moisture above this threshold, the microbes revert relatively quickly from dormancy to their active state.

2.6. Model Simulation Setup

We collectively refer to Equations 1, 2, 5, 10 and 11 as the “model,” with variables and symbols summarized in Table 1. We first analyze the system using a dynamical systems framework (e.g., Strogatz, 2024), to determine steady states and stability conditions for the key variables C , H , B_C , and B_H , treating soil moisture(s) as constant. This formulation is analogous to controlled laboratory experiments with fixed moisture conditions and facilitates characterization of the model's long-term behavior and stability.

We next examined the model's dynamics under simulated periodic drying and wetting cycles that replicate an experimental design in which soil moisture is elevated to a prescribed level and subsequently allowed to decline through drying. Soil moisture input is represented as discrete rainfall pulses of fixed magnitude h_0 (this raises the soil moisture to a prescribed level) occurring at a predetermined interval τ (hence, rainfall frequency = $1/\tau$ d^{-1}), enabling analysis of how rainfall frequency and magnitude influence the substrate (C , H) and microbial pools (B_C and B_H). We ran the simulation for 3,000 days to allow the model to reach a steady state (periodic or fixed) and report the time series and phase portrait of the substrate-microbe pairs.

To increase realism in the environmental forcing conditions, we then introduce rainfall intermittency by simulating Equation 1 using a stochastic approach (Porporato & Yin, 2022), as already explored by Bertagni et al. (2021), without the dynamic biomass and organic carbon pools. This stochastic rainfall forcing allows us to replicate the field conditions in which rainfall frequency and magnitude are random. In this framework, rainfall ($R(t)$) is modeled as pulses of random depth occurring as a marked Poisson process, with a frequency λ (d^{-1}), and each event has an exponentially distributed random depth of rainfall with mean α (cm) (Porporato & Yin, 2022). Here, the simulation length is also 3,000 days. However, we only report 2,000 days of model simulation to eradicate the influence of initial conditions on result interpretation.

We then estimate how the long-term average contribution of HOB to microbial biomass evolves with varying climatic regimes in both dormancy and no-dormancy models, and quantify their relative abundance as $B_H/(B_H + B_C)$. For the long-term averages, simulation length was 200 years, and this provides us with substantial data for a statistical summary, elucidating the influence of microbial dormancy and the relative contribution of HOB

biomass. Finally, we explore a data-model comparison and discuss uncertainties and extensions of the modeling framework.

3. Results

3.1. Steady State and Stability Analysis

To gain an understanding of the long-term behavior of the model, we first performed an analysis of the steady states (or fixed points) and the stability of the model variables (H^* , C^* , B_H^* , and B_C^*), assuming that soil moisture (s) remains constant, as it would under controlled laboratory conditions. The proposed model has three fixed points and their analytical expressions as a function of soil moisture (s) are presented in Table 3. The first fixed point is characterized by $B_H = 0$, namely, no HOB contribution to microbial biomass. The second fixed point occurs at $B_C = 0$, namely, no CDB contribution to microbial biomass. The third fixed point represents a coexistence scenario, where both microbial classes contribute to biomass generation.

Figure 2 illustrates the physically meaningful steady state values of the model variables (H^* , B_H^* , C^* , and B_C^*) and their corresponding stability (depicted by solid and dashed lines for stable and unstable, respectively) as a function of soil moisture for loamy sand. The first fixed point ($B_H^* = 0$) corresponds to zero HOB biomass and cessation of H_2 uptake, giving a steady state H_2 concentration at atmospheric level, H_a . This fixed point is unstable (dashed blue lines, Figure 2), except at high soil moisture, partly attributed to the low diffusivity of H_2 to microbial hotspots under well-watered conditions and simultaneously, a low decomposition rate of H_2 by HOB, k_H .

The second fixed point ($B_C^* = 0$) is unstable across most soil moisture conditions, indicating that complete loss of CDB biomass is improbable. The exception occurs at low soil moisture, within the interval bounded by the hydrogen oxidation and carbon decomposition activity thresholds, s_{ws} and s_w , where the fixed point is stable. Here, CDB activity ceases while limited HOB activity persists, reflecting HOB's greater tolerance to water stress (Figure A1a). This fixed point is also characterized with no physically meaningful steady state values for soil carbon and C^* except within the narrow moisture range where the fixed point is stable and C^* attains very low values (see black line in Figure 2c). The third fixed point, characterized by the coexistence of CDB and HOB, is more representative of observed field conditions and the corresponding stability analysis confirms that this fixed point is stable across a wide range of soil moisture, indicating that such coexistence is the most probable configuration of HOB and CDB.

To obtain the filled area shown in the steady-state values of the model variables in the figure, we varied the H_2 decomposition rate (k_H^*) using values derived from exponential fits to laboratory experimental data reported by Reji et al. (2025) for Forest (sandy loam) and Meadow (silty loam) soils. These parameter choices represent contrasting soil ecosystems characterized by relatively high (forest) and low (meadow) microbial decomposition rates.

3.2. Impacts of Drying-Wetting Sequences

We proceeded to analyze the response of the model's substrate-microbe pair under varying lengths of drying period (τ) between successive wetting events, as well as differing rewetting (h_0) magnitudes. We examined three distinct configurations of drying periods, τ and rewetting magnitude, h_0 , corresponding to: (a) $\tau = 300$ days and $h_0 = 20$ mm, (b) $\tau = 60$ days and $h_0 = 20$ mm, and (c) $\tau = 25$ days and $h_0 = 35$ mm. These configurations result in total average annual rainfall amounts of approximately 20, 120, and 490 mm, respectively, thereby representing environmental conditions characteristic of hyper-arid, arid, and semi-arid regions, respectively (D'Odorico et al., 2006).

Soil moisture losses occur due to evapotranspiration $ET(t, s)$ and leakage $L(t, s)$ as defined in Equation 1, while rainfall, $R(t)$, is in the form of periodic pulses (defined by their frequency $1/\tau$), carrying a fixed amount of rainfall, h_0 . Therefore, Figure 3 presents the time series of soil moisture, s and the model variables (H , C , B_H , and B_C) under drying-wetting cycles for $h_0 = 35$ mm and τ of 25 days

A more detailed view of the dynamics is depicted on the right-hand side, which contains the model dynamics for 100 days (a typical growing season), between day 1900 and day 2000. In this detailed view, we show that the model predicts pulses of microbial growth for B_C following wetting events that favor the carbon substrate decomposition (Figure 3c), with a subsequent decline in during dry periods. By contrast, B_H increases during dry

Table 2

Model Parameters Used in Simulations, Unless Otherwise Specified

Parameter	Symbol	Value	Units	Reference
Maximum added litter	$ADD_{\max}$	3.2	$\text{gC m}^{-3} \text{d}^{-1}$	Finzi et al. (2002)
Minimum added litter	$ADD_{\min}$	0	$\text{gC m}^{-3} \text{d}^{-1}$	—
C decomposition rate	k_C^*	1.8×10^{-3}	$\text{m}^3 \text{d}^{-1} (\text{gC})^{-1}$	Assumed
H_2 decomposition rate	k_H^*	3.2×10^{-4}	$\text{s}^{-1} (\text{m}^3 \text{gC}^{-1})^2$	Assumed ^a
HOB mortality rate	m_H	5×10^{-3}	d^{-1}	Xu et al. (2014)
CDB mortality rate	m_C	5×10^{-3}	d^{-1}	Xu et al. (2014)
Respired carbon fraction by CDB	r_C	0.5	—	Manzoni and Porporato (2007)
Respired carbon fraction by HOB	r_H	0.5	—	Manzoni and Porporato (2007)
Carbon-hydrogen nutrient ratio ^b	Π	12	$\text{gC}(\text{gH})^{-1}$	Assumed
Rooting depth	Z	30	cm	Porporato and Yin (2022)
Average rainfall frequency	λ	0–1	d^{-1}	Porporato and Yin (2022)
Average rainfall depth	α	1.5	cm	Porporato and Yin (2022)
Atmospheric concentration of H_2	H_a	530	ppb	Novelli et al. (1999)
Dormancy transition factor	χ	0.1	—	—
Drying period	τ	(see text)	days	Assumed
Fixed rainfall amount	h_0	(see text)	cm	Assumed

^aSee appendix for estimation of the H_2 decomposition rate. ^bAssumption: 1:1 hydrogen and carbon consumption and the element atomic weight.

conditions due to a higher H_2 availability. The magnitude of net changes in either B_C or B_H diminishes after repeated cycles as the variables tend to a periodic steady state. When either h_0 is reduced, or τ is larger, B_C initially exhibits similar growth and decline patterns. However, after repeated cycles, B_C sharply decays toward zero (see Figures 4a and 4b), as the initial biomass following rewetting events becomes insufficient to sustain the population through the subsequent drying period.

Figure 4 presents phase portraits of substrate–microbe pairs generated from three representative drying–wetting model simulations, with the green dot representing the initial condition. For the drying period and rainfall magnitude configuration of $\tau = 300$ days and $h_0 = 20$ mm, we observed that the H- B_H (H_2 concentration–microbe) orbit reaches a periodic steady state, as illustrated in the top row of Figure 4, column (a), while the C- B_C pair reaches a fixed steady state as B_C collapses towards zero, as shown in the bottom row. This simulation uses low rainfall magnitude and long drying periods, so soil moisture declines progressively past the activity thresholds of CDB and HOB. Below s_w , CDB undergoes significant decay while HOB continues to H_2 oxidation and carbon decomposition at reduced rates. Below s_{ws} , HOB activity ceases and H_2 concentration approaches its atmospheric value (530 ppb). Following rewetting, soil moisture rises to a level favorable for HOB but suboptimal for CDB, limiting CDB growth. Hence, over repeated drying and wetting cycles CDB biomass and B_C progressively decline towards zero.

Table 3

Steady-State Solutions for Substrates (C^* and H^*) and Microbial Biomass (B_C^* and B_H^*) as a Function of Soil Moisture

Variable	Fixed points I	Fixed points II	Fixed points III
C^*	$\frac{m_C}{(1-r_C)k_C}$	$\frac{m_H}{\Pi(1-r_H)k_H H^*}$	$\frac{m_C}{(1-r_C)k_C}$
H^*	H_a	$H_a - \frac{Z \text{ADD}(s)}{\Pi g r r_H}$	$\frac{(1-r_C)m_H k_C}{\Pi(1-r_H)m_C k_H}$
B_C^*	$\frac{\text{ADD}(s)(1-r_C)}{m_C r_C}$	0	$\frac{(1-r_C)}{m_C r_C} \left[\text{ADD}(s) + m_H B_H^* \left(1 - \frac{1}{(1-r_H)} \right) \right]$
B_H^*	0	$\frac{\text{ADD}(s)(1-r_H)}{m_H r_H}$	$\frac{-g_r m_H k_C (1-r_C) \mp g_r \Pi H_a k_H m_C (1-r_H)}{m_C m_H k_H Z}$

Note. X^* represents the fixed points of a generic variable X .

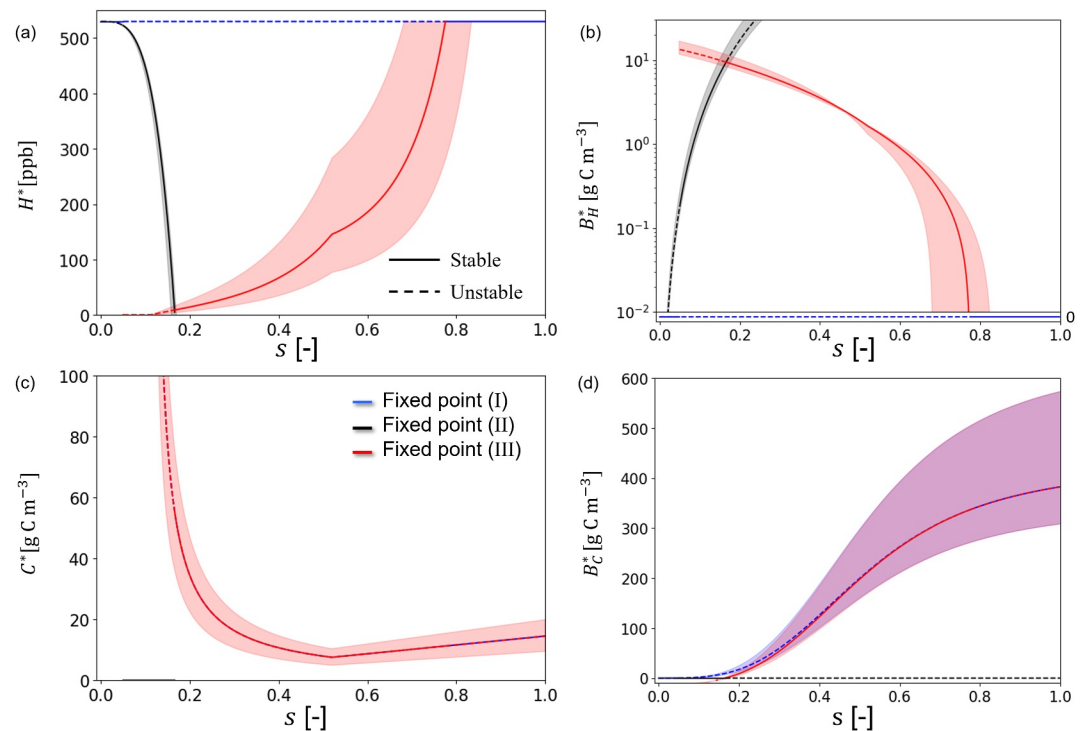


Figure 2. Example of the steady state solutions of the model variables (a) hydrogen concentration H^* , (b) microbial biomass by hydrogen-oxidizing bacteria, B_H^* , (c) carbon, C^* , and (d) microbial biomass by carbon-decomposing bacteria, B_C^* as a function of soil moisture (s) for loamy sand. Dashed lines represent regions where the fixed point is unstable, while solid lines indicate regions where the fixed point is stable. The horizontal lines at the bottom of (b) and (d) are used to represent $B_H^* = 0$ and $B_C^* = 0$, respectively. Panel (b) is in Log scale. The filled area is obtained through variation of parameters associated with specific soil ecosystems, particularly k_H^* , as detailed in Appendix A. Model parameters used are described in Table 2.

Under the conditions of $h_0 = 20$ mm, $\tau = 60$ days, the H- B_H pair similarly converges to a periodic steady state, as in the simulations with $h_0 = 20$ mm, $\tau = 300$ days. However, two notable differences emerge: B_H reaches a higher biomass due to more frequent soil moisture levels for optimal HOB activity, and H does not approach atmospheric values during drying, since soil moisture remains above the s_{ws} , sustaining continuous HOB activity. On the other hand, the C- B_C pair similarly converges to a fixed steady state when compared to the simulations with $\tau = 300$ days. However, it takes more rewetting cycles for B_C to collapse toward zero.

Finally, under the conditions of $h_0 = 35$ mm, $\tau = 25$ days, both substrate-microbe pairs (H- B_H and C- B_C) achieved a periodic steady state, highlighting the significant effect of low-stress levels and optimal microbial activity on microbial biomass accumulation. Notably, maximum B_H in this scenario is lower than in the $\tau = 300$ days and $h_0 = 20$ mm, due to limited H_2 diffusion immediately after rewetting, but as the soil subsequently dries, conditions improve. In contrast, rewetting brings soil moisture to levels optimal for CDB, enabling sustained carbon decomposition and biomass growth. As a result, the C- B_C reaches a periodic steady state, unlike in the previous two configurations where B_C collapsed toward zero due to prolonged suboptimal conditions.

3.3. Microbial Response to Stochastic Soil Moisture and H_2 Uptake

A more realistic complex representation of hydrologic forcing is achieved by considering rainfall as a random process in time, that is, via a stochastic modeling approach (Porporato & Yin, 2022). Figure 5a presents a time series of soil moisture for a loamy sand, with the rainfall input represented as instantaneous pulses with exponentially distributed random rainfall magnitude, occurring as a marked Poisson process. We consider an intermediate climatic condition characterized by a rainfall frequency, $\lambda = 0.2$ d⁻¹ and an average rainfall magnitude, $\alpha = 15$ mm, which results in an average annual rainfall of 1,100 mm, representing a subhumid ecosystem. Figure 5b shows the corresponding time series of the H- B_H substrate-microbe pair (Equation 2 and 12) and Figure 5c shows the time series for the C- B_C pair (Equation 6 and 13).

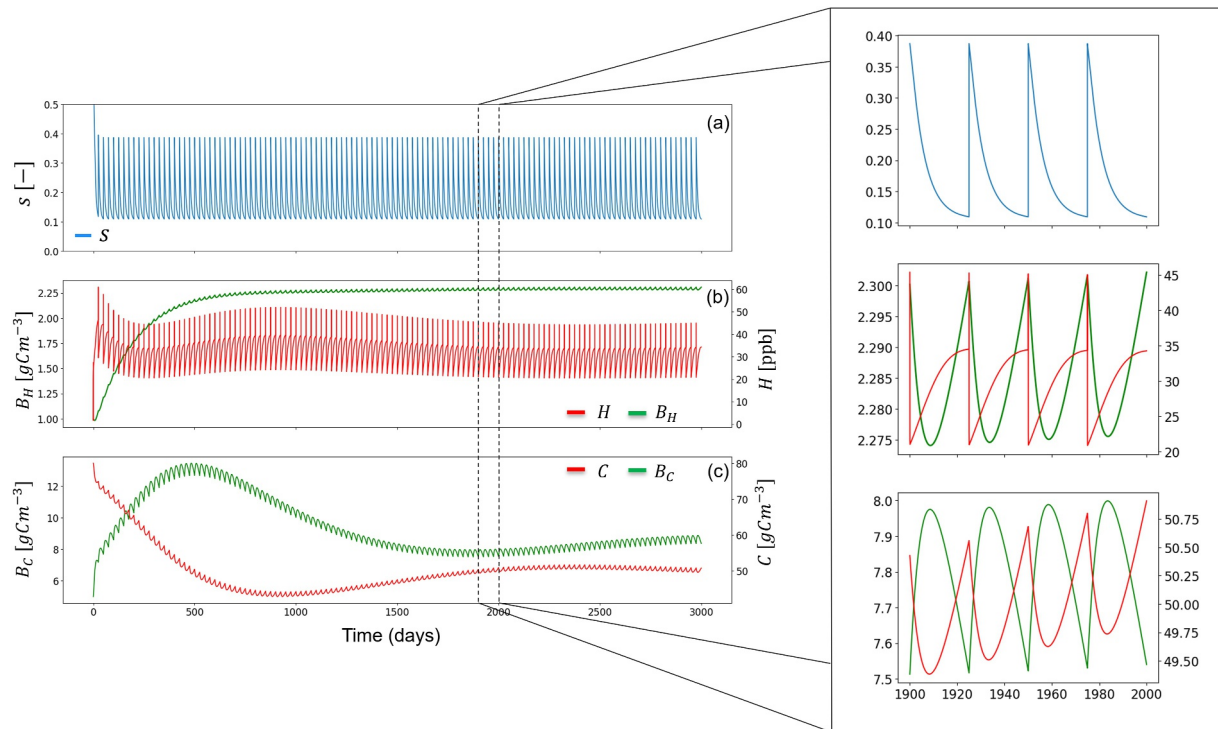


Figure 3. Example of model simulations time series for a loamy sand following drying-wetting cycles for instantaneous rainfall, $h_0 = 35$ mm, and length of dry period, $\tau = 25$ days for (a) soil moisture, s (b) concentration of H_2 , H and microbial biomass by hydrogen-oxidizing bacteria, B_H , and (c) organic carbon substrate, C and microbial biomass by carbon-decomposing bacteria, B_C . The zoomed-out section from day 1900 to day 2000 is provided to elucidate the response of the model variables to soil moisture jumps.

The critical role of soil moisture in influencing the dynamics of H is highlighted in Figure 5b, where we observe several abrupt fluctuations in H corresponding to rapid changes in the biological oxidation of H_2 following rainfall events. To evaluate the effects of incorporating microbial biomass and organic carbon components when estimating the biological sink of H_2 , we compared our model results (red line, Figure 5b) with those obtained from the model by Bertagni et al. (2021) (black line, Figure 5b), which does not account for dynamic carbon substrate and microbial biomass. The key distinction lies in the amplitude of H_2 concentration oscillations: our model predicts significantly larger-amplitude fluctuations than the more constrained oscillations produced by Bertagni et al. (2021) formulation. Additionally, the strong coupling between B_H and H was evident: an increase in HOB biomass consistently corresponded to enhanced H_2 oxidation, resulting in lower soil H and vice versa. Similarly to previous H_2 modeling approaches, for example, Bertagni et al. (2021), Ehhalt and Rohrer (2013) and Yashiro et al. (2011), we observe that the H_2 diffusive flux is in equilibrium with the biological oxidation (i.e., negligible time derivative in Equation 2, or $F = Z \cdot BO$) confirming the validity of the quasi steady-state approximation for H_2 even in conditions of variable microbial biomass.

Figure 5c illustrates the dynamics of C (red line) and B_C (green line). We observed that the accumulation of C is driven by the low decomposition activity of B_C under low soil moisture conditions, alongside the continuous addition of plant residue (ADD). Once moisture levels become favorable, B_C initiates substantial decomposition of C , leading to a decline in the substrate concentration and an increase in microbial biomass.

3.4. Effect of Microbial Dormancy

To examine the impacts of microbial dormancy, we consider a hydrological regime typical of an arid environment, characterized by rainfall frequency $\lambda = 0.03 \text{ d}^{-1}$, and average rainfall magnitude $\alpha = 15$ mm, which results in an average annual rainfall of 165 mm. To account for uncertainties in the values of soil moisture threshold that triggers microbial dormancy, we explored different soil moisture levels for s_{dorm} , ranging from s_{ws} to s_w .

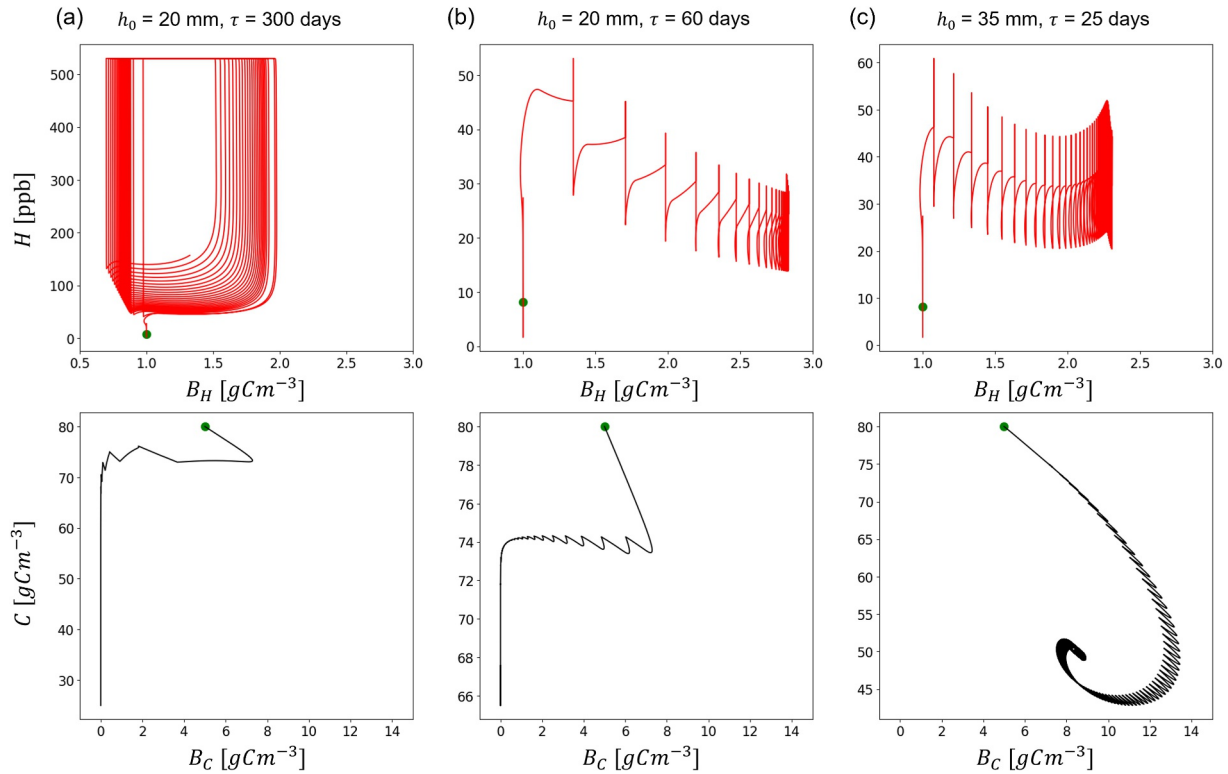


Figure 4. Phase portraits for the substrate-microbe pairs are shown for the H- B_H pair (first row) and C- B_C pair (second row) for different instantaneous rainfall (h_0) and length of dry period (τ) values of (a) $h_0 = 20$ mm, $\tau = 300$ days, (b) $h_0 = 20$ mm, $\tau = 60$ days, and (c) $h_0 = 35$ mm, $\tau = 25$ days. A green dot represents the initial conditions.

Figure 6a presents the time series of soil moisture and the effectiveness of the dormancy strategy in HOB biomass is shown in Figure 6b. During extended low soil moisture periods, dormancy mitigates the sharp biomass decline seen in the no-dormancy model (black line). The value of s_{dorm} impacts both the dormancy duration and overall biomass accumulation, and we present the summary of the simulation results (over 200 years of data) in Figure 7. Based on these results, the model suggests the presence of an optimal condition for biomass preservation via microbial dormancy, where biomass loss occurs as a cost when dormancy is initiated either too early or too late.

3.5. Aridity Controls on B_H and Microbial Dormancy

Here we explore the hydrological conditions under which dormancy becomes necessary for the survival of HOB. To achieve this, we ran a series of 50-year simulations of the model under varying hydrological conditions, as quantified by the dryness index (DI), and evaluated the long-term average contribution of HOB to microbial biomass ($\langle B_H \rangle$), as well as its relative abundance $\langle B_H \rangle / (\langle B_H \rangle + \langle B_C \rangle)$. The DI is defined as the ratio of the long-term average of the potential evapotranspiration rate $\langle ET_{\text{max}} \rangle$ to the average rainfall rate $\langle R \rangle$, where $\langle \cdot \rangle$ represents the long-term average of a variable. Hence, $\langle R \rangle = \alpha \lambda$ represents the long-term average of the rainfall rate (Porporato & Yin, 2022). DI can be used as a measure of physical water scarcity. Low DI values ($DI < 1$) indicate regions classified as humid environments, $1 < DI < 5$ indicate regions classified as subhumid to semiarid, while high values ($DI > 5$) represent regions classified as arid to hyper-arid (D'Odorico et al., 2006). Model simulations reveal an interesting nonlinear trend in the plot of $\langle B_H \rangle$ as a function of DI, as shown in Figure 8a. Initially, as DI increases, $\langle B_H \rangle$ also increases in both models, reaching a peak in regions approaching arid conditions. However, as DI surpasses 6, the contribution of HOB to microbial biomass starts to decline. This decline is far more pronounced in the no-dormancy model than in the dormancy model, once again highlighting the importance of the dormancy strategy in preserving HOB biomass under extreme environmental stress.

Furthermore, in semi-arid regions ($4 < DI < 6$), the dormancy strategy leads to a slightly smaller B_H compared to the no-dormancy model (Figure 8a). This can be attributed to the frequent fluctuations of soil moisture around the

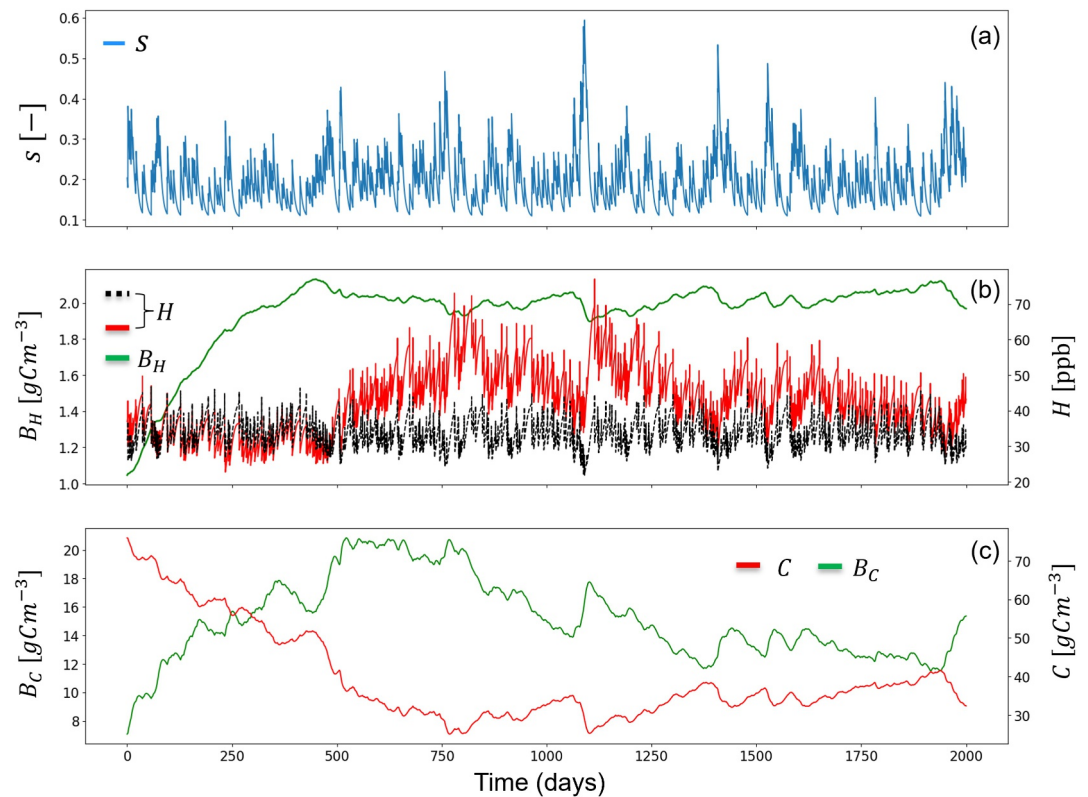


Figure 5. Example of time series for a loamy sand under subhumid climate conditions ($\lambda = 0.2 \text{ d}^{-1}$ and $\alpha = 15 \text{ mm}$) for (a) soil moisture, s , (b) depth-averaged concentration of H_2 , H and microbial biomass by hydrogen-oxidizing bacteria, B_H , and (c) organic carbon substrate, C and microbial biomass by carbon-decomposing bacteria, B_C . The dashed black line in (b) represents the dynamics of H_2 following the formulation proposed by Bertagni et al. (2021) without bacterial biomass, while the red line is produced from the numerical solution of Equation 2.

set dormancy threshold (s_{dorm}), which may induce excessive cost for the drought-avoidance strategy. Collectively, long-term simulation suggests that microbial dormancy becomes essential for the competitive survival of soil microbes, specifically, HOB in semi-arid to arid regions ($\text{DI} > 5$).

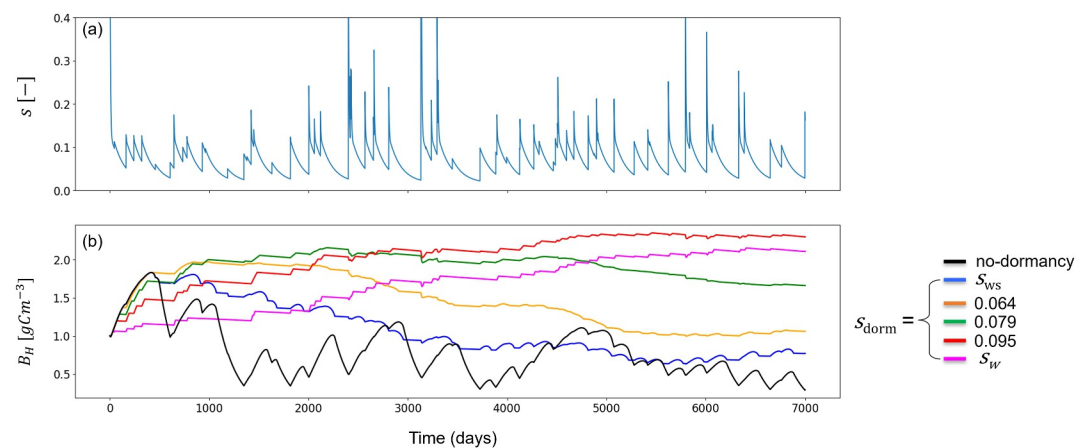


Figure 6. Example of time series for a loamy sand, simulated under arid climate conditions ($\lambda = 0.03 \text{ d}^{-1}$ and $\alpha = 15 \text{ mm}$) for (a) soil moisture, s , and (b) microbial biomass by hydrogen-oxidizing bacteria, B_H for different values of s_{dorm} and the no-dormancy model (represented by the black line).

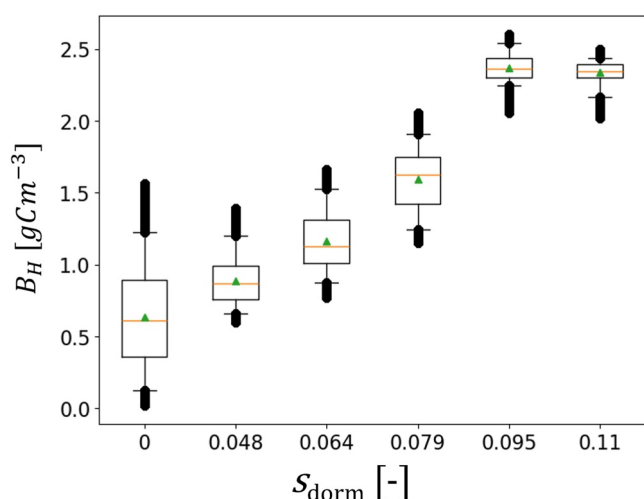


Figure 7. Box plots summarizing 200 years of simulation data for B_H , excluding an initial transient period of 5,000 days and extending beyond the time series shown in Figure 6. The mean values are indicated by green triangles, the black points are outliers beyond the 5th and 95th percentile whiskers, and the no-dormancy model is plotted on $s_{\text{dorm}} = 0$.

formly distributed between the minimum and maximum measured ($55,770 \text{ gCm}^{-3}$ and $424,580 \text{ gCm}^{-3}$, respectively). The same was done for B_C (337 gCm^{-3} and $5,377 \text{ gCm}^{-3}$, respectively). For each B_C value, B_H values were set as a fraction (assumed to be between 1% and 20%) and this resulted in 5,000 model simulations. For soil moisture, Meredith et al. (2016) reported measurements for a well-drained site and a poorly drained site. Here, we used the mean.

Figure 9, shows the simulation results, where the simulation average is shown as a red line and the red area is one standard deviation from the average. For comparison, the black line represents estimates when V_d depends only on abiotic drivers (soil moisture, temperature and snow) based on the formulation of Bertagni et al. (2021).

The results indicate that explicitly incorporating biotic drivers such as soil carbon (C) and the biomass of HOB (B_H) helps explain a substantial portion of the observed variability in deposition velocity. The simulation average (red line) accurately reproduces the seasonal dynamics of H_2 uptake. In particular, the model shows improved agreement with observations during the summer of 2011 and the winter of 2012, with most measured values falling within one standard deviation of the simulations. It is important to note that both models overestimate H_2

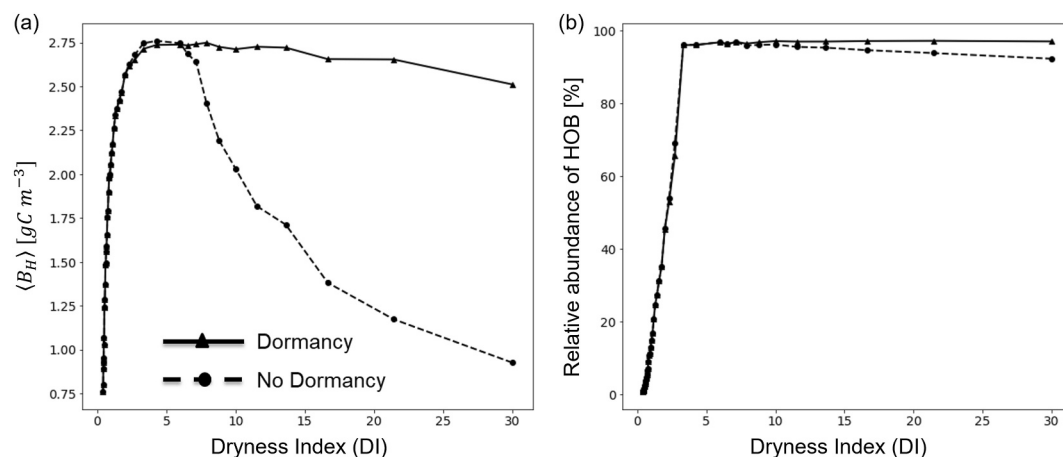


Figure 8. (a) Long-term average contribution of hydrogen-oxidizing bacteria (HOB) to microbial biomass, $\langle B_H \rangle$, and (b) Relative abundance of HOB, as a function of dryness index for the dormancy and no-dormancy model ($\text{ET}_{\text{max}} = 4.5 \text{ mm d}^{-1}$, $s_{\text{dorm}} = 0.095$).

The relative abundance of HOB increases with DI, going from humid to hyper-arid conditions, as illustrated in Figure 8b. In hyper-arid environments, where the overall bacterial biomass is low, the no-dormancy model shows a slight decline in relative abundance, whereas the dormancy model stabilizes at approximately 95%. Such high contributions of HOB to microbial biomass have been documented in the literature (Ji et al., 2017; Jordaan et al., 2020; Lynch et al., 2014; Ortiz et al., 2021).

3.6. Model Application to Atmospheric Fluxes

We evaluate the applicability of our model by estimating the deposition velocity (V_d), a key metric of the soil's capacity to act as a sink for atmospheric H_2 . This quantity is defined as the ratio of the H_2 flux (F) to the atmospheric H_2 concentration (H_a), that is, $V_d = F/H_a$ (Bertagni et al., 2021; Ehhalt & Rohrer, 2009). The derivation of V_d for our model is reported in Appendix A3. Specifically, we perform a data-model comparison using V_d observations from the Harvard forest reported by Meredith et al. (2016). Model simulations are initialized using representative values of soil carbon (C) and microbial biomass (B_C) based on soil experiments conducted at the same site (DeAngelis, 2023). Because these data sets are not temporally aligned with the H_2 measurements, we conducted simulations over multiple combinations of observed values for C, B_C , and B_H . We used 10 different values for C, uni-

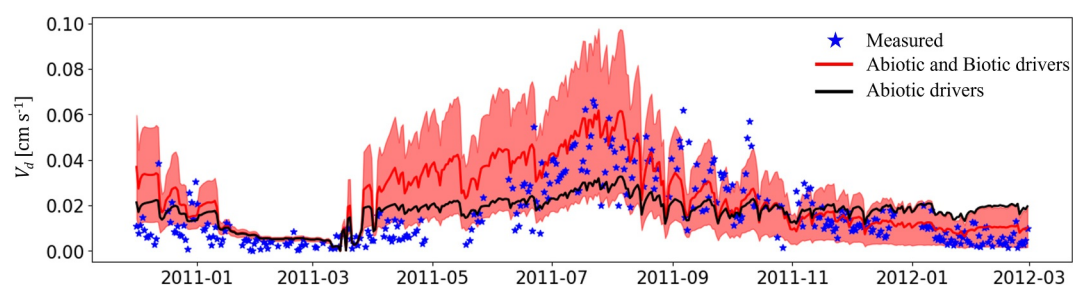


Figure 9. Time series of deposition velocity (V_d) at Harvard Forest from December 2010 to February 2012. The red line represents the average from 5,000 model realizations with the shaded area indicating ± 1 standard deviation. The black line represents estimates based solely on abiotic drivers (soil moisture, temperature, and snow), while the blue stars correspond to field measurements reported by Meredith et al. (2016).

uptake during the spring of 2011. This discrepancy can be partly attributed to neglecting increased microbial mortality under cold conditions, as well as the temperature response of microbial activity derived from Ehalt and Rohrer (2011), which likely overestimates microbial activity near freezing conditions.

4. Discussion

4.1. Influence of Soil Moisture and Biotic Drivers on H_2 Uptake

Modeling efforts have incorporated abiotic drivers (e.g., soil moisture, temperature) in estimating the atmospheric H_2 sink (Bertagni et al., 2021), and more recently, Karbin et al. (2026) represented biotic drivers via a rate modifier. However, these studies lack explicit representation of biotic drivers as dynamic microbial biomass and carbon pools, a gap this study attempts to address. To this end, we extend the estimation of the biological H_2 oxidation (BO) to include HOB biomass (B_H) and soil carbon (C), and investigate how soil hydrology drives the proposed model, and in turn, how these biotic drivers influence H_2 concentration and deposition velocity (V_d).

Simulation results suggest that moisture regimes and their fluctuations strongly influence model dynamics. Under constant soil moisture, HOB and CDB coexist over a broad moisture range consistent with reports of their ubiquitous presence across diverse soil ecosystems (Bay et al., 2021; Greening et al., 2016; Greening & Grinter, 2022; Islam et al., 2020). At high moisture, restricted H_2 diffusion limits H_2 uptake and thus, HOB biomass growth, while at low soil moisture values, constrained carbon decomposition, limits the existence of CDB but not HOB, unless moisture falls below the HOB activity threshold. This low moisture observation is consistent with reports of low carbon content (e.g., Dunkerley & Brown, 1997; Wang et al., 2010) and HOB dominance in low moisture environments such as deserts (Bay et al., 2021; Ji et al., 2017; Jordaan et al., 2020).

Drying and wetting cycles have also been widely employed to investigate various characteristics of soil microbes and substrates (Blagodatskaya & Kuzyakov, 2013; Brangari et al., 2020; Magid et al., 1999; Mikha et al., 2005; Salazar et al., 2018; Tang et al., 2016; Van Gestel et al., 1993). Model simulation results under drying-wetting cycles suggest that the H- B_H substrate-microbe pair consistently reaches a periodic steady state, defined as a variable pair returning to the same values at the end of each cycle, though maximal biomass concentration depends on moisture residing within the optimal HOB activity range. The C- B_C reaches a periodic steady state only when the soil moisture is sufficiently high for CDB to decompose carbon, as in the third case examined. This observed dynamics for C- B_C has been similarly reported by (Brangari et al., 2020), but that of H- B_H remains unverified owing to the unavailability of measured data. Our results for H- B_H should therefore be interpreted with caution until further evidence becomes available.

To better emulate field observations, rainfall events were then modeled as a marked Poisson process, capturing randomness in both magnitude and frequency. Simulation results show the instantaneous influence of moisture on H_2 concentration, with explicit representation of biotic drivers producing higher oscillatory amplitudes relative to the more confined oscillations of the abiotic-only model (Bertagni et al., 2021). Similar to observations from laboratory experiments (Drewer et al., 2026; Ehalt & Rohrer, 2011; Reji et al., 2025; Smith-Downey et al., 2006) and field studies (Buzzard et al., 2022; Cowan et al., 2025; Meredith et al., 2016; Nagai et al., 2024), soil moisture has been identified to be the dominant factor in H_2 uptake, and more recently, Drewer et al. (2026) reported that

carbon content can become a dominant factor in high-labile carbon soils like peatland. Notably, the higher oscillatory amplitude observed due to biotic drivers cannot presently be verified owing to the limited availability of field measurements. Hence, further investigation is therefore warranted in future modeling studies and field campaigns.

The influence of microbial dormancy has been reported in modeling studies (Blagodatskaya & Kuzyakov, 2013; He et al., 2015), but not in the context of hydrogen uptake. Here, we incorporate dormancy to examine HOB behavior under environmental stress, given reports that H_2 oxidation serves as a survival strategy under such conditions (Greening et al., 2022; Greening & Grinter, 2022; Jordaan et al., 2020; Ortiz et al., 2021). Simulation results suggest that models neglecting dormancy may underestimate microbial biomass, an observation similar to that reported in the literature (He et al., 2015; Salazar et al., 2018), and that HOB biomass in arid regions can constitute up to 95% of the total microbial biomass. For instance, if we assume a one-to-one mapping between microbial population and biomass generation, this finding aligns with the reports of Ji et al. (2017) and Ortiz et al. (2021), that 90% of bacteria surveyed in Antarctic deserts encode hydrogenases to oxidize H_2 . In addition, our results reveal an optimal point for dormancy transition; however, this finding should be interpreted with caution, as we considered only soil moisture as a proxy for dormancy, while other factors may also contribute to microbial dormancy.

In the context of data availability, several studies have reported field measurements of H_2 uptake, expressed as either flux rates or deposition velocities, and have examined the roles of biotic and abiotic controls, as well as ecosystem characteristics (e.g., land use and crop type). For example, Cowan et al. (2025) and Lallo et al. (2008) observed higher H_2 uptake in forest soils compared to grassland and mineral soils, respectively. However, their findings do not identify soil moisture or temperature as the sole drivers of H_2 flux variability. In addition, Bartyzel et al. (2013), Cowan et al. (2025) and Meredith et al. (2017) reported pronounced seasonal variability, with higher uptake rates during summer due to warm summer temperatures and optimal moisture for H_2 uptake, than winter (for instance, presence of snow limits diffusion of H_2 and winter temperatures can freeze microbial horizons). However, it is important to note that these reported field data lack complete experimental observations for the model variables (C , H , B_C , B_H) described in this work.

In a bid to test our model simulations against field data, we obtained representative data for the biotic factors described in this work from DeAngelis (2023) and proceeded to estimate the deposition velocity (V_d) of H_2 and compared it with data from Harvard Forest (Meredith et al., 2016). Collectively, our simulation results represent an improvement over the simulations with only abiotic drivers for V_d . Nonetheless, a robust data-model comparison requires several additional considerations. First, temporal alignment of comprehensive observational data sets during field campaigns is essential. Second, issues of spatial representativeness arise because the eddy-covariance method used to estimate H_2 fluxes integrates measurements over a relatively large footprint (0.7–1 km, Meredith et al., 2017), relying on atmospheric turbulence metrics that introduce inherent variability. Furthermore, the associated soil moisture, snow, and rainfall data do not specify the spatial correspondence to the flux footprint. Third, the remaining modeling limitations and unaccounted complexities (e.g., variable depth-averaging, atmospheric and turbulence interactions, plants, etc.) can also contribute to discrepancies. These limitations highlight the potential for future extensions and refinement of our model, as discussed next.

4.2. Model Uncertainty, Limitation, and Extension

Generally, modeling uncertainties arise from multiple factors, which subsequently influence the model's internal dynamics and predictive capabilities (e.g., Arriola and Hyman (2009), Smith (2024), and Soize (2017)). A key source of such uncertainty in our modeling effort pertains to the assumed decomposition rates of soil carbon and hydrogen, k_C^* and k_H^* , respectively. These rates are largely soil-type dependent and although they could, in principle, be constrained through laboratory experiments, they are in general different in field conditions (e.g., Catalán et al. (2016) and references therein for soil carbon, and Ehhalt and Rohrer (2011) and Morfopoulos et al. (2012) for H_2).

In this study, the parameters k_C^* and k_H^* are selected to ensure numerical stability and to confine the model's fixed points to physically meaningful values. Recent work by Reji et al. (2025) provides suitable values of k_H^* across different soil types, as summarized in Appendix A. Although the sensitivity of model outcomes to these parameters is acknowledged, a comprehensive uncertainty quantification would be required to rigorously assess the robustness of the model predictions under parameter variability. Such analyses have been employed in related

studies (e.g., Bradford et al., 2016; Clifford et al., 2014; Wang & Hsieh, 2002), but conducting a similar framework is outside the scope of the present work.

The limited availability and challenges associated with obtaining observational data for key model variables—such as quantifying the specific contribution of HOB to total microbial biomass or determining the ratio of the active to dormant microbial fractions, also pose significant constraints on the full validation of the proposed model. Beyond data availability constraints, model limitations also stem from several underlying assumptions. For instance, Equations 4, 6 and 7 adopt a multiplicative (nonlinear) formulation to estimate substrate decomposition by soil microbes; alternative flux relationships could offer a simplification to this formulation. A further limitation arises from Equation 7, which assumes that HOB co-metabolizes organic carbon and H_2 , an assumption that can may not hold for many HOB classes capable of independent carbon decomposition for growth. Further modeling developments and comprehensive data acquisition efforts are essential for refining the model performance and achieving better alignment with the observed daily variability in substrate and biomass related quantities.

Provided that more detailed models have been shown to outperform traditional simpler formulations and can elucidate previously ambiguous patterns in soil microbial dynamics and biogeochemical fluxes (Hagerty et al., 2022; Manzoni & Schimel, 2024; Čapek et al., 2023), the model presented herein can be further extended to account for additional complexities. These may include:

- Enhanced representation of microbial dormancy—incorporating additional environmental and physiological factors beyond soil moisture that influence the transition to dormant states (e.g., nutrient availability, temperature, etc.), as demonstrated in some previous studies (He et al., 2015; Wang et al., 2014).
- Incorporation of spatial representation. For instance, Zheng et al. (2022) highlighted dynamic transitions between diffusion- and reaction-limited regimes, resulting in deviations of mean-field estimates from spatially averaged decomposition rates. Likewise, Borer et al. (2019) emphasized the influence of microbial hotspots in governing substrate decomposition and shaping the persistence of different bacterial functional groups.
- Incorporating eco-evolutionary processes which account for the taxon-specific decomposition rates within microbial communities offers a promising avenue for model refinement (Manzoni & Schimel, 2024). Such an approach allows for dynamic shifts in community composition in response to variations in soil moisture or organic carbon inputs, thereby enhancing the model's ability to capture biologically realistic feedback and adaptive responses in soil microbial processes (e.g., Brangarí et al., 2020; Rocci et al., 2024; Weverka et al., 2023).
- Rainfall seasonality, as opposed to homogeneous rainfall fluctuations explored here as well as accounting for the influence of temperature and particularly, the impact of snow, which introduces a higher diffusive barrier. For example, both Cowan et al. (2025) and Meredith et al. (2016) observed seasonal dependence in H_2 flux and V_d measurements.
- The soil moisture balance equation is derived through depth averaging, which removes the dependence of soil moisture on depth to focus on temporal rather than spatial variation. This model could therefore be extended to incorporate depth-dependent variation in soil moisture and other model variables. Data reported by Hou et al. (2025) demonstrate that soil H_2 concentration varies with depth, suggesting that incorporating such depth dependence would improve the model effectiveness. However, increased simulation runtime and computational demand may present a limitation of such an extension.
- The model can also be extended to explore feedback mechanisms of hydrogen oxidation on the cellular volume of soil microbes, particularly to investigate whether cytosolic metabolic water released during H_2 oxidation might improve the hydration needs of HOB (Greening et al., 2022; Ortiz et al., 2021) and thus be included in the gamut of strategies for HOBs in very dry environments.

In summary, while we have noted some sources of uncertainties, limitations and extensions to this modeling framework, it is highly probable to note that the results presented in this study is simply one possible realization of microbial behaviors in soil ecosystems, and our results does not entirely capture the intrinsic complexity existent in soil microbial systems. Therefore, our intentions are not to present absolute microbial reality, but to help sharpen questions that are otherwise difficult to formulate or rigorously test in the laboratory or through field campaigns.

5. Conclusions

The extent to which soils serve as atmospheric H_2 sinks is attracting significant research attention, motivated by the fundamental question of how various factors contribute to, influence, or constrain this process. Existing modeling efforts (e.g., Bertagni et al., 2021; Paulot et al., 2021) aimed at understanding the fate and implications of a hypothetical increase in H_2 emissions lack explicit representation of HOB dynamics. The mathematical model presented in this study therefore extended the estimation and characterization of the biological sink of atmospheric hydrogen by explicitly incorporating the dynamics of both HOB biomass and the availability of soil organic carbon and exploring how this biological sink is affected by varying hydroclimatic conditions.

Our model simulation results suggest that both HOB and CDB are ubiquitously present (Steady-state and corresponding stability analysis, Figure 2) and contribute to microbial biomass in the soil, with HOB tending to dominate microbial biomass in arid to hyper-arid regions, while CDB dominates under well-watered (sub-humid–humid) conditions (drying-wetting cycles and stochastic soil moisture simulations, Figures 3–5). Introducing microbial dormancy into the model appeared to increase the presence of HOB in arid and hyper arid regions (Figures 6–8) and points to a possible optimum condition for the onset of dormancy (Figure 7), though this result warrants further scrutiny given the assumptions involved. In terms of data–model comparison, our intention to incorporate HOB biomass and soil carbon to estimate H_2 biological sink appears beneficial, as reflected in improved alignment between simulated H_2 deposition velocity (V_d) with observational data from Harvard Forest (Figure 9); however, this comparison is currently based on a single site and should not be taken as conclusive validation of the model.

These findings advance our understanding of the mechanisms governing the removal of atmospheric H_2 , provide guidance for field observation campaigns by highlighting key variables relevant to H_2 flux estimations, and contribute to broader assessments of the environmental sustainability of a hydrogen-based energy future. Future work can extend the present model towards a more comprehensive understanding of the complex influence of biotic and abiotic factors on H_2 soil sink, and investigate the ecological benefits of H_2 oxidation for microbial cells (cytosolic moisture, maintenance energy, etc.), especially in arid regions where HOB constitute a dominant fraction of the microbial biomass.

Appendix A

A1. Estimation of H_2 Decomposition Rate

Laboratory experiments reported by (Reji et al., 2025) were used to constrain appropriate values of k_H^* , as reported in Table 2. Recalling Equation 2, we simplify its formulation to reflect the representative laboratory experimental setup described in the referenced study. Under conditions where H_2 production and the flux (F) of H_2 into the soil column are neglected, Equation 2 reduces to

$$nZ \frac{d[(1-s)H]}{dt} = -Z(BO). \quad (A1)$$

For constant soil moisture (s), soil organic carbon (C), and HOB biomass (B_H), the analytical solution of Equation A1 follows a simple exponential decay. The solution can be expressed as, $H(t) = H_a e^{-\delta t}$, where $\delta = (k_H^* B_H C) / (n(1-s))$ is the effective decay constant with dimensions of $[T^{-1}]$.

Figure A1 shows the temporal evolution of H_2 concentration, with solid lines representing exponential fits to the data based on the analytical solution described above. The decay constant δ was estimated as 0.075 min^{-1} , 0.042 min^{-1} , and 0.031 min^{-1} for Forest, Pine Barrens, and Meadow soils, respectively. By algebraically rearranging the expression for δ , we obtain the corresponding values for k_H^* to be $5.77 \times 10^{-4} \text{ s}^{-1}(\text{m}^3 \text{gC}^{-1})^2$, $2.7 \times 10^{-4} \text{ s}^{-1}(\text{m}^3 \text{gC}^{-1})^2$, and $2.3 \times 10^{-4} \text{ s}^{-1}(\text{m}^3 \text{gC}^{-1})^2$ for Forest, Pine Barrens, and Meadow soils, respectively. The values of k_H^* obtained for the Forest and Meadow soils are subsequently used to estimate the lower and upper bounds of the steady-state values of the model variables presented in Figure 2.

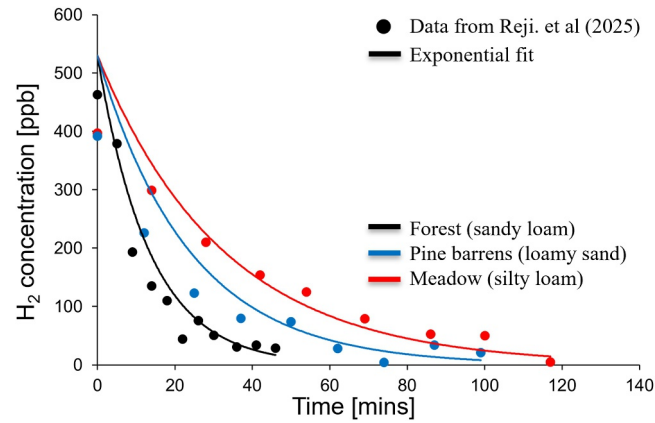


Figure A1. Time series of H_2 concentrations for Forest, Pine Barrens, and Meadow soils. Points represent data from (Reji et al., 2025) and solid lines are exponential fits representative of the analytical solution of Equation A1.

A2. Functional Forms Used in the Model

The soil-dependent reduction functions that represent the response of the potential decomposition rate of HOB and CDB to soil moisture, $f_H(s)$, can be expressed as

$$f_H(s) = \frac{1}{N}(s - s_{ws})^{\beta_1}(1 - s)^{\beta_2}, \quad (A2)$$

where s_{ws} is the soil-dependent lower threshold for HOB activity. N is a normalization constant such that $\max(f_H) = 1$. This maximum occurs in the optimal moisture conditions for bacterial activity (s_{opt}). The power exponent coefficients are $\beta_1 \approx 0.4$ and $\beta_2 = \beta_1(1 - s_{opt})/(s_{opt} - s_{ws})$ (Bertagni et al., 2021).

The response of CDB decomposition to soil moisture, $f_C(s)$ can also be expressed as

$$f_C(s) = \begin{cases} 0 & s \leq s_w \\ \frac{s - s_w}{s_{fc} - s_w} & s_w \leq s \leq s_{fc} \\ \frac{s_{fc}}{s} & s > s_{fc} \end{cases} \quad (A3)$$

Soil dependent values for s_{fc} , s_{opt} , s_w , s_{ws} , and s_{dorm} can be obtained through the soil water retention curve (Porporato & Yin, 2022). Example of the reduction functions ($f_H(s)$ and $f_C(s)$) for loamy sand is presented in Figure A2a. Figure A2b shows the modification made to $f_H(s)$ used for the dormancy and no-dormancy models (see Section 3.4).

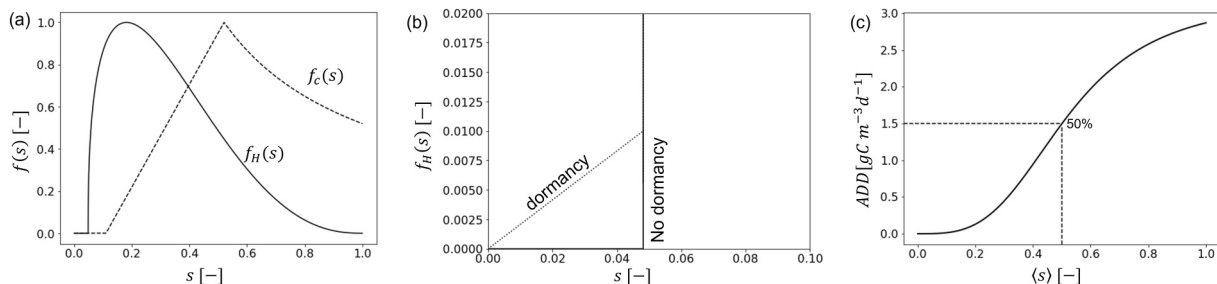


Figure A2. (a) Example of reduction functions $f_H(s)$ (solid line) and $f_C(s)$ (dashed line) for a loamy sand, (b) The modified representation of $f_H(s)$ for the dormancy and no-dormancy models, and (c) Plant residue input (ADD) with respect to soil moisture (s).

The input of carbon into the soil ADD can be expressed as

$$\text{ADD} = \text{ADD}_{\max} + \frac{\text{ADD}_{\min} - \text{ADD}_{\max}}{1 + \left(\frac{s}{s_{fc}}\right)^a}, \quad (\text{A4})$$

where s_{fc} is the soil-dependent field capacity and $a \approx 3.3$ is derived by assuming a logistic relationship (see Figure A1) between $\text{ADD}_{\min} = 0$ (air-dry soil) to $\text{ADD}_{\max} = 3.2 \text{ gC m}^{-3} \text{ d}^{-1}$ (temperate forest) (Finzi et al., 2002; Manzoni & Porporato, 2007). Such a dependence considers the well-known dependence of ecosystem productivity on average soil moisture conditions. Figure A2c shows ADD with respect to soil moisture.

A3. Deposition Velocity

An analytical relationship for the deposition velocity can be expressed as

$$V_d = \frac{g_T V_{BD}}{g_T + V_{BD}}, \quad (\text{A5})$$

where $V_{BD} = Z * k_H * C * B_H$, Z is the soil depth, k_H is the decomposition rate of H_2 as described after Equation 4, C is soil carbon and B_H is the biomass of HOB. g_T is the total conductance through the diffusive barriers and the soil, and can be mathematically expressed as

$$\frac{1}{g_T} = \frac{1}{g_d} + \frac{1}{g_s}, \quad (\text{A6})$$

where g_d is the conductance of the diffusive barrier and g_s is the conductance of the soil. These two conductances are:

$$g_d = \frac{D_d}{d}, \quad g_s = \frac{D_s(s)}{\ell}, \quad (\text{A7})$$

where D_d and D_s are the diffusivities, d is the depth of the diffusive barrier (litter or snow) and ℓ is a diffusive layer length-scale. While this is fixed to a constant value in Bertagni et al. (2021), here, we also include the influence of biotic parameters in its calculation. Through dimensional analysis (Barenblatt, 2003), ℓ can be calculated using the H_2 diffusivity in soil (D_s with dimension $[\text{L}^2/\text{T}]$) and the decomposition rate of H_2 ($\omega = k_H C B_H$ with dimensions $[1/\text{T}]$), so that $\ell = \sqrt{D_s/\omega}$. With this formulation, we have also explicitly included biotic factors in estimating the characteristic length scale of H_2 diffusion through the soil.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Availability Statement

The data set used for this research is available in (Meredith et al., 2016) and python codes for the numerical solution and analysis are available in (Olaitan et al., 2026).

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