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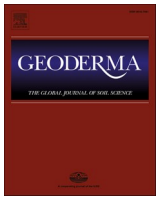

Characterizing environmental drivers of the soil hydrogen sink through controlled laboratory experiments

Julia Drewer [a,*], Nicholas Cowan [a], Aurelia Bezanger [a], Mark Hanlon [a], Toby Roberts [a], Saeed Karbin [b], Ruby Devlin [a,c], Alex Tweedie [a,c], Rujuta Nalavade [b], Eiko Nemitz [a]

[a] UK Centre for Ecology and Hydrology Edinburgh, Bush Estate, Midlothian EH26 0QB, UK
[b] School of Biological Sciences, University of Aberdeen, Aberdeen AB24 3UU, UK
[c] School of GeoSciences, The University of Edinburgh, Edinburgh EH8 9XP, UK

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ABSTRACT

Microbial uptake in soils is the dominant natural sink of atmospheric hydrogen (H_2); however, the environmental controls governing this process remain poorly constrained across different soil types and land uses. This study investigates H_2 fluxes with a diverse set of soils using controlled laboratory incubations designed to isolate the effects of soil moisture, soil physical properties, carbon pools, pH, and temperature. Topsoils from 11 sites were sieved, repacked, and subjected to a moisture gradient from saturation to near-dryness, with H_2 fluxes regularly measured. Across all soils, moisture was the primary control of H_2 uptake. Uptake initially increased as soils dried from saturation, peaked at intermediate moisture levels (10 to 40% water-filled pore space), and then declined again under both saturated and near-dry conditions. Organic content-rich systems behaved differently to mineral soils. Peatland soil showed exceptionally strong H_2 uptake across a wider moisture range, driven by its porous structure and large dissolved organic carbon (DOC) pool. When included in regression models, DOC content emerged as a major predictor of flux, contributing significantly to an overall model explanatory power of $R^2 = 0.51$ when paired with other variables. Investigations revealed that forest litter acted as a strong H_2 sink, with uptake an order of magnitude higher than soils (by mass) and remained active even at sub-zero temperatures. These results demonstrate that H_2 uptake is strongly regulated by soil physical structure and moisture in mineral soils, but also by labile carbon and organic-layer properties in high-carbon environments. The findings highlight the importance of explicitly representing peatlands, the availability of labile carbon pools, and surface organic layers in models of the global H_2 budget and emphasise the need for more field measurements in carbon-rich and understudied ecosystems.

1. Introduction

Atmospheric molecular hydrogen (H_2) is an abundant trace gas with a global mean concentration of approximately 550 ppb in 2024 and an atmospheric lifetime of around two years (Paulot et al., 2024; Pétron et al., 2024). Although H_2 itself is not a direct greenhouse gas, it indirectly affects climate by being a precursor for stratospheric water vapour (H_2O), boosting tropospheric ozone (O_3) production and through its competition with methane (CH_4) and carbon monoxide (CO) for the hydroxyl radical (OH), thereby influencing the oxidative capacity of the atmosphere (Ocko and Hamburg, 2022; Sand et al., 2023; Warwick et al., 2023). As national energy strategies increasingly consider H_2 as a major component of low-carbon energy systems, there is growing concern that leakage during production, storage, and distribution could increase atmospheric H_2 levels over coming decades (Ocko and Hamburg, 2022; Rezaei et al., 2025). Increasing H_2 emissions from 1990 to 2020 have been attributed to anthropogenic sources (Ouyang et al., 2025). This has renewed scientific focus on the processes governing the global H_2 budget and particularly the dominant role of soils as a biological H_2 sink.

Soils represent the single largest sink of atmospheric H_2, accounting for approximately 70 to 90% of global removal (Rhee et al., 2006; Morfopoulos et al., 2012; Ouyang et al., 2025). This sink is driven predominantly by high-affinity hydrogen-oxidising bacteria (HOB), which are capable of oxidising H_2 at sub-atmospheric mixing ratios. Metagenomic, transcriptomic, and biochemical studies have demonstrated

* Corresponding author.
E-mail address: juew@ceh.ac.uk (J. Drewer).

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that high-affinity H_2 oxidation is phylogenetically widespread, occurring across *Actinobacteria*, *Acidobacteria*, *Proteobacteria*, and various candidate phyla (e.g. Meredith et al., 2013; Khdhiri et al., 2017), though the ecological function of these groups in different soil environments remains poorly constrained.

Despite its global importance, the strength of the soil sink varies markedly across ecosystems, land uses, and soil types. To understand how terrestrial systems contribute to global H_2 removal, investigation of determinants of soil H_2 uptake in diverse environments and land uses is required (Hou et al. 2025). Field measurements consistently show large spatial heterogeneity, with uptake rates differing by more than an order of magnitude between mineral soils, forest floors, peatlands, and agricultural landscapes (Smith-Downey et al., 2008; Simmonds et al., 2011; Cowan et al., 2025a). This variability is driven by a combination of physical and biogeochemical factors that influence both the transport of H_2 through the soil matrix and the capacity of soils to consume H_2 once it reaches reactive zones. Among the most widely recognised drivers are soil moisture, porosity, texture, soil organic carbon (SOC), dissolved organic carbon (DOC), pH, and land management practices (Schuler and Conrad, 1991; Baril and Constant, 2023; Cowan et al., 2025a).

The impact of SOC on the soil H_2 sink is particularly understudied, but it is believed to be a significant driver of HOB activity and a large contributor to the spatial variability of H_2 uptake (Baril and Constant, 2023). SOC influences soil structure, aeration, and water retention, all of which affect gas diffusion. Carbon-rich soils (e.g., forest soil) may present stronger resource competition for microbes, leading to higher reliance on alternative energy sources such as H_2 (Reji et al., 2025). Furthermore, DOC levels can influence redox conditions and respiration rates, thereby affecting the ability of soils to act as a sink for atmospheric H_2. In very carbon-rich soils, enhanced microbial respiration can reduce oxygen availability and generate microscale environments that differ sharply from bulk soil conditions. The spatial heterogeneity of soils further complicates interpretation. Organic horizons, rooting, and plant litter layers in forest ecosystems create multiple physical barriers between the atmosphere and the mineral soil, each of which can alter gas transport pathways and influence sink strength.

Diffusion constraints are often the primary control on atmospheric H_2 uptake, particularly in mineral soils. H_2 must diffuse from the atmosphere into the soil profile, thus, conditions that restrict gas movement (such as high water-filled pore space (WFPS), high clay content, or compaction) constrain potential for uptake (Bertagni et al., 2021). Conversely, sandy or well-structured soils with high porosity generally exhibit higher uptake potential, subject to moisture limitations (Cowan et al., 2025a, Reji et al., 2025). However, field flux measurements inherently couple with multiple environmental drivers such as soil moisture, temperature, diffusivity, surface litter and microbial composition, making it challenging to attribute variability to specific controlling processes. Soil bulk density (BD) and the arrangement of pore networks further influence gas-phase diffusion and can differ substantially between soils formed under contrasting parent materials and land management regimes. These physical properties are typically stable on decadal timescales but can be influenced by tillage, organic amendments, and vegetation cover. Measuring soil pore networks, which strongly influence H_2 uptake, is a major challenge because most methods disturb soil structure in the field. Even when soils are collected, the natural pore networks are altered, meaning they may not fully represent real field conditions.

While field measurements provide crucial insight into real-world H_2 flux, they also present challenges for disentangling the effects of individual environmental drivers. Soil moisture, DOC, temperature, and porosity often covary in the field, and surface organic layers complicate the interpretation of chamber measurements by introducing diffusion barriers or additional reactive compartments. As a result, although field flux studies are essential for quantifying ecosystem-level H_2 uptake, they are limited in their ability to identify mechanistic controls (Cowan et al., 2025a). Controlled laboratory experiments offer a complementary approach that enables the isolation of specific environmental drivers under standardised conditions. By repacking soils to appropriate bulk densities, controlling temperature and moisture, and eliminating confounding surface layers, laboratory incubations allow direct assessment of how soil physical and chemical properties influence H_2 uptake.

In this study, we performed a controlled laboratory incubation experiment using soils collected from eleven sites covering arable land, grasslands, temperate and tropical forests, and a peatland. These soils span wide ranges in texture, SOC content, DOC concentrations, bulk density, and pH, providing a diverse basis for investigating the physical and biogeochemical factors influencing atmospheric H_2 uptake by soils. By rewetting soils to saturation and monitoring H_2 fluxes as they dried, we characterised moisture-flux relationships for each soil and quantified how soil properties modified these responses.

2. Methods

2.1. Soil collection and preparation

A total of eleven field sites were selected based on maximising variability amongst a variety of locations with ongoing field measurements and access for researchers (Table 1). At each site, multiple soil subsamples of surface soil (from the top 10 cm) were taken across an area of approximately 20 m^2 and combined to form a composite sample representative of the topsoil. Soils were transported back to the laboratory where they were air-dried and sieved (2 mm) to remove large roots and stones. Dried soils were stored at room temperature in air-tight boxes between preparation stages. For incubation, approximately 800 g of dried soil from the mineral soil sites and 300 g from the Greylake peat soil (due to vastly different soil densities and hydration properties of peat materials) were repacked into cylindrical incubation vessels (19 cm in diameter, 10 cm in height) at an approximate field bulk density. Soils were then rewetted to ~100% water-filled pore space (WFPS) by adding deionised water. Following saturation, the soils were allowed to air-dry slowly at constant laboratory temperature (20 °C) while H_2 fluxes were measured throughout the drying period to capture a wide range of WFPS (over 1 to 4 weeks) (Fig. 1a). WFPS was calculated gravimetrically by weighing soils at each sampling event and relating water mass to pore space volume determined from bulk density and soil particle density (SPD). Per site, 3 to 10 replicates were used.

For an additional experiment, one of the sites (Glencorse birch forest) was sampled again and this time the top layer (1 cm) of plant litter was separated from the soil underneath, both substrates prepared as described above, and incubated separately. In this instant, moisture content was kept constant, and temperature reduced from +20 °C to −6 °C over the course of the experiment.

Table 1
A summary of all field sites from which topsoil was extracted for laboratory incubation measurements.

Site	ID	Land use Type	Country	Location (degree Latitude/degree Longitude)
Aberdeen pH5	P5	Arable	UK	57.19, 2.21
Aberdeen pH7	P7	Arable	UK	57.19, 2.21
Borneo, Sabah, Kinabatangan	BO	Forest	Malaysia	5.14, 118.04
Easter Bush	EB	Grassland	UK	55.87, −3.21
Fenswood Farm Clay	FC	Arable	UK	51.42, −2.67
Fenswood Farm Loam	FL	Arable	UK	51.42, −2.67
Glencorse	GC	Forest	UK	55.85, −3.22
Greylake Peat	GL	Peatland	UK	51.11, −2.87
Sri Lanka, Kandy region, Central province	SL	Forest	Sri Lanka	6.97, 80.59
Thetford Forest	TF	Forest	UK	52.42, 0.88
Weybourne	WB	Grassland	UK	52.95, 1.12

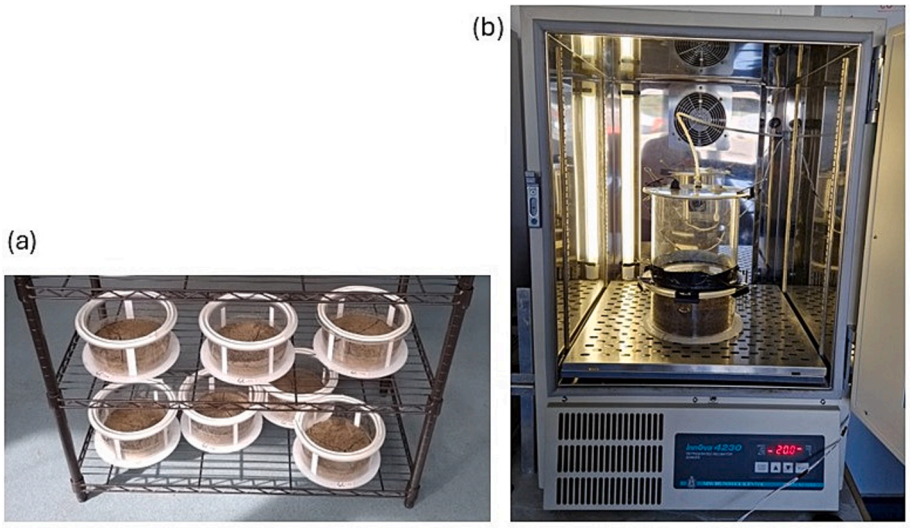

Fig. 1. (a) Following saturation, the soils were allowed to air-dry slowly at constant laboratory temperature (20 °C). (b) During measurements, air was sampled from a sealed chamber placed within in an incubator at constant temperature.

2.2. Hydrogen flux measurements

Fluxes were determined from the rate of change in headspace H_2 concentration during chamber closure. A three-way tap was used to sample air from the chamber, removed using a 100 mL syringe at $t = 0$, 1, 2, 3, 5, 7 and 10 min after chamber enclosure while the chambers were placed in an incubator at constant temperature (Fig. 1b). 20 mL glass vials were filled using a double-needle system to flush the vials with 5 times their volume (Drewer et al., 2021). Hydrogen concentrations in the samples were analysed using an Agilent 8890 gas chromatograph equipped with a pulsed discharge helium ionisation detector (GC-PDHID) and a 7697A headspace autosampler, following the method of Cowan et al. (2025a). Each analytical run included at least three sets of four certified calibration standards spanning the atmospheric concentration range from below ambient to about 1.7 times ambient levels (~200 ppb to 900 ppb), with certificates accurate to ±5%. Instrumental noise (σ) was approximately 15 ppb H_2, corresponding to an analytical flux detection limit of 0.02 nmol kg^{-1} s^{-1}, calculated following the method of Cowan et al. (2025b).

Fluxes were calculated using linear and non-linear regression methods using the HMR package for the statistical software R (Pedersen et al., 2010). By convention, positive fluxes represent emission from the soil, and negative fluxes indicate that the soil acts as a sink (i.e. uptake). Fluxes of H_2 were calculated using both linear regression and a non-linear regression with a negative exponential form of curvature which calculates the rate of change of a gas concentration at $t = 0$ (Eqs. (1)–(3). The concentration C at time t is given by Eq. (1), where C_0 is the initial concentration, C_{eq} is the value at equilibrium and k is a constant. dC/dt is the initial rate of change in concentration at $t = 0$ in nmol kg^{-1} s^{-1}, calculated using Eq. (2). F is gas flux from the soil (nmol kg^{-1} s^{-1}), ρ is the density of air in mol m^{-3}, V is the headspace volume of the chamber in m^3 and m is the mass of dry soil (at 105 °C) within the chamber in kg.

$$C_t = C_{eq} - (C_{eq} - C_o)\exp(-kt) \quad (1)$$

$$\frac{dC}{dt} = k(C_{eq} - C_o) \quad (2)$$

$$F = \frac{dC}{dt} \times \rho \times \frac{V}{m} \quad (3)$$

The default method was to use non-linear regression for flux calculations where the criteria of Cowan et al. (2025a) were met: (i) k is not unrealistically large in Eq. (2) (as defined and limited by the HMR package in R), (ii) the flux estimated by linear regression is larger than the analytical uncertainty of the method (0.02 nmol kg^{-1} s^{-1}) and (iii) the 95% confidence interval (95% C.I.) of the model fit is less than 5 times the magnitude of the flux estimated using linear regression (removes poor-fitting outliers).

2.3. Analysis of soil properties

Bulk density was measured at each site during the collection of soils for the incubation experiments. Soil was taken from the top 10 cm using a metal ring of known volume (d = 7.5 cm, h = 5 cm) which was carefully inserted into the ground to minimise compaction. Samples were oven-dried at 105 °C for three days until constant weight. Soil particle density (SPD) was determined using a water pycnometer method. Approximately 25 g of oven-dried soil (105 °C) was added to the pycnometer, and the combined mass was measured. SPD was calculated using standard pycnometer equations corrected for water density at the measured temperature. Soil pH was measured using a lab-based pH meter (MP 200, Mettler Toledo GmbH, Schwerzenbach, Switzerland), where 20 mL of deionised water were added to a 10 g sub-sample of soil, shaken and left to rest for 60 min prior to measurement.

Soil particle size distribution was assessed using a dry-sieving method suitable for coarse textural separation. Air-dried soils were gently disaggregated by hand and passed through a nested sieve stack (2 mm, 1 mm, 500 μm, 250 μm, and 63 μm). Each sieve fraction was weighed to determine the percentage contribution of coarse sand (>1 mm), medium/fine sand (1 mm–250 μm), and silt-plus-clay (<250 μm). Because the <250 μm fraction includes both silt and clay, results are presented as bulk texture classes rather than full particle size distributions.

Sub-samples of 10 g of soil were dried at 105 °C until constant weight, milled using a ball mill (MM200 ball mill, Retsch, Haan, Germany) and analysed for total carbon using an elemental analyser (Flash SMART, Thermo Fisher Scientific, MA, USA). Soil organic carbon fractions were determined following the physical and chemical fractionation scheme of Zimmermann et al. (2007). Air-dried soils were separated into particulate and mineral-associated pools through a series of density, ultrasonic, and size-based steps. First, particulate organic matter (POM) was isolated by density separation using sodium polytungstate solution (ρ = 1.6 g cm^{-3}). Samples were gently shaken, centrifuged, and the floating light fraction (POM) was removed, rinsed, dried, and weighed. The remaining heavy fraction was subjected to ultrasonic dispersion to disrupt aggregates and release occluded organic matter. The applied

energy level followed Zimmermann et al. (2007) to standardise aggregate disruption. After dispersion, suspensions were wet-sieved at 63 μm to separate sand-associated organic matter from the combined silt & clay fractions. The silt- and clay-associated organic matter was recovered by sedimentation, dried, and weighed. All fractions were milled and analysed for carbon content using dry combustion on an elemental analyser (Flash SMART, Thermo Fisher Scientific, MA, USA). Fractional carbon masses were summed to verify recovery relative to bulk soil carbon.

2.4. Statistical analysis

All data analysis was carried out using the statistical software R (version 4.5.1) and R studio (R Core Team, 2025). Multiple regression models were fit to H_2 flux using lm() function in the R package "stats" (R Core Team, 2025). Relationships between H_2 flux and environmental variables (WFPS, OC, DOC, texture, pH, SPD) were evaluated using linear models. A simplified general additive model (GAM) was used to generate a model fit to flux data to help visualise non-linear responses to soil moisture (expressed as WFPS), implemented using the "mgcv" package for R (Wood, 2025). The analysis of soil data including and excluding the peat soil (Greylake) was carried out separately due to its markedly distinct organic matter characteristics and DOC concentrations. For regression analysis, all reported R^2 values are adjusted for the number of predictors.

3. Results

3.1. Soil properties

The soils from the field sites spanned a wide range of textures and properties (Table 2). Mineral soils varied from coarse-textured to fine-textured. Sand content ranged from 25% in the Borneo soil to more than 85% in the Sri Lanka and Thetford Forest soils, while clay content ranged from 7.5% to 27.5%. The two Fenswood soils represented the greatest contrast within a single site, with the clay soil (FC) containing nearly three times more clay than the corresponding loam (FL). Soil pH varied from moderately acidic to alkaline (5.13–7.91), with the Aberdeen pH 5 and pH 7 soils providing a paired comparison under otherwise similar conditions (Watson et al. 2024). Soils correspond to the pH 4.5 and 7.5 experimental plots in the long-term trials which were the extremes (lowest and highest pH at the same site). However, upon remeasuring the pH in extracted soils prior to the lab incubations, pHs were closer to 5 and 7, hence the naming convention in this study. Particle density (SPD) also showed modest variability (1.90 to 2.65 g cm^{-3}), with the Greylake peat exhibiting the lowest SPD due to its high organic matter content.

Soil organic carbon (SOC) concentrations differed markedly among sites. Mineral soils generally contained between 20 g kg^{-1} and 180 g kg^{-1} SOC, whereas the Greylake peat had substantially higher SOC (576 g kg^{-1}). Dissolved organic carbon (DOC) showed an even stronger variability: DOC concentrations were low in mineral soils (0.19–3.46 mg L^{-1}), intermediate in managed or semi-natural systems (1 to 2 mg L^{-1}), and extremely elevated in the peat soil (52.34 mg L^{-1}), indicating a highly labile carbon pool (Table 2).

3.2. Flux response to soil moisture gradient

Fluxes of H_2 measured from the incubations ranged from slightly above zero to −1.07 nmol kg^{-1} s^{-1} with 78% of all measurements above the detection limit of the measurement method. The flux data followed a log-normal distribution, with large variability observed between replicates (Fig. 2). Across all soils, atmospheric H_2 uptake generally increased as soils dried from saturation; however, variability in individual measurements was relatively large, especially when flux magnitude remained close to the detection limitations of the method. At high moisture content (WFPS >60%), most soils showed suppressed uptake, reflecting a strong diffusion limitation under near-saturated conditions.

Across all sites, the relationship between WFPS and H_2 uptake was characterised using site-specific generalised additive models (GAMs) based on the measured data, allowing for representation of non-linear and asymmetric responses (Fig. 2, Table 3). Maximum uptake of H_2 occurred at low to intermediate moisture contents with modelled optimum WFPS values ranging from 13.0% (P7) to 40.4% (P5), with most sites clustering between 20 and 30% WFPS. However, not all soils reached WFPS <10% due to some of the soils not fully drying out at ambient temperatures. Across the temperate mineral soils (P5, P7, EB, FC, FL, GC, WB, TF), the driest conditions (0 to 20% WFPS) typically exhibited moderate to strong uptake, with mean fluxes between −0.05 and −0.15 nmol kg^{-1} s^{-1}. The GC and WB sites exhibited relatively high uptake capacities compared to other temperate mineral soils (0.256 and 0.263 nmol kg^{-1} s^{-1}, respectively) at intermediate moisture levels (36 to 38% WFPS), whereas FL and EB showed moderate uptake (0.198 and 0.095 nmol kg^{-1} s^{-1}) with a lower optimal WFPS (16 to 23%). These results show that, while the general shape of the moisture response is consistent across temperate mineral soils, both the magnitude of uptake and the position of the optimum WFPS varies strongly between soils.

The tropical soils (SL and BO) exhibited substantially lower uptake rates compared to temperate systems, with maximums of 0.028 and 0.023 nmol kg^{-1} s^{-1}, respectively. Their optimum WFPS values (21.4% for SL and 32.3% for BO) fell within the broader range observed for temperate soils, but the overall response curves were flatter, due to lower overall sink strength. In contrast to the mineral soils, the peat soil (GL) displayed a distinctly different response. The GAM predicted a very low optimum moisture content (6.4% WFPS) and the highest uptake rate of all sites (0.393 nmol kg^{-1} s^{-1}). H_2 consumption in the peat soil occurred under very dry conditions, with lower uptake at higher moisture contents.

Table 2
A summary of the soil properties measured at all field sites from which topsoil was extracted for laboratory incubation measurements. Results represent a mean of 3 replicates for each parameter (standard deviation of mean included).

Site	ID	Sand	Clay	Silt	pH	SPD	SOC	DOC
		%	%	%		g cm^{-3}	g kg^{-1}	mg L^{-1}
Aberdeen pH5	P5	67.5	7.5	25	5.13 ± 0.03	2.45 ± 0.03	114.6 ± 0.7	3.46 ± 0.08
Aberdeen pH7	P7	70	7.5	22.5	7.46 ± 0.08	2.49 ± 0.02	117.6 ± 0.4	2.94 ± 0.15
Borneo, Sabah Kinabatangan	BO	25	15	60	5.79 ± 0.02	2.65 ± 0.47	68.9 ± 1.7	0.19 ± 0.01
Easter Bush	EB	62.5	12.5	25	5.67 ± 0.11	2.57 ± 0.07	77.8 ± 2.0	0.76 ± 0.12
Fenswood Farm Clay	FC	42.5	27.5	30	6.49 ± 0.06	2.50 ± 0.07	100.6 ± 1.5	1.46 ± 0.15
Fenswood Farm Loam	FL	55	10	35	7.46 ± 0.10	2.55 ± 0.03	92.3 ± 1.6	1.50 ± 0.776
Glencorse	GC	77.5	10	12.5	6.18 ± 0.34	2.56 ± 0.12	69.6 ± 1.1	0.52 ± 0.21
Greylake Peat	GL	80	15	5	5.98 ± 0.03	1.90 ± 0.06	576.0 ± 10.4	52.34 ± 7.10
Sri Lanka, Kandy region, Central province	SL	90	7.5	2.5	5.56 ± 0.05	2.38 ± 0.05	172.2 ± 4.0	1.86 ± 1.04
Thetford Forest	TF	87.5	7.5	5	5.58 ± 0.09	2.61 ± 0.19	29.2 ± 0.5	1.70 ± 0.25
Weybourne	WB	67.5	12.5	20	7.91 ± 0.05	2.63 ± 0.04	60.1 ± 3.7	2.06 ± 0.15

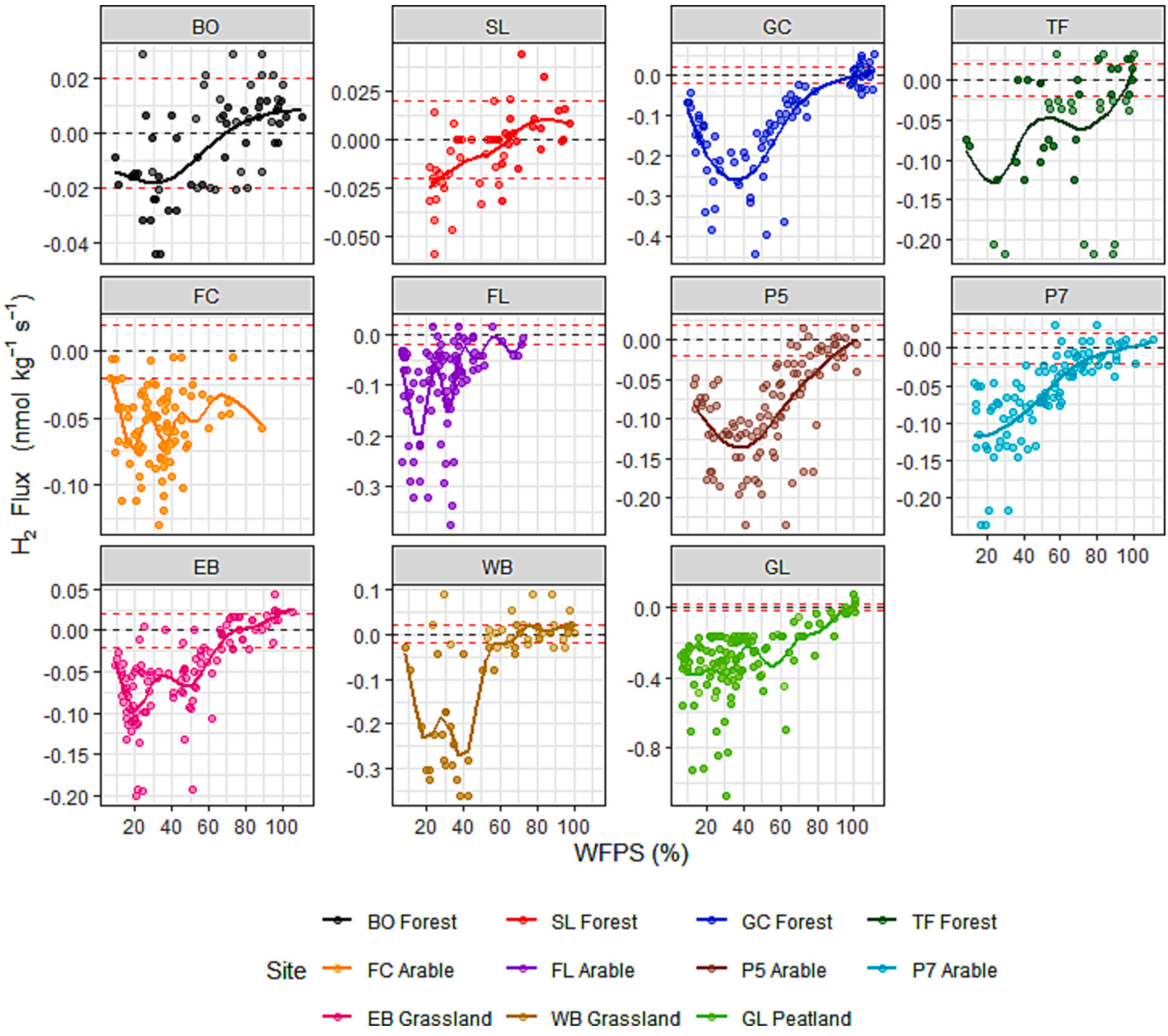

Fig. 2. All individual hydrogen (H_2) flux measurements from the incubation chambers are plotted against water filled pore space (WFPS). A simplified general additive model (GAM) is fit to help visualise non-linear responses to soil moisture (expressed as WFPS). The analytical uncertainty of the method is included for reference (red dashed line). Note different scales of the y-axes. Details of sites in Table 1.

3.3. Regression analysis between flux and soil properties

Multiple linear regression revealed soil moisture was the strongest predictor of H_2 flux for mineral soils (all soils excluding the Greylake peat) (Fig. 3a, Table 4). Overall, the regression was only able to explain approximately 30% of the variation in H_2 flux from the mineral soils ($R^2 = 0.30$), which was dominated by correlation with the single parameter of soil moisture ($R^2 = 0.20$, $p < 0.0001$). Generally, in mineral soils uptake decreased with increasing moisture content. Individually, other soil properties did not strongly predict differences in H_2 flux between the different soils, with R^2 values ranging from 0.01 to 0.04. Sand content and pH both had negative coefficients, indicating that sandier soils and less acidic conditions tended to increase H_2 uptake.

Inclusion of the peat soil (Greylake), which has uniquely high DOC and low SPD values, revealed a different set of drivers in comparison to the mineral soils (Fig. 3a, Table 4). The overall patterns however remained consistent. Soil moisture remained a strong predictor ($p < 0.0001$), and sand content continued to have a significant negative association with flux. However, SOC and DOC both emerged as additional strong predictors. DOC had a strongly negative coefficient ($p < 0.0001$, Table 4), indicating that soils with higher DOC concentrations exhibited substantially stronger H_2 uptake. This relationship remained robust after controlling for moisture and physical properties, highlighting DOC as an important driver of uptake in the soil. However, SOC has a significant positive coefficient (Table 4) for both data sets with and without the peatland soils, suggesting that a high carbon content can reduce H_2 uptake where carbon is not in a labile form.

The multiple linear regression fits of H_2 flux and soil parameters provide a relatively noisy model by which to predict flux with an R^2 of 0.52 and 0.30 for the full dataset and mineral soil only subset, respectively. When the peat soil is included, the model is dominated by the DOC parameter, thus the Greylake peat soil acts as an outlier which has strong influence on the predicted outputs (Fig. 3b). While soil moisture is a strong predictor of H_2 flux in the mineral soils, the mean negative flux of the mineral soils is broadly comparable (ranging from −0.004 to −0.11 nmol kg^{-1} s^{-1}) in contrast to the peatland soil, which is

Table 3
A summary of generalised additive model (GAM) fitting between H_2 flux and water filled pore space (WFPS). The maximum H_2 uptake from 0 to 100% WFPS is reported as well as the predicted WFPS at which maximum uptake occurs.

Site	ID	n	Modelled maximum soil uptake (nmol kg^{-1} s^{-1})	Modelled Optimum WFPS (%)
Aberdeen pH5	P5	98	0.137	40.4
Aberdeen pH7	P7	92	0.117	13.0
Borneo, Sabah Kinabatangan	BO	55	0.023	32.3
Easter Bush	EB	92	0.095	22.9
Fenswood Farm Clay	FC	180	0.073	19.6
Fenswood Farm Loam	FL	186	0.198	16.9
Glencorse	GC	74	0.256	38.2
Greylake Peat	GL	235	0.393	6.4
Sri Lanka, Kandy region, Central province	SL	38	0.028	21.4
Thetford Forest	TF	57	0.136	23.1
Weybourne	WB	66	0.263	36.2

significantly larger in magnitude (−0.29 nmol kg^{-1} s^{-1}).

3.4. Direct comparison of pH effect on flux

Soil properties of the two soils from Aberdeen (P5 and P7) were broadly similar in all aspects except for pH. These soils represent two long-term plots where the impact of pH on agricultural activity is being investigated (Watson et al. 2024). These soils correspond to the extremes (lowest and highest pH at the same site). The range of H_2 flux observed for both sites during the change of WFPS was broadly similar, with peak in uptake (negative flux) occurring at 40.4% WFPS region for P5 (0.137 nmol kg^{-1} s^{-1}) and at 13% WFPS region for P7 (0.117 nmol kg^{-1} s^{-1}) (Fig. 2). Despite similarities in flux magnitude between the soils and the relatively high variability in measured flux between replicates, there is a distinct difference in the shape of the H_2 flux response curve to WFPS between the different soils. Under wet (saturated) conditions, both soils observe flux close to the detection limit of the measurement method (e.g. zero flux). Under very dry conditions, H_2 uptake measured from the P5 soil begins to recede, while the variability in flux measured in the P7 soil increases. These results indicate that while both soils respond to changing WFPS, other soil properties such as pH may influence the magnitude and rate of these changes across the moisture gradient.

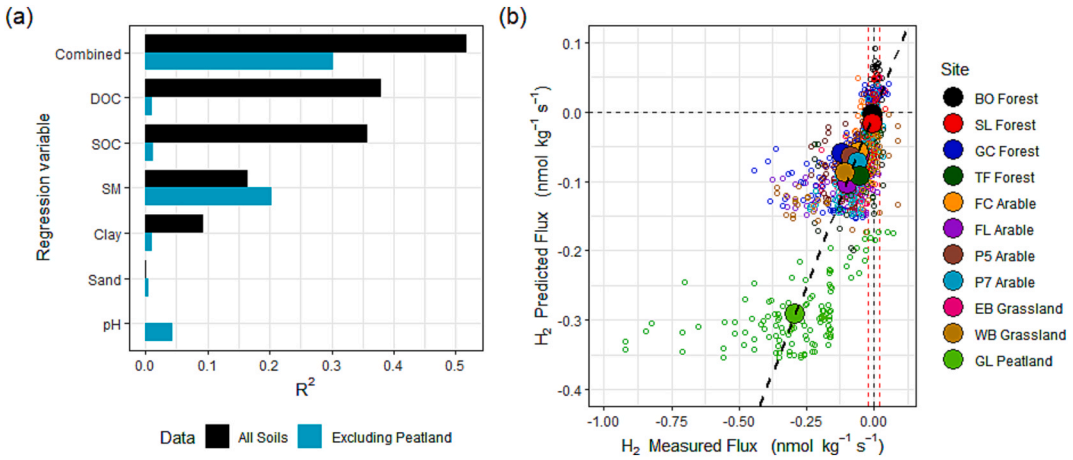

Fig. 3. (a) The R^2 values of linear regression applied between H_2 flux and individual measured soil parameters, and multiple linear regression applied to all parameters combined. Model fitting was applied to all soils, and separately to mineral soil data excluding the peatland (Greylake) soils. (b) Flux predicted using the multiple linear regression fit between H_2 flux and all soil parameters for all soils against measured H_2 flux. Large points indicate the mean for each site. Red dashed vertical lines indicate the analytical uncertainty of the measurement method.

Table 4
A summary of fitting parameters of multiple linear regression models used to fit H_2 flux data (nmol m^{-2} s^{-1}) and all soil parameters. Model fitting was applied to all soils, and separately to mineral soil data excluding the peatland (Greylake) soils. Significance levels are *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Variable	Unit	Estimate	Std Err	t-value	Pr (>|t|)	Significance
All Soils						
Intercept		−0.3828	0.3491	−1.0960	0.2731	
WFPS	%	0.0019	0.0001	18.0070	<0.0001	***
Clay	%	0.0014	0.0007	2.1240	0.0338	*
Sand	%	−0.0006	0.0003	−1.9310	0.0537	
pH		−0.0058	0.0036	−1.6240	0.1046	
SPD	g cm^{-3}	0.0898	0.1259	0.7140	0.4755	
SOC	g kg^{-1}	0.0008	0.0003	2.9860	0.0029	**
DOC	mg L^{-1}	−0.0102	0.0012	−8.2200	<0.0001	***
Excluding Peatland						
Intercept		−1.2210	0.3641	−3.3530	0.0008	***
WFPS	%	0.0014	0.0001	17.4130	<0.0001	***
Clay	%	0.0020	0.0005	3.7050	0.0002	***
Sand	%	−0.0001	0.0002	−0.6350	0.5259	
pH		−0.0136	0.0030	−4.5460	<0.0001	***
SPD	g cm^{-3}	0.4124	0.1325	3.1110	0.0019	**
SOC	g kg^{-1}	0.0013	0.0002	5.2820	<0.0001	***
DOC	mg L^{-1}	−0.0026	0.0035	−0.7450	0.4564	

3.5. The impact of plant litter and temperature on H_2 sink

A dedicated experiment was carried out on the soil from the Glencorse Forest (GC) site, where surface plant litter (approximately 1 cm depth) was collected separately from the underlying mineral soil. A temperature ramp from + 20 °C to −6 °C was carried out on both substrates, with H_2 flux investigated for each material at each set temperature. WFPS could not be established for the plant materials, but gravimetric water content was kept constant throughout all measurements via a misting spray of deionised water. The H_2 flux measured from the mineral soil was close to detection limits, but a trend was still observed of uptake being higher with higher temperature. The lowest uptake from the mineral soil was observed in sub-zero conditions, where flux measured was not significantly different from zero (Fig. 4). The H_2 uptake per mass of material was consistently larger in the plant litter than for the soil (Fig. 4). At −6 °C (the lowest temperature at which the incubator could provide a stable setting) the lowest H_2 uptake in the plant litter (mean flux of −0.14 nmol kg^{-1} s^{-1}) is still greater than the highest uptake measured from the soil (−0.015 nmol kg^{-1} s^{-1} at 5 °C) (Fig. 4).

The H_2 flux measured from both the soil and plant litter correlated strongly with temperature, with uptake increasing under warmer conditions. The response was close to linear in nature over the temperature range investigated (−6 to 20 °C), with a near three-fold scale in flux magnitude observed for both materials (R^2 of 0.60 and 0.59 for linear regression fit between temperature and H_2 flux for soil and plant litter materials, respectively).

4. Discussion

Despite the diversity of soil types analysed in this study, which included temperate mineral soils, tropical forest soils, arable systems, and a peatland rich in organic material, the experiments revealed several consistent patterns in terms of drivers of H_2 flux. Previously, forests were considered to have the largest capacity to remove atmospheric H_2, based on the greater H_2 uptake in deciduous forests > grasslands > arable soils (Ehhalt & Rohrer, 2009; Khdhiri et al., 2017). However, our study showed that soil physicochemical parameters had a stronger influence than land use as such.

Moisture was the dominant control across all mineral soils, aligning with the view that gas diffusivity governs much of the variability in H_2 uptake (e.g. Bertagni et al., 2021). Previously the optimum soil moisture content for H_2 uptake activity has been reported to be between 6 and 20% (Smith-Downey et al., 2006). The moisture response curves obtained from the drying experiments in our study demonstrate that atmospheric H_2 uptake is primarily diffusion-limited, with a clear optimum at intermediate soil water contents. In mineral soils, peak uptake consistently occurred between 5 and 40% WFPS across all sites, regardless of differences in texture, pH, or organic carbon content. Above this moisture range, uptake declined rapidly as the diffusion of atmospheric H_2 into the soil matrix became restricted. This pattern closely mirrors those reported in field studies, where saturated soils typically exhibit little or no uptake due to severely limited gas transport (e.g. Cowan et al., 2025a). The consistent moisture-flux behaviour across most mineral soils reinforces the conceptual model in which H_2 uptake is largely governed by the physical structure of the soil, particularly diffusivity and the balance between air- and water-filled pore space (Yonemura et al., 1999, Yonemura et al., 2000, Myagkiy et al., 2020). The weak, but statistically significant correlation between H_2 flux with sand content and SPD in the multiple regression models further supports this interpretation. Sandier soils with lower particle density showed stronger uptake at equivalent moisture levels. Conversely, finer-textured soils and soils with higher density and organic content exhibited lower uptake, likely due to lower potential for diffusivity between soil and atmosphere. At very low moisture contents, uptake decreased for most soils (e.g., BO, GC, P5, WB), suggesting that the desiccation effect may reduce microbial activity and limit uptake under extremely dry conditions. However, under very low moisture levels, measurable H_2 oxidation has still been observed in ours as well as other studies (Reji et al., 2025).

The H_2 uptake observed in high-labile carbon soils and plant litter differed considerably from that of mineral soils, highlighting the need to consider litter layers and carbon content in both process understanding and modelling frameworks. The Greylake peat soil (GL) displayed patterns of H_2 uptake that diverged strongly from the mineral soils. Peat soils are fundamentally different to mineral soils, dominated by large, fibrous organic particles and a high degree of structural heterogeneity. These characteristics are consistent with both the strong uptake at moderate moisture and the rapid collapse of the sink under saturation. The regression results highlight the importance of SOC as a driver of H_2 uptake in organic-rich systems. When the peat soil was included in the analysis, DOC emerged as one of the strongest predictors of flux, with a highly significant negative coefficient. Even though we only included one peat soil in this study, we believe it is worth noting and warrants further investigation in future studies. The fact that SOC content was negatively correlated with H_2 uptake (e.g. high SOC content reduces the H_2 sink if DOC is small) suggests that total carbon content is less relevant than the type of carbon (e.g. labile or microbially available carbon) and

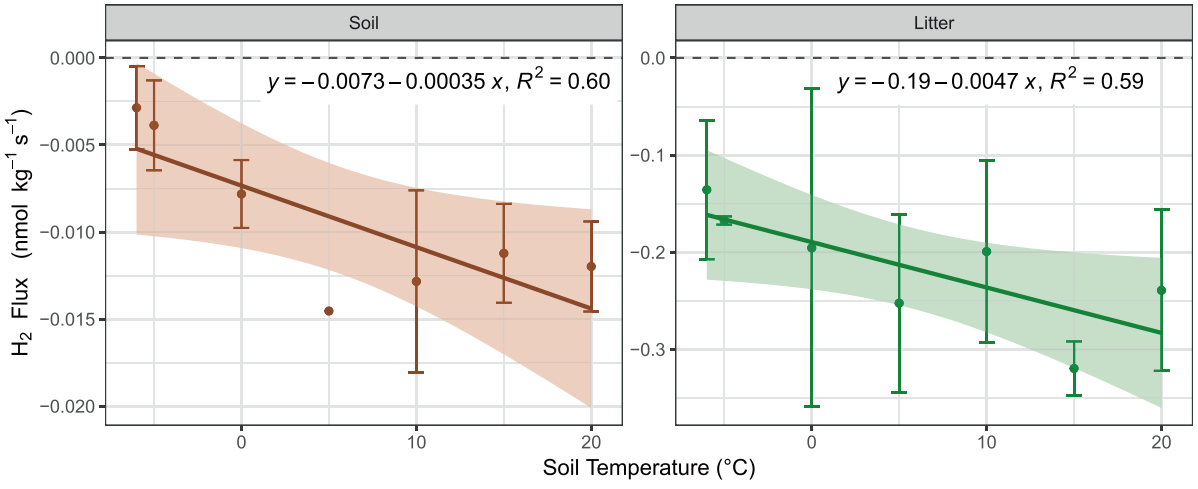

Fig. 4. Linear regression between mean flux and soil temperature measured from separated plant litter and mineral soil from the Glencorse Forest (GC) site are presented. Shaded areas represent the standard error in the regression fit.

associated biogeochemical processes. It has previously been reported that the bacterial H_2 uptake activity can be reduced by the addition of carbon to soil (Baril and Constant, 2023) with further studies recommended to confirm these findings (Hou et al., 2025). It has also previously been shown that H_2 oxidation rates scaled with average SOC content within the drier range of the moisture gradient (Reji et al., 2025). A recent study presented integration of microbial activity rate modifiers derived from the decomposability of SOC as a proxy for potential microbial activity (Karbin et al., 2026). In our study, the peat soil dominated the overall model when included, increasing total model explanatory power from $R^2 = 0.30$ to $R^2 = 0.52$, but also highlighted the limited ability of simple regression models to capture the diversity of the drivers of microbial H_2 uptake in soils, especially with a small number of soils to draw comparisons from.

Soil pH optima have been mentioned previously in relation to H_2 uptake (Schuler and Conrad, 1991). The paired Aberdeen soils (P5 and P7) provided an opportunity to assess the effect of pH on H_2 uptake while minimising confounding factors. Although the soils differed by more than 2 pH units, their moisture–flux curves were similar in magnitude, and pH did not emerge as a significant predictor in either the mineral-only or full regression models. This suggests that pH is not a major determinant of H_2 uptake under the controlled laboratory conditions used here. However, subtle differences in moisture response shape between P5 and P7 indicate that pH may influence microbial community composition or H_2 oxidation processes in ways that are not fully captured by simple models. Investigating soil microbial communities across pH gradients might hence be necessary to address this fully (Hou et al., 2025). Our results support the conclusion that pH effects, while present, are secondary to moisture and pore structure and may only impact H_2 uptake potential significantly when at extreme ends of the pH scale.

Temperature dependency of H_2 uptake has previously been described in laboratory studies with optimum temperatures for soil uptake reported to be 10–30 °C (Smith-Downey et al., 2008). The temperature experiment carried out on the Glencorse Forest soil and organic layer showed in addition that plant litter can act as a substantial H_2 sink. In our case, the temperature response in the flux data presented is not influenced by water content changing, but questions remain as to how to accurately compare water retention capability and its effects in terms of microbial response in a variety of materials. Litter uptake fluxes were an order of magnitude larger than soil uptake fluxes (by mass of material) at all temperatures, though comparisons were not made of expected flux in the field based on the mass ratio of materials by area coverage. While there is still some uncertainty regarding how this finding relates to real-world conditions, there are several implications to consider. First, in forest environments where litter layers are especially thick and spatially extensive, a substantial portion of atmospheric H_2 consumption may occur above the mineral soil surface. This could lead to misinterpretation of fluxes and their drivers measured using flux chamber and soil coring techniques that do not distinguish litter from soil contributions. Second, the temperature response of the litter was much stronger than that of the mineral soil, suggesting that climate variability or seasonal temperature patterns may disproportionately affect H_2 uptake in forested or high-carbon landscapes. Third, the structural properties of litter (porosity, low particle density, and high surface area) create a highly favourable environment for both diffusion and microbial activity, likely explaining the strong uptake. This is an example that the microbial activity is not diffusion limited and shows the strength of microbial activity in driving H_2 uptake. The finding that uptake in plant litter is still relatively large under sub-zero temperatures is particularly noteworthy, as it implies that even when mineral soil uptake is diffusion-limited under frozen or near-frozen conditions, H_2 oxidation may continue at the surface where organic surface materials are present (e.g. forests and uneven/drained peatlands). This might have an impact on the representation of soils in high-latitude areas as they are often regarded frozen soils with no uptake in sub-zero temperature. Together, these results emphasise that surface organic layers should be explicitly accounted for in both field measurements and process-based models. Our findings highlight a paradigm shift from the Ehhalt and Rohrer model (Ehhalt and Rohrer (2013)): rather than viewing the topsoil litter simply as a physical barrier to diffusion, these findings position it as a synergistic contributor to the total soil uptake.

While laboratory incubations provide a powerful means of isolating environmental controls, several limitations must be considered when extrapolating results to field contexts. The sieving and repacking of soils disrupt natural structure, homogenise aggregates, and remove root channels that play important roles in gas diffusion and atmospheric exchange. As such, absolute flux values measured here should not be interpreted as representative of *in-situ* conditions. Instead, the results should be viewed as mechanistic insights into how soil properties and environmental drivers interact. The moisture gradient imposed in the incubations may also differ from naturally occurring moisture variation in rate, pattern, and spatial distribution. In field soils, drying progresses unevenly, and microbial communities may respond differently to slow seasonal drying than to the controlled, uniform drying imposed in laboratory settings. The limited explanatory power of the regression models ($R^2 = 0.30$ for mineral soils) reflects the complexity of H_2 uptake processes, as well as the difficulty of capturing non-linear interactions among soil structure, carbon pools, and microbial activity using simple statistical models. The stronger model performance when including peat ($R^2 = 0.52$), with the caveat of it being a small sample size, nevertheless highlights the challenge of combining soils with fundamentally different functional characteristics into a single model framework. Ultimately, laboratory incubations are most valuable for identifying key drivers and generating hypotheses that can be tested under field conditions. The relationships observed and emphasised in this study relate to moisture, total SOC and DOC availability, and porosity of soils, which we recommend further investigation of when carrying out field measurements, model parameterisations, and process-based understanding in future studies.

Current models of the global H_2 cycle often treat soil uptake as a function of soil moisture, diffusivity, and a single biological sink term (Bertagni et al., 2021; Ehhalt and Rohrer, 2013; Morfopoulos et al., 2012; Smith-Downey et al., 2008). Several models have attempted to incorporate the influence of SOC on microbial H_2 uptake. The model developed by Morfopoulos et al. (2012) considers the dynamics of soil vegetation cover, aiming to indirectly capture the effects of SOC content on H_2 uptake. In contrast, Paulot et al. (2021) adopted a modification of the Ehhalt model by introducing a constant that depends on SOC content, following a Michaelis-Menten relationship. This was a step forward in directly accounting for SOC, but it does not consider the impact of the composition of the organic matter (e.g. whether it is labile) on potential microbial activity. The results from our study suggest that this approach may not be sufficient for capturing the diversity of soil types and surface materials. In particular, i) litter layers and peatlands appear to behave as distinct functional classes and require separate parameterisation, ii) labile carbon appears to be important driver of H_2 uptake while total carbon content of soils may reduce uptake depending on availability to microbial processes and impact on soil structure and aeration, iii) texture and density parameters should be included in models as modifiers of diffusivity beyond moisture alone and iv) plant litter can significantly impact uptake in forest ecosystems and should be treated as an independent reactive compartment. Incorporating these factors into spatially explicit models could significantly improve predictions of atmospheric H_2 removal, particularly in heterogeneous landscapes and carbon-rich environments. To achieve this, further efforts to measure H_2 flux in field conditions are required, with more focus on areas where data is limited, especially areas where the magnitude and drivers of H_2 flux are still poorly understood such as the tropics, the southern hemisphere, forests and peatlands. Furthermore, global warming is expected to reduce average SOC (Sáez-Sandino et al., 2024; Wang et al., 2023) with effects on H_2 oxidation uncertain due to limited understanding of

the mechanisms. Ultimately, validation of models is still highly reliant on a few datasets, and further efforts are required to expand global data inventories. In addition, models ought to include a more detailed representation of organic matter and labile carbon as potentially strongest predictors of controlling microbial activity.

5. Conclusions

Despite substantial variability in texture, pH, carbon content and ecosystem origin, soil moisture emerged as the dominant control on H_2 uptake in mineral soils with the other soil parameters influencing the moisture response and magnitude of uptake. In mineral soils H_2 consumption is primarily limited by gas diffusivity. In contrast, the organic-rich soil included in this study behaved fundamentally differently. The peat soil showed exceptionally high H_2 uptake at moderate moisture, reflecting both its porous, heterogeneous structure and large labile carbon pool. DOC emerged as a key predictor of flux indicating that labile carbon, rather than bulk soil carbon alone, influences microbial H_2 oxidation in organic-rich systems.

Surface organic layers further complicate ecosystem-level H_2 dynamics. The results of this study demonstrate that plant litter can act as strong H_2 sink, with uptake rates an order of magnitude higher than soil (by mass). Litter also retained substantial uptake capacity at sub-zero temperatures, suggesting that surface organic layers may dominate H_2 consumption during cold periods when mineral soil diffusion is restricted. These findings imply that litter layers must be explicitly accounted for in field flux measurements and process-based models, particularly in forests and peatlands.

Overall, the results indicate that current global models of the soil H_2 sink require refinement. Improvements should include: (i) explicit treatment of peatlands and organic layers as distinct functional classes; (ii) incorporation of DOC or carbon-quality metrics in high-carbon soils; (iii) inclusion of texture and density effects on diffusivity; and (iv) representation of litter as a reactive compartment in forested environments. Expanding field measurements in poorly studied systems, especially forests, peatlands, and tropical soils, will be crucial for validating these refinements and improving predictions of the terrestrial H_2 sink under future atmospheric and climatic conditions.

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CRediT authorship contribution statement

Julia Drewer: Writing – original draft, Supervision, Project administration, Funding acquisition, Conceptualization. **Nicholas Cowan:** Writing – review & editing, Visualization, Supervision, Formal analysis, Data curation. **Aurelia Bezanger:** Writing – review & editing, Investigation. **Mark Hanlon:** Writing – review & editing, Investigation. **Toby Roberts:** Writing – review & editing, Investigation. **Saeed Karbin:** Writing – review & editing, Investigation. **Ruby Devlin:** Writing – review & editing, Investigation. **Alex Tweedie:** Writing – review & editing, Investigation. **Rujuta Nalavade:** Writing – review & editing, Investigation. **Eiko Nemitz:** Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

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

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Data statement

The dataset is currently being prepared for submission to The Environmental Information Data Centre (EIDC) https://eidc.ac.uk/ for open access depository.

Data availability

Data being prepared for submission to Environmental Information Data Centre EIDC https://eidc.ac.uk/

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