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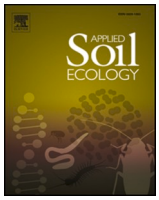

Linking soil structure and microbial communities to predict CO_2 emissions from drained arable peatlands

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ABSTRACT

Understanding interactions between soil structure, microbial communities, and greenhouse gas dynamics is critical for predicting carbon losses from drained agricultural peatlands. This study tested the hypothesis that land use alters soil structure and microbial communities, thereby shaping CO_2 flux, using high-resolution XCT, microbial profiling, and gas and soil measurements across winter wheat, sugar beet, and bare soil treatments on a productive UK farm on peatland. Bare soil exhibited the highest pore connectivity and gas diffusivity (Dp/D_0: 0.08–0.10 in dry conditions), declining to near-zero during wet periods in October. Fungal alpha-diversity (Shannon index: 2.8–3.2) was significantly higher in cropped soils compared to bare soil (2.0–2.5), with sugar beet supporting the most diverse fungal communities. *Sordariomycetes* dominated fungal assemblages (50–75 % relative abundance), while *Actinobacteria* and *Vicinamibacteria* consistently comprised 20–30 % of bacterial communities. Soil moisture strongly regulated diffusivity ($R^2 = 0.93$, $p < 0.001$), driving seasonal shifts in gas transport and microbial dynamics. Fungal communities showed stronger treatment differentiation ($R^2 = 0.24–0.49$) than bacterial communities, with distinct assemblages observed in sugar beet at 20 cm depth ($R^2 = 0.489$, $p = 0.011$). An XGBoost machine learning model explained 82 % of the variance in CO_2 concentrations, identifying key fungal (OTU_15_F, OTU_6_F) and bacterial (OTU_901, OTU_5115) taxa as top predictors. These results highlight that crop selection can alter microbial diversity by up to 60 % and drive tenfold changes in soil gas diffusivity, underscoring the importance of integrating soil structural and microbial metrics into greenhouse gas models. Such insights can guide sustainable peatland management strategies that balance productivity with carbon conservation.

1. Introduction

Global efforts to mitigate climate change increasingly recognise the importance of understanding carbon dynamics in agricultural systems (Allan et al., 2023; Kamyab et al., 2024). Peatlands are exceptional carbon reservoirs, storing nearly one-third of the world's soil carbon despite covering only 3 % of the land surface (Harenda et al., 2018; Joosten et al., 2012; Nath et al., 2024). However, the conversion of peatlands to arable land has drastically altered their ecological function, transforming these carbon sinks into significant sources of CO_2 (Lång et al., 2024; Page and Baird, 2016). This shift highlights the urgent need to identify strategies for managing peatland agriculture in a way that minimises its contribution to greenhouse gas emissions while maintaining productivity (Lloyd et al., 2023).

Traditionally, studies on CO_2 flux from arable peatland soils have focused on environmental factors, such as soil moisture, temperature, and pH, or management practices like fertilization and tillage (Dutta and Dutta, 2016). Crop type also influences emissions, as root exudates,

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residue quality, and nutrient demands vary between crops, affecting soil carbon dynamics (Gui et al., 2023; Ma et al., 2022; Yang et al., 2020). However, an often-overlooked factor is the soil microbiome, the diverse community of microorganisms driving organic matter decomposition, nutrient cycling, and greenhouse gas fluxes (Jansson and Hofmockel, 2020). These microbial processes underpin carbon release or sequestration, yet their specific roles in agricultural peatlands remain poorly understood (Jansson and Hofmockel, 2020; Levine et al., 2011). Microbes in the soil are the primary producers of greenhouse gases (GHG) such as CO_2, nitrous oxide (N_2O), and methane (CH_4) (Singh et al., 2010). These gases are released as by-products of various microbial metabolic processes, including respiration, denitrification, nitrification, and methanogenesis (Kolb and Horn, 2012; Li et al., 2024). Microbial activity is influenced by factors such as the availability and quality of organic matter, nutrient levels, moisture and temperature (Cruz-Paredes et al., 2021; Jansson and Hofmockel, 2020). These elements are essential for microbial function, as they provide the necessary energy for microbial metabolism and growth (Jansson and Hofmockel, 2020; Neira et al., 2015). They are additionally influenced by soil physical properties such as soil porosity, moisture content, texture, and compaction as those determine the movement of nutrients, energy, and oxygen through the soil (Neira et al., 2015).

Recent advances in high-throughput sequencing and bioinformatics have revealed that soil microbial communities are sensitive to environmental change and responsive to crop type, with different crops selecting distinct microbial consortia through root exudates and rhizosphere interactions, potentially altering CO_2 production (Andersen et al., 2013; Bahram et al., 2018). For example, different crops can select for distinct microbial consortia through root exudates and rhizosphere interactions, potentially altering the soil's capacity to generate CO_2 (Gui et al., 2023). However, how these microbial shifts interact with soil physical structure to regulate gas transport and emissions in agricultural peatlands remains poorly understood (Philippot et al., 2024; Tiemeyer et al., 2016). Most studies examine either microbial composition (e.g., (Levine et al., 2011; Li et al., 2024; Yang et al., 2024) or soil structure (e.g., (Buragienė et al., 2019) in isolation, overlooking their combined influence, a critical gap given that structural changes in drained peat can directly affect aeration, moisture distribution, and microbial metabolism (Lång et al., 2024). This study addresses this gap by jointly analysing soil microstructure and microbial communities across contrasting crop types on cultivated peat providing an integrated view of their role in driving CO_2 emissions. We combine field measurements of CO_2 concentrations, soil physicochemical properties, and microbial community composition with 3D X-ray computed tomography (XCT) to quantify pore network structure. Using statistical and machine learning models (XGBoost), we test the extent to which microbial composition can predict CO_2 dynamics. Crucially, we also explore the mechanistic links between microbial communities and soil physical structure, focusing on air-filled porosity, gas diffusivity, and connected pore domain volume. By assessing both predictive performance and biophysical constraints on respiration, we aim to identify how soil structure moderates' microbial activity and contributes to emergent CO_2 flux patterns.

Additionally, we explore the potential of microbial biomarkers specific operational taxonomic units (OTUs) correlated with CO_2 flux to improve the predictive power of greenhouse gas models and better represent microbial contributions to peatland carbon cycling. Given the mounting pressures on peatlands from agriculture and climate change, our study aims to provide a novel perspective on the interplay between crops, microbes, and CO_2 flux in one of the planet's most critical ecosystems. We hypothesised that (i) crop type alters soil structure and microbial community composition, (ii) these changes influence CO_2 flux through their effects on gas transport and microbial activity, and (iii) integrating structural and microbial predictors into greenhouse gas models increases their predictive accuracy (Fig. 1).

2. Materials and methods

2.1. Study area and soil sampling

This study was conducted from June to October 2024 on a working arable farm on peatland in the Fenlands of eastern England. The region has a mean temperature of 10 °C and receives 600–800 mm of precipitation annually. The soils are high in organic matter and are considered very fertile. Three fields representing different land-use treatments were selected: (i) sugar beet (*Beta vulgaris*) - 13.71 ha (52°30′27.3″N 0°24′17.5″E); (ii) bare field (left uncultivated for one year) - 9.62 ha (52°50′41.5″N 0°40′03.10″E) opposite the sugar beet field, and (iii)

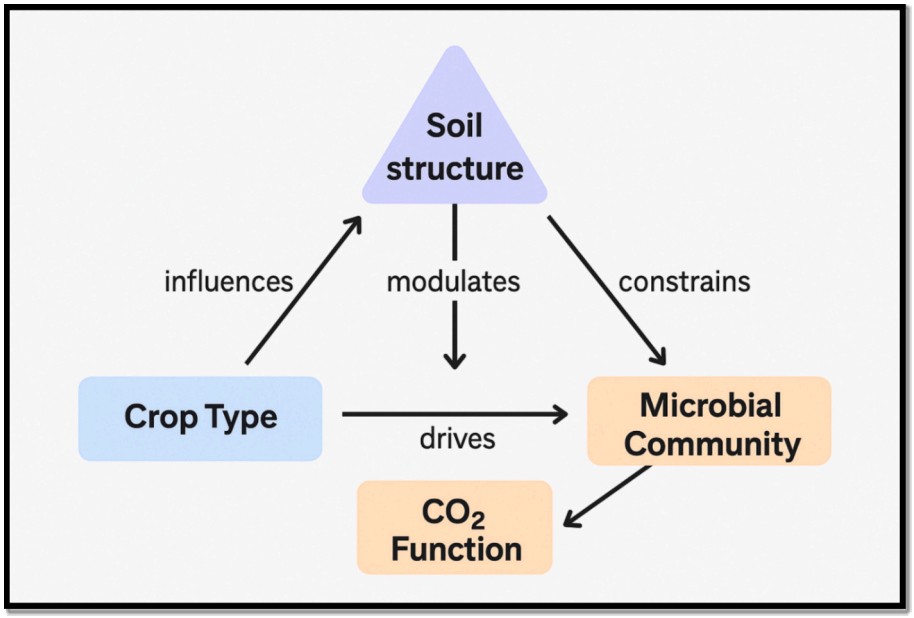

Fig. 1. Conceptual framework linking crop type, soil structural connectivity (Conn.D), microbial community composition, and CO_2 emission dynamics in productive UK peat soils. This study explores functional relationships among these components using integrated structural, microbial, and gas datasets from a working farm system.

winter wheat field (*Triticum aestivum*) - 6.6 ha (52°51′47.9″N 0°38′96.8″E) located about 150 m from the sugar beet field measured.

Sampling points were selected to capture both the spatial heterogeneity of the fields and the effects of land use on soil properties and CO_2 emissions. The Big W sampling design (Munroe, 2018) was employed because it provides cost-effective yet statistically robust coverage for on-farm trials. Within each field, the W transect was laid across a 250 m grid to ensure representation of field-scale variability. Sampling locations were positioned at each turning point of the W (two ends, centre, and two intermediate points), covering different topographic positions and management zones. At each location, composite soil samples were obtained by pooling 3–5 subsamples within a 0.1–1 m radius to reduce microsite variability and improve representativeness. This design ensured that selected points reflected both within-field variability and treatment-specific conditions, providing a scientifically rigorous basis for comparing the influence of different crops on peat soil structure, microbial communities, and CO_2 emissions.

Sampling was carried out during the peak growing season to capture active microbial and soil processes. The winter wheat field received 220 kg/ha/year of ammonium nitrate, while the sugar beet fields were fertilized with 200 kg/ha/year of ammonium nitrate.

2.2. CO_2 emission measurements

CO_2 flux were measured using a portable LI-COR Biosciences LI-8100 A single-chamber soil flux system (LI-COR Biosciences, Lincoln, Nebraska) equipped with a closed-chamber design allowing air circulation within the sealed chamber, which has a diameter of 20 cm (Madsen, Xu et al. 2009). Measurements were conducted at soil depths of 5 cm, 10 cm, and 20 cm at five systematically distributed locations within each field plot, encompassing all crop types. Data collection was repeated every two weeks from June to September. CO_2 flux was calculated based on the rate of concentration change within the chamber.

2.3. Soil physicochemical properties

Soil moisture was determined using ML3 ThetaProbe soil moisture sensor (ThetaKit, Delta-T, Great Britain). Soil temperature at the time of sampling was recorded using an in-field thermometer probe HI 98509–01 (Hanna Instruments Pty Ltd). Both soil moisture and temperature measurements were taken at depth; 5 cm, 10 cm and 20 cm at locations adjacent to the CO_2 measurement positions within each field. Soil pH was measured in a 1:2.5 soil-to-water suspension using a calibrated pH meter.

2.4. DNA extraction and sequencing

At each site, soil cores were taken from depths of 5 cm, 10 cm and 20 cm using a standardized auger at locations adjacent to the CO_2 measurement positions. Samples were collected in five replicates for each depth and land-use treatment from the five sampling positions indicated above, providing spatial replication across the field. To minimise cross-contamination, tools were sterilised between samples with 70 % ethanol. Soil samples were placed in sterile containers, transported on ice, and stored at −20 °C prior to analysis. Total DNA was extracted from 0.25 g of soil using the DNeasy PowerSoil Kit (Qiagen) following the manufacturer's protocol. For bacteria the V3–V4 hypervariable region of the 16S ribosomal RNA (rRNA) gene was amplified using primers [CCTAYGGGRBGCASCAG,GGACTACNNGGGTATCTAAT] and for fungal the internal transcribed spacer for the endophytic region (ITS1-1F) [CTTGGTCATTTAGAGGAAGTAA,GCTGCGTTCTTCATCGATGC] was amplified. DNA quality was assessed with a NanoDrop™ 1000 spectrophotometer (Thermo Scientific™), and only samples with 260/280 ratios ~1.8 and 260/230 ratios 2.0–2.2 were retained. Target regions were PCR-amplified using barcoded primers, and amplicons of the expected size were verified by agarose gel electrophoresis. Equimolar products were pooled, end-repaired, A-tailed, and ligated with Illumina adapters. Library quality was checked by Qubit, qPCR, and an Agilent Bioanalyzer. No extraction blanks or PCR negative controls were submitted, but all library preparation and sequencing followed Novogene's standard quality control protocols. Sequencing was performed on an Illumina NovaSeq 600 PE250 platform.

To analyse the microbial community composition in each sample, raw sequences were quality-filtered, clustered into operational taxonomic units (OTUs) at 97 % similarity, and taxonomically assigned using the Silva 138.1 annotation database for 16S rRNA data and Unite v9.0 annotation database for ITS data. Microbial diversity indices, including Shannon and Simpson indices, were calculated using QIIME2.

2.5. Elemental and isotopic analysis

Samples were placed in a freezer overnight and then freeze dried for 24 h using a Mini Lyotrap freeze dryer. 1 mg samples were weighed using a Sartorius CP2P microbalance and encapsulated within tin cups. The samples were then analysed for total carbon (TC), total nitrogen (TN) and the isotopes of both carbon ($\delta^{13}C$ (‰)) and nitrogen ($\delta^{15}N$ (‰)) in the Stable Isotope Laboratory at the University of Leicester using a Sercon ANCA GSL elemental analyser interfaced to a Sercon Hydra 20-20 continuous flow isotope ratio mass spectrometer. Carbon isotope results are expressed relative to VPDB (Vienna Pee Dee Belemnite). Nitrogen isotope results were expressed relative to atmospheric nitrogen.

2.6. X-ray computed tomography and image analysis

Soil core and aggregate samples were scanned using a v|tome|x M 240 kV X-ray CT scanner (Baker and Hughes Digital Solutions GmbH, Germany) at Rothamsted Research, Harpenden. The soil core sample was scanned using micro-focal X-ray tube and soil aggregates samples were scanned with nano-focal tube. The samples placed in a sample holder and the holder was fixed on the specimen stage of the scanner. All soil core samples were scanned with a 0.5-mm copper filter on the micro-focal X-ray tube, at a potential energy of 120 kV, current of 150 μA with a spatial resolution of 37 μm. During the scan, the specimen stage rotated through 360° at a rotation step increment of 0.16° collecting a total of 2200 projection images. Exposure time of each projection image was 83 ms with image averaging of 3, and a skip of 1, and each core scanned for 1 h 40 min as a multiscan mode. After scanning, soil cores were air-dried at room temperature for one week. Six aggregates (2–3 mm) were randomly selected from each core and scanned using a nano-focus X-ray tube (60 kV, 240 μA, 2.5 μm voxel size). Each scan captured 1700 projections over 45 min, with images reconstructed in *phoenix datos|x* software (Baker and Hughes Digital Solutions GmbH, Germany). Beam hardening correction (level 4) and motion corrections were applied, and multi-scan routines were merged to generate continuous 3D volume data.

Image stacks were processed in ImageJ, and segmentation was performed using the Huang thresholding method, which separates pore space from the solid phase based on grayscale intensity. Soil pore network architecture was analysed using 3D X-ray computed tomography (XCT) at a voxel resolution of 40 μm. After image segmentation and binarization, connectivity was assessed using the Euler characteristic (χ) and a derived metric called Conn.D, defined as the volume of the largest connected pore domain (in mm^3). This was calculated by identifying the largest 26-connected cluster of pore voxels and summing their volume. Conn.D reflects the effective percolating volume through which gas or water can move and serves as a proxy for soil physical continuity. This metric is particularly valuable in highly porous peat soils, where total porosity alone may not distinguish functionally disconnected structures.

2.7. Soil gas diffusivity estimation

Soil gas diffusivity (Dp) was estimated to assess gaseous exchange potential in relation to soil moisture and air-filled porosity across different crop treatments and sampling dates. Relative gas diffusivity (Dp/D_0), the ratio of soil gas diffusivity to that in free air, was calculated using the Millington–Quirk model:

$$\frac{D_p}{D_0} = \left(\frac{\theta_a}{\phi}\right)^{1.5} \quad (1)$$

where θ_a is the air-filled porosity, φ is total porosity derived from bulk density with an assumed particle density of 1.4 g cm^{-3} (Faoziah et al., 2019). The exponent 1.5 captures the nonlinear effects of tortuosity and constriction in gas flow pathways as soils become wetter and air-filled porosity decreases. Volumetric water content (θ) was measured in situ and used to calculate $\theta a = \phi - \theta$ at three depths (5, 10, and 20 cm) across five sampling dates from June to October 2024.

2.8. Machine learning model for CO_2 emission prediction

To identify key predictors of CO_2 flux across treatments, we implemented an Extreme Gradient Boosting (XGBoost) regression model using the *xgboost* package (version 1.7.8.1) in R (Chen and Guestrin, n.d). Input variables were selected based on their ecological relevance to peatland carbon cycling and their statistical contribution to model performance. Specifically, soil physicochemical properties (pH, temperature, moisture, total nitrogen, and total carbon) and microbial community composition (OTU relative abundances) were included due to their known influence on CO_2 fluxes. Prior to model training, variance and correlation filtering ($r < 0.75$) was applied to reduce dimensionality and avoid multicollinearity, retaining only variables showing significant variation across treatments. The model was trained with LOOCV (Leave-One-Out Cross-Validation) to minimise overfitting, and performance was evaluated using R^2, and root mean square error (RMSE). Variable importance was assessed using the gain metric, which reflects each feature's contribution to predictive power, and further interpreted with SHAP (SHapley Additive exPlanations) values to determine both the strength and direction of predictor influence. This approach enabled ranking of influential microbial taxa and soil structural parameters, identifying potential microbial biomarkers of carbon cycling in peat systems. Importantly, XGBoost's ability to capture complex, non-linear interactions provided mechanistic insights beyond those accessible to linear or univariate models, offering a robust framework for modelling greenhouse gas emissions from agricultural peatlands (Grinsztajn et al., 2022).

2.9. Data availability

Data from this experiment is shared in the supplementary material. All metagenomic sequence data generated in this study have been deposited in the NCBI Sequence Read Archive (SRA) as raw FASTQ files under BioProject accession number PRJNA1345951 for 16S rRNA amplicon data (BioSample accessions SAMN52822337–SAMN528 22396) and BioProject accession number PRJNA1346049 for ITS amplicon data (BioSample accessions SAMN52823209–SAMN528 23268).

3. Results

3.1. Bacteria community composition

Bacterial communities were dominated by a stable core microbiome across all treatments and soil depths. *Actinobacteria* and *Vicinamibacteria* consistently accounted for 20–30 % of the community, while *Alphaproteobacteria* and *Thermoleophilia* together represented 15–25 % (Fig. 2a & b). *Gammaproteobacteria* maintained relatively stable abundances (~5–7 %) across all samples. *Acidimicrobiia* were more abundant in wheat fields, particularly at shallow depths, whereas the diverse "Others" category (~25 %) indicated substantial background diversity. The overall stability of these dominant taxa suggests a resilient core bacterial microbiome, with subtle treatment-specific variations likely reflecting localised environmental adaptations.

3.2. Fungal community composition

Fungal communities were strongly dominated by *Sordariomycetes*, which comprised 50–75 % of sequences across all treatments and depths, with peak abundances observed in sugar beet fields at 10 cm depth (Fig. 2c & d). *Leotiomycetes* formed the second most abundant group, with consistent representation in wheat field samples across all depths. *Eurotiomycetes* were more prevalent in bare fields (5 cm) and in wheat fields, while *Leotiomycetes* showed a more uniform distribution in sugar beet than in wheat soils. Despite some field-specific variations, the overwhelming dominance of *Sordariomycetes* represents the most prominent compositional feature of the fungal communities in these agricultural peatland soils.

3.3. Bacterial and fungal alpha diversity

Here, alpha-diversity reflects the richness and evenness of microbial species within each treatment, while beta-diversity highlights the differences in community composition between crop types and bare soil. Bacterial diversity across different land use treatment conditions and soil depths was assessed using the Abundance-based Coverage Estimator (ACE) and Shannon diversity index (Fig. 3a & b). The ACE index measures species richness, while the Shannon index accounts for both richness and evenness within microbial communities. Bacterial alpha diversity, as assessed by ACE and Shannon indices, did not differ significantly across soil depths (5, 10, and 20 cm) or among field types (B, S, and W) (Fig. 3a & b; Tukey's HSD; all $p > 0.05$). For ACE diversity, the greatest positive mean difference was observed between the S field at 20 cm depth and the B field at 5 cm depth (Fig. 3a; $p = 0.28$), while the largest negative difference occurred between the S field at 5 cm and S field at 20 cm (Fig. 3a; $p = 0.12$). Similarly, Shannon diversity showed its largest positive difference between the W field at 10 cm and the S field at 5 cm (Fig. 3b; $p = 0.12$), and its largest negative difference between the W field at 5 cm and the W field at 10 cm (Fig. 3b; $p = 0.22$). Despite numerical variations across treatments and depths, the wide confidence intervals and high adjusted *p*-values indicate that bacterial alpha diversity remained broadly similar across the peatland soils.

Fungal Alpha diversity, measured by Shannon and ACE indices, showed no significant differences across soil depths (5, 10, and 20 cm) or field types (B, S, and W) (Fig. 3c & d; Tukey's HSD; all $p > 0.05$). However, pairwise comparisons among certain treatment groups revealed significant differences (Fig. 3d). For Shannon diversity, the largest positive difference was observed between the W field at 10 cm and the S field at 20 cm (Fig. 3d; $p = 0.002$), indicating significant higher diversity in wheat soils at this depth. Similarly, the W field at 20 cm and 5 cm showed significantly higher Shannon values compared with S field at 20 cm (Fig. 3d; $p = 0.006$ and 0.005, respectively). Though these differences were not consistent across other pairwise comparisons, the overall patterns suggest that both land use treatment and depth influence fungal diversity and richness, potentially reflecting shifts in fungal community structure in response to environmental condition.

3.4. Bacterial beta diversity

The ADONIS (PERMANOVA) test, based on Bray-Curtis dissimilarity indices, also revealed significant differences in bacterial community composition across land use treatments and soil depths (Supplementary Table 1). The most pronounced differences were observed in the Sugar

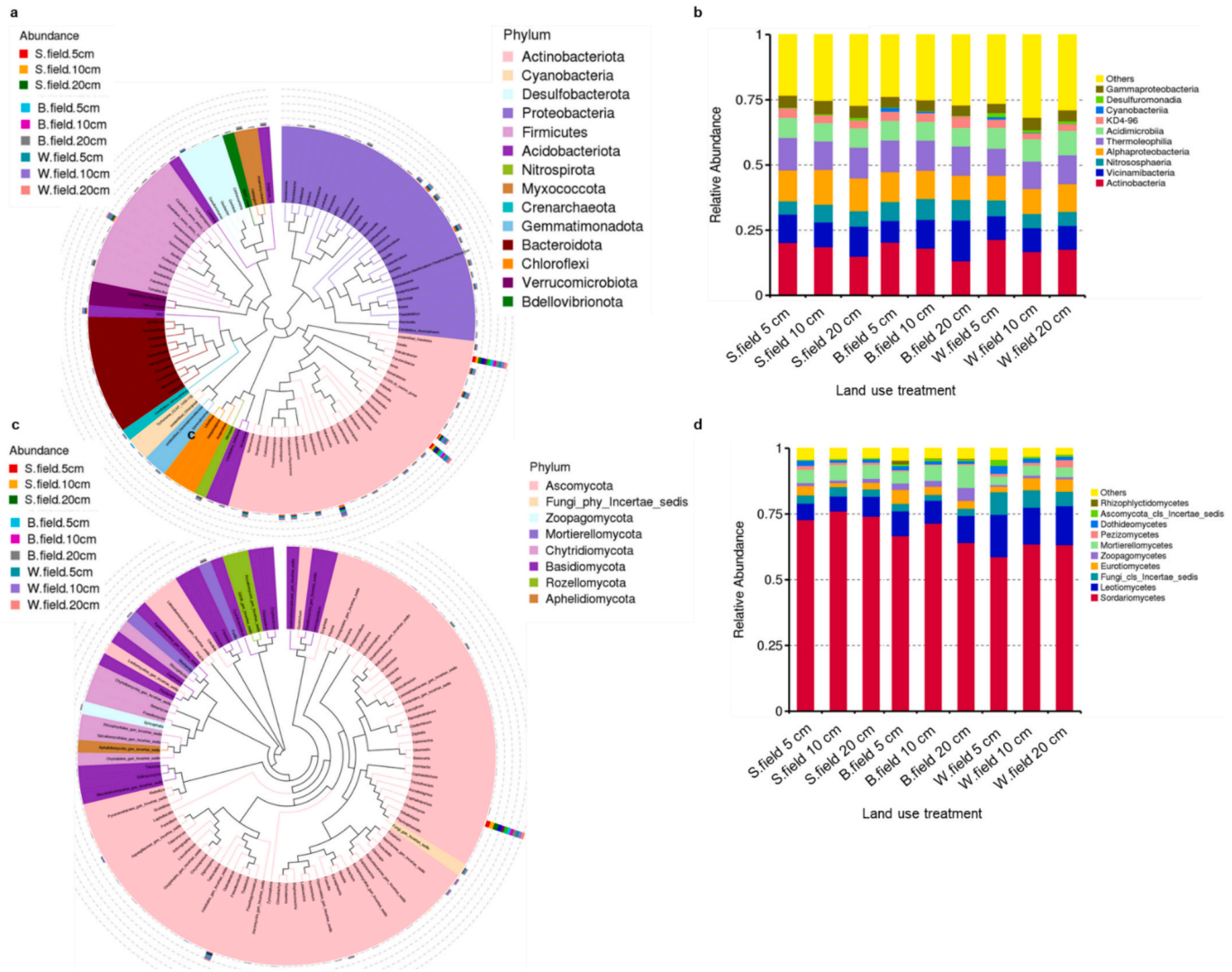

Fig. 2. Taxonomic Composition of Soil Microbial Communities Across Different Land-Use Treatments and Soil Depths (a) Phylogenetic tree of bacterial communities at the phylum level, showing relative abundances across different land-use treatments and soil depths.
(b) Bar plot depicting the relative abundance of bacterial phyla in different groups.
(c) Phylogenetic tree of fungal communities at the phylum level, displaying relative abundances across different land-use treatments and soil depths.
(d) Bar plot illustrating the relative abundance of fungal taxa at the class level in different groups.
Samples are categorized by land-use type and depth, with different colours representing taxonomic groups.

beet field at 5 cm, which significantly differed from all other land use treatments and depths (Supplementary Table 1).

In contrast, within-field comparisons revealed vertical homogeneity in bacterial communities at deeper depths. No significant differences were observed between Sugar beet field.10 cm and Sugar beet field.20 cm ($F = 1.12$, $R^2 = 0.12$, $p = 0.338$) or within bare field and wheat field samples across depths (all $p > 0.1$) (Supplementary Table 1).

The strongest dissimilarity was observed between bare field at 20 cm of depth and wheat field at 20 cm of depth ($F = 4.58$, $R^2 = 0.36$, $p = 0.006$), suggesting substantial horizontal heterogeneity at this depth (Supplementary Table 1).

Overall, these findings indicate that bacterial communities exhibit both horizontal (land use treatment) and vertical (soil depth) structuring, with the most distinct community at sugar beet field at 5 cm of depth. The results suggest that environmental filtering and stochastic processes shape microbial communities, with potential implications for microbiome-mediated soil functions such as CO_2 emissions.

3.5. Fungal beta diversity

PERMANOVA analysis of Bray-Curtis dissimilarities revealed significant differences in fungal communities across land use treatments ($p < 0.05$), with R^2 values ranging from 0.24 to 0.49, indicating that 24–49 % of the variation was attributable to land use (Supplementary Table 2). The strongest dissimilarity was between sugar beet field at 20 cm of depth and wheat field at 20 cm of depth ($R^2 = 0.489$, $p = 0.011$) (Supplementary Table 2).

Within-field depth comparisons showed no significant differences in fungal community composition (all $p > 0.05$), suggesting vertical homogeneity in fungal distribution within each land use type. For example, sugar beet field samples exhibited high similarity across depths ($p > 0.49$, $R^2 < 0.1$), a trend also observed in bare field, and wheat field samples (Supplementary Table 2).

Among land use treatments, the wheat field had the most similar fungal communities ($R^2 = 0.159$–0.244, $p < 0.05$), while bare field and wheat field showed moderate differentiation ($R^2 = 0.249$–0.323, $p < 0.01$) (Supplementary Table 2). These results align with relative

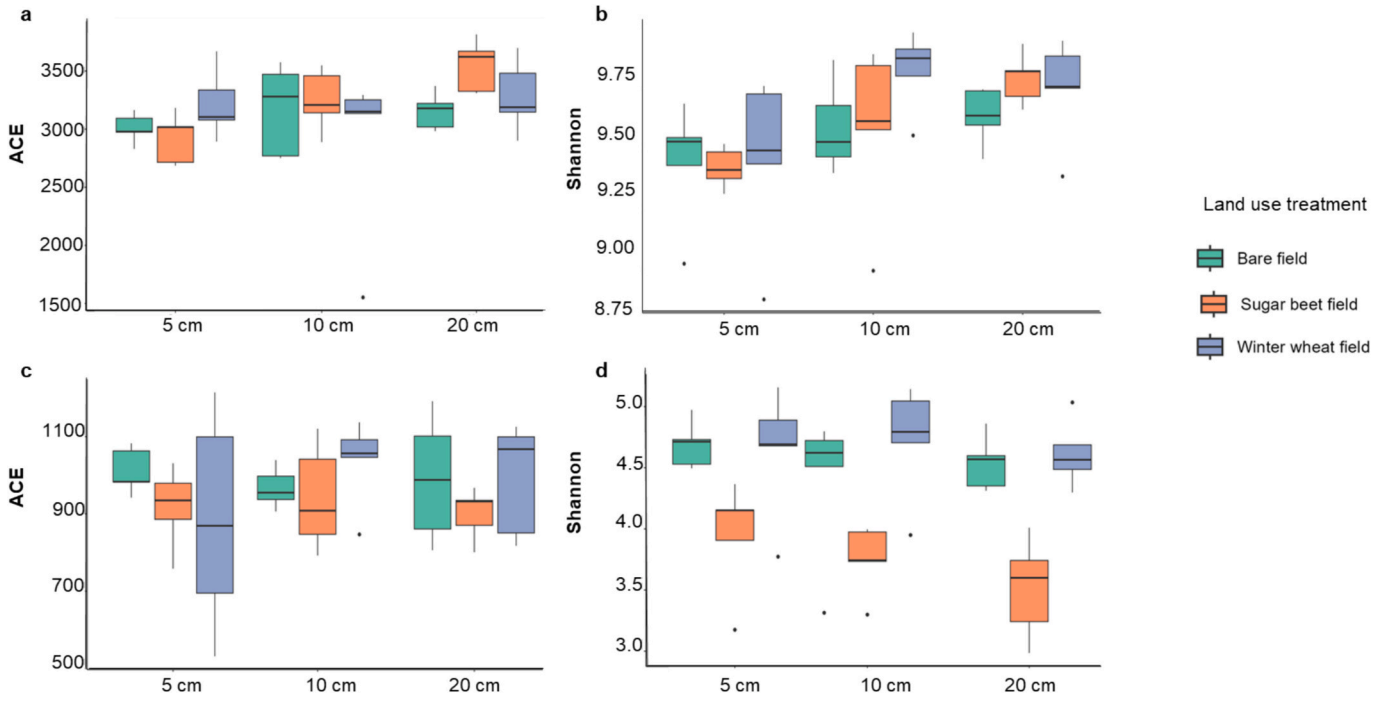

Fig. 3. Alpha-diversity of soil microorganisms across different land-use treatments. Overall comparison of species alpha-diversity among the four groups. (a) Boxplots display the ACE diversity index for bacteria (b), the Shannon diversity index for bacteria (c), the ACE diversity index for fungi (d), and the Shannon diversity index for fungi.

abundance patterns, where *Sordariomycetes* consistently dominated, while taxa such as *Eurotiomycetes*, *Mortierellomycetes*, and *Leotiomycetes* varied in representation between land use treatments rather than soil depths (Fig. 2d).

3.6. Canonical correspondence analysis of microbial communities and environmental variables

Canonical Correspondence Analysis (CCA) was performed to assess the influence of environmental variables on microbial community composition, using both bacterial (16S rRNA) and fungal (ITS) sequencing data. The analysis focused on three land use treatments—Bare field (B), Winter wheat field (W), and Sugar beet field (S)—at a soil depth of 20 cm. The CCA biplots (Fig. 4a & b) illustrate the relationships between microbial community structure and key soil properties, including soil moisture, pH, soil temperature, bulk density, porosity percentage, electrical conductivity, and CO_2 emissions.

Distinct clustering of samples suggested that both bacterial and fungal communities were structured by land-use treatment and soil depth, with environmental gradients further shaping their composition (Fig. 4a & b). For bacterial communities, soil moisture, total nitrogen percentage (Total N) and total carbon percentage (Total C) exhibited a strong positive correlation with the microbial composition. These parameters directly influence bacterial metabolic activity and growth, as moisture availability determines nutrient diffusion rates and cellular processes, while C and N availability controls energy and biosynthesis pathways. Sugar beet samples aligned more closely with these vectors, suggesting that enhanced nutrient cycling under sugar beet cultivation creates favourable conditions for diverse bacterial communities (Fig. 4a). Wheat samples were more dispersed along CCA2, suggesting root exudate-driven selection of specific bacterial consortia, consistent with known rhizosphere effects on microbial assembly (Fig. 4a).

CO_2 flux were closely linked to the microbial communities in bare soil plots across both datasets (Fig. 4a & b), reinforcing the observation that areas with minimal plant cover exhibited distinct microbial compositions contributing to higher respiration rates (Xin et al., 2022). Soil pH also influenced both bacterial and fungal communities, with a greater effect observed in bacterial composition (Fig. 4a & b). Overall, these results highlight that both chemical (moisture, Total N, Total C, pH) and physical (bulk density, porosity) soil parameters jointly structure microbial communities, with direct implications for CO_2 flux dynamics in agricultural peatlands.

3.7. Comparison between fungal and bacterial community influence on CO_2 emissions

Overall, both bacterial and fungal communities exhibited strong responses to soil moisture, pH, and CO_2 flux, with fungi showing a greater sensitivity to soil structure (bulk density, porosity) (Fig. 4a & b). The results indicate that both microbial groups contribute to soil respiration, but their interactions with environmental factors differ. These findings highlight the importance of considering both bacterial and fungal communities in predictive models of CO_2 flux from arable peatlands.

3.8. Seasonal variability in soil gas diffusivity under different crop treatments

Fig. 5 illustrates temporal variations in relative soil gas diffusivity (D_P/D_0) across three agricultural treatments sugar beet, bare soil, and wheat at soil depths of 5 cm, 10 cm, and 20 cm during the growing season (June to October 2024). Relative diffusivity increased markedly from June to August, reflecting seasonal soil drying. The bare soil consistently exhibited the highest diffusivity values (ranging up to ~0.7), indicative of lower moisture retention and greater air-filled pore spaces, likely due to the absence of plant cover. In contrast, the sugar beet treatment maintained the lowest diffusivity (typically <20 cm), attributed to higher moisture retention facilitated by crop canopy shading and root-mediated water uptake dynamics. Wheat exhibited intermediate diffusivity profiles, highlighting the influence of crop type and growth stage on soil moisture and gas transport properties. These results emphasize that crop management significantly modulates soil

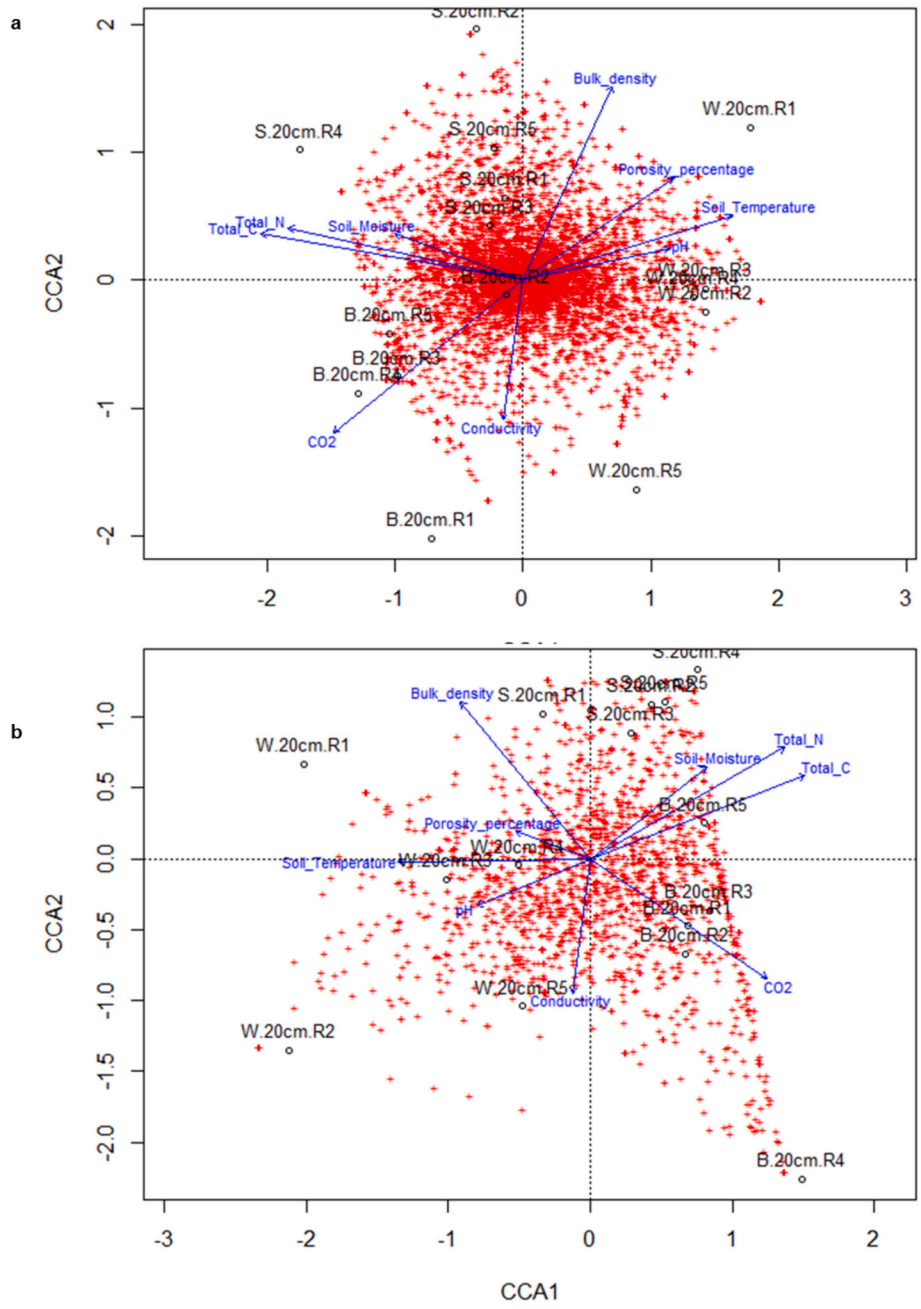

Fig. 4. Canonical Correspondence Analysis (CCA) Biplot of (a) Bacteria community composition and environmental variables (b) Fungal community composition and environmental variables. The CCA biplot illustrates the relationships between microbial (bacterial and fungal) community composition and environmental factors, including CO_2 emissions, soil moisture, total nitrogen percentage (Total N), total carbon percentage (Total C), pH, soil temperature, bulk density, porosity percentage, and conductivity. Red points represent individual microbial taxa, while black circles denote sample sites. The arrows indicate the direction and strength of environmental gradients influencing microbial distribution. Bare soil (B), winter wheat (W), and sugar beet (S) samples are labelled according to crop type and depth (20 cm). CO_2 emissions are strongly associated with soil moisture, Total N and Total C, while other variables contribute to microbial community structure across different land uses. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

structure and moisture conditions, thereby affecting microbial respiration dynamics and potential soil CO_2 emissions.

3.9. Relationship between pore connectivity (Conn.D) and cropping systems

Analysis of pore connectivity (Conn.D), measured using X-ray computed tomography (XCT), revealed differences among treatments, reflecting changes in soil pore network characteristics associated with crop type. The average Conn.D was highest in the bare soil (13.2 mm^3), followed by wheat (12.4 mm^3), and lowest in the sugar beet (7.4 mm^3). Greater Conn.D values indicate a more extensive interconnected pore space, potentially facilitating more efficient gas diffusion and influencing microbial respiration dynamics. However, statistical analyses indicated no significant treatment effect on Conn.D ($P > 0.05$), suggesting that observed differences in connectivity were subtle or masked by soil heterogeneity at the field scale. Despite the lack of significant differences, the observed trends in connectivity may contribute to explaining the higher diffusivity and elevated soil CO_2 concentrations measured under bare soil compared to the cropped treatments.

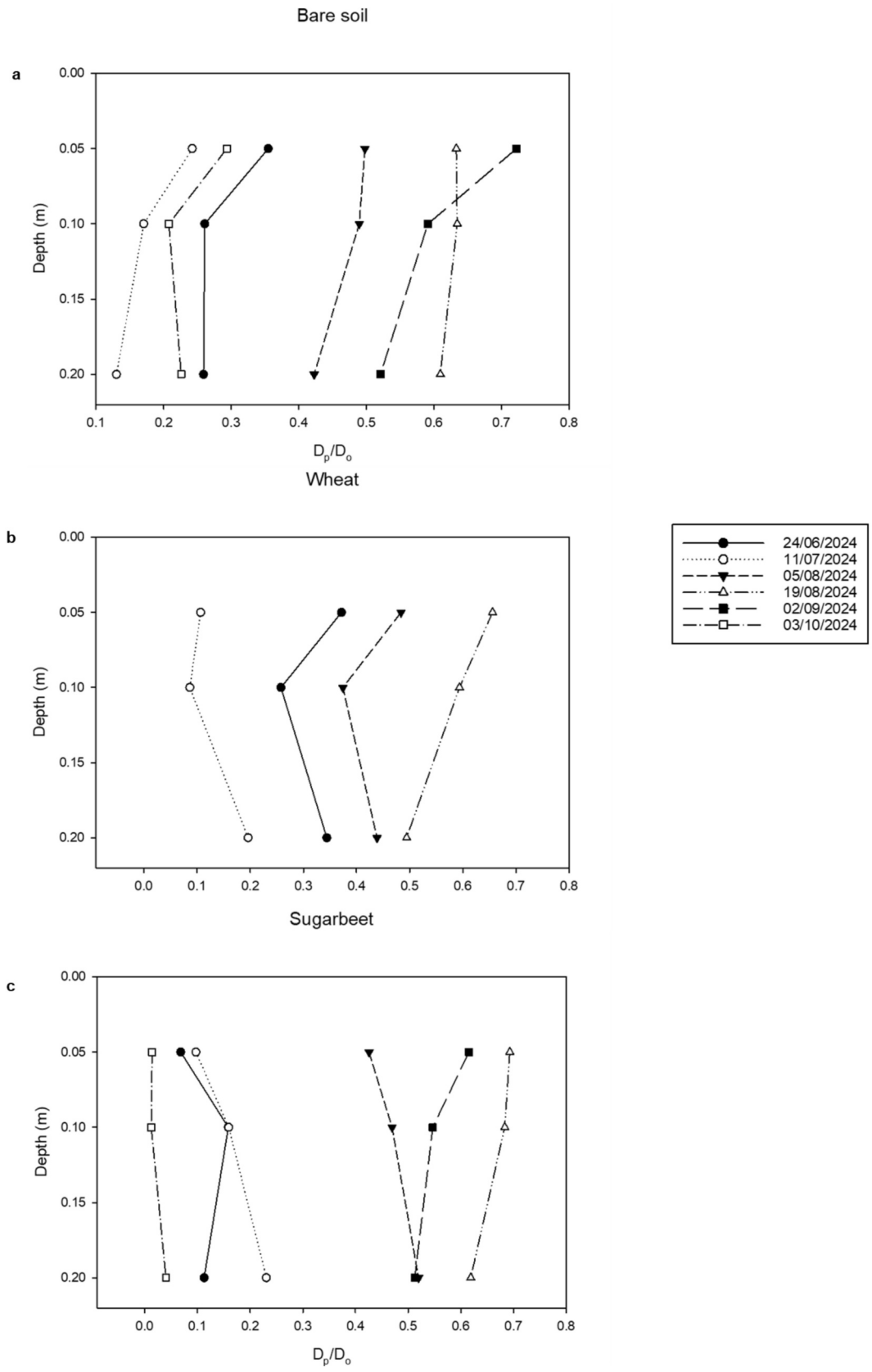

Fig. 5. Temporal and spatial variation in relative soil gas diffusivity D_p/D_o by depth under different treatments: (a) Bare soil, (b) Wheat, and (c) Sugar beet. Each line represents a different sampling date across the growing season from June to October 2024, at three depths (5 cm, 10 cm, and 20 cm). Dp/Do was calculated using the Millington–Quirk model based on measured air-filled porosity.

3.10. Predictive modelling identifies potential biomarkers of soil microbial communities linked to CO_2 emissions

To evaluate whether soil bacterial and fungal community characteristics can serve as biomarkers for CO_2 flux from arable peat soils, an XGBoost regression model was developed using bacterial and fungal operational taxonomic unit (OTU) relative abundances alongside soil physicochemical properties (pH, soil moisture, soil temperature) (Fig. 6). OTU counts were normalised to relative abundance prior to modelling, accounting for differences in sequencing depth across samples. To mitigate overfitting given the limited training dataset, LOOCV was employed to assess the model's predictive accuracy across different classification levels.

The model demonstrated a strong predictive performance (R^2 = 0.82), with predicted CO_2 concentration values aligning well with actual measurements along the 1:1 reference line (Fig. 6a). However, the model exhibited a high Root Mean Square Error (RMSE = 37.39), with greater variability observed in predictions at higher CO_2 concentrations. This pattern suggests potential non-linearity in the data or the influence of unaccounted environmental factors on soil respiration dynamics (Fig. 6a).

The feature importance analysis revealed specific microbial taxa particularly OTU_6_F (*Syncephalis_sp*, OTU_15_F (*Hypocreales_sp*), OTU_901 (*Vicinamibacterales*), OUT_116_F (*Microascales_sp*), and OTU_5115 (*KD3-10*) along with land use treatment (Bare soil) and soil temperature, as the strongest predictors of soil CO_2 concentration (Fig. 6b). This underscores the critical role of microbial community composition and soil physical properties such as temperature and land use in driving CO_2 emissions, with bacterial and fungal OTUs exhibiting varying degrees of influence. These findings highlight the potential of microbial indicators in understanding and predicting soil carbon flux dynamics.

4. Discussion

This study reveals how soil structure and microbial communities jointly influence CO_2 flux in cultivated peatlands. By integrating XCT-derived pore metrics, microbial profiling, and in situ gas measurements, we demonstrate that specific pore characteristics and microbial taxa are key predictors of CO_2 flux. These findings provide a novel, mechanistic framework for improving greenhouse gas models in agricultural peat soils.

Soil CO_2 concentrations measured across treatments were consistently low, typically ranging between 420 and 700 μmol mol^{-1}. These values are notably lower than concentrations commonly reported in organic-rich or poorly drained systems, where CO_2 levels can exceed 2000–5000 μmol mol^{-1} (Blodau and Moore, 2003). Several interacting factors likely contributed to this observation. First, soil structure analyses revealed high total porosity and well-connected pore domains across treatments, especially in the bare soil and sugar beet plots. These structural conditions facilitate rapid gas exchange, which can prevent in situ accumulation of CO_2 despite active microbial and root respiration. Second, measurements were made during daytime hours, when soil respiration is ongoing but CO_2 is rapidly effluxing to the atmosphere. Midday sampling may therefore underestimate transient CO_2 build-up that occurs overnight or under low-diffusion conditions. Bare soil plots, in particular, lacked recent root inputs and showed microbial communities dominated by oligotrophic taxa with potentially lower metabolic rates. Finally, sensor placement and small-scale heterogeneity could also have affected detection, especially in peat soils where gas production and diffusion can vary across millimetre scales. Taken together, these results suggest that the low measured concentrations reflect high gas diffusivity, rapid turnover, and spatial heterogeneity, rather than an absence of microbial activity. This reinforces the importance of interpreting soil gas measurements within the context of physical structure and ecological dynamics, particularly in porous, high-carbon systems like drained peat soils.

Although no statistically significant differences were found in connectivity (Conn.D) among treatments, subtle variations in pore structure may still lead to meaningful functional differences in gas diffusivity and microbial habitat characteristics. Statistical tests based solely on mean comparisons can sometimes mask ecologically relevant nuances, particularly in inherently heterogeneous soil environments where small structural differences can yield disproportionately large effects on microbial activity and greenhouse gas fluxes. Future research employing higher replication or advanced non-linear analytical approaches may provide deeper insights into these subtle but functionally critical differences.

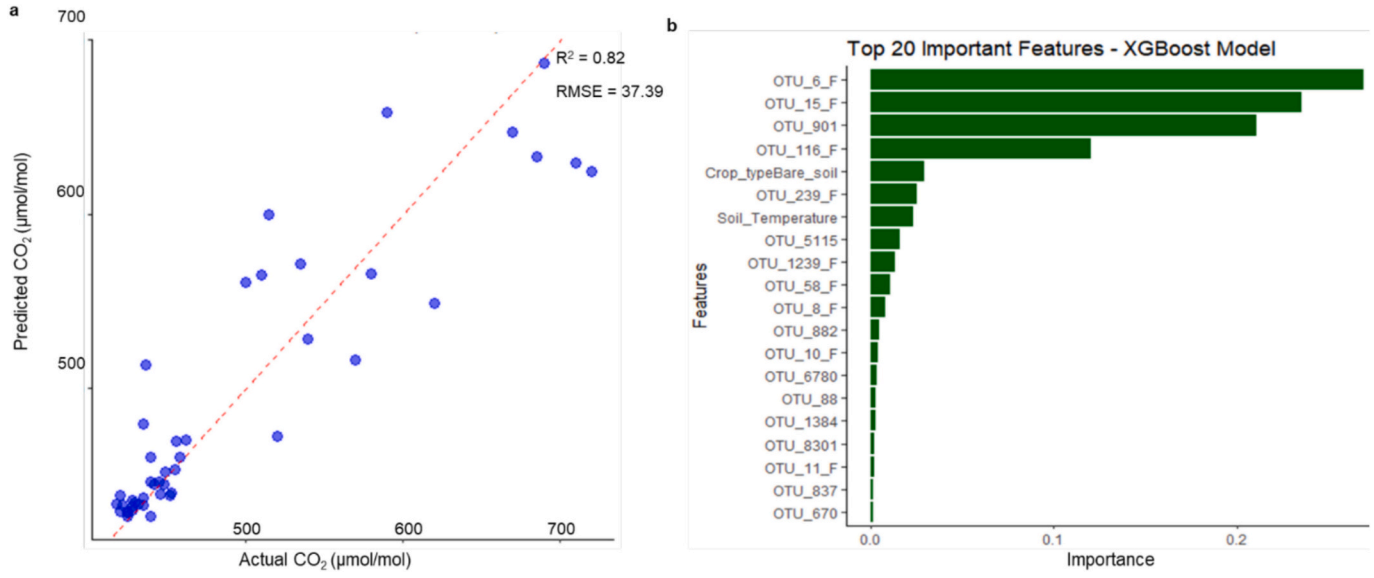

Fig. 6. Model evaluation (a) Predicted vs. actual CO_2 emissions using an XGBoost model with leave-one-out cross-validation (LOOCV). The red dashed line represents the ideal 1:1 relationship. (b) Top 20 most important features contributing to CO_2 emission predictions based on the XGBoost model. The most influential features include OTU_6_F, OTU_15_F, OTU_901, OTU_116_F, crop type, OTU_239_F and soil temperature indicating the strong impact of bacterial and fungal communities on CO_2 emissions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.1. Depth-dependent diversity patterns

The alpha diversity analyses (Fig. 3) provided critical insights into the vertical stratification of microbial communities. For bacteria, the higher richness and evenness observed at mid-depths (10 cm) across multiple land use treatments suggests optimal conditions for bacterial diversity at this soil horizon. This pattern could be explained by a balance of resources—sufficient oxygen availability compared to deeper soils, coupled with more stable moisture and temperature conditions than surface layers (Eilers et al., 2012; Fierer et al., 2003).

In contrast, fungal diversity tended to increase with depth. This inverse pattern between bacterial and fungal diversity with depth highlights the different ecological strategies and environmental preferences of these microbial groups (Bahram et al., 2015; Li et al., 2019). Fungi, with their filamentous growth form, may be better adapted to exploit deeper soil horizons where oxygen levels are reduced but where more recalcitrant carbon sources persist (Baldrian et al., 2012; Crowther et al., 2014).

These depth-dependent diversity patterns suggest that land management practices altering soil physical structure, such as tillage intensity and depth, could differentially impact bacterial versus fungal communities across the soil profile. Consequently, agricultural management decisions should consider these vertical microbial distribution patterns to optimize beneficial soil ecological functions while minimizing disruption to key microbial groups that contribute to soil health and carbon sequestration.

4.2. Environmental drivers of microbial community structure

The CCA (Fig. 4) revealed that soil moisture, total nitrogen percentage and total carbon percentage emerged as the predominant factors shaping both bacterial and fungal communities, particularly in the sugar beet field. This finding underscores the fundamental importance of water availability, nitrogen and carbon content in regulating microbial metabolism and community assembly in peatland soils (Fenner and Freeman, 2011; Zhalnina et al., 2015). Mechanistically, soil moisture regulates microbial dynamics by influencing substrate solubility, enzyme diffusion, and oxygen availability. High moisture creates more anaerobic microsites, favouring anaerobic or facultative anaerobes, while well-drained conditions enhance aerobic respiration and the proliferation of fast-growing taxa (Manzoni et al., 2012; Zhang et al., 2013).

The stronger response of fungal communities to soil physical properties (bulk density, porosity) compared to bacteria highlights their greater sensitivity to soil structural architecture. This can be attributed to the hyphal growth strategy of fungi, which relies on interconnected pore networks for foraging and colonization (Harris, 2003; Rillig and Mummey, 2006). Reduced pore connectivity likely impedes fungal hyphal extension and nutrient acquisition, while more connected and aerated soils facilitate fungal proliferation. This mechanism explains why management practices altering pore size distribution and connectivity may disproportionately affect fungal community dynamics (Lehmann et al., 2017; Six et al., 2006).

Difference in microbial community structure across land-use treatment further reflects underlying soil structural heterogeneity. CCA indicated that moisture, temperature, and pH were primary environmental gradients shaping microbial composition, this is consistent with studies in drained peat and organic soils (Andersen et al., 2013; Urbanová and Bárta, 2014). In the bare soil plots, where pore connectivity and diffusivity were highest, distinct microbial assemblages adapted to aerobic conditions were observed. Such conditions promote faster decomposition rates and elevated CO_2 flux by supporting aerobic heterotrophs capable of rapid substrate turnover (Smith et al., 2005). Conversely, in the sugar beet plots with lower connectivity and diffusivity, restricted oxygen exchange likely limited aerobic decomposition, favouring microaerophilic or facultative anaerobic microbes and resulting in intermediate CO_2 flux (Du et al., 2023). In wheat plots, the combination of moderate structural properties and active root systems may have suppressed microbial respiration through rhizosphere competition for oxygen and labile carbon substrates, explaining the lower CO_2 flux observed (Lecomte et al., 2018). Overall, these findings suggest that environmental factors such as moisture, nutrient availability, and pore structure interact to regulate microbial metabolism through mechanisms that control substrate accessibility, redox gradients, and spatial colonization pathways (Lacroix et al., 2021). This mechanistic understanding strengthens the link between soil physical conditions, microbial community structure, and greenhouse gas fluxes in managed peatland systems.

4.3. Microbial respiration, CO_2 diffusivity, and soil moisture

Microbial respiration is tightly regulated by soil gas diffusivity because oxygen availability and CO_2 removal are essential for sustaining microbial metabolism (Jin and Jury, 1996; Moldrup et al., 2000). Reduced gas diffusivity limits oxygen supply, creating hypoxic or anaerobic conditions that suppress aerobic respiration and shift microbial processes toward anaerobic pathways such as denitrification and methanogenesis (Butterbach-Bahl et al., 2013; Kuzyakov and Blagodatskaya, 2015), consistent with microscale oxygen limitation theory (Or et al., 2007; Sexstone et al., 1985; Tecon and Or, 2017). Recent research has demonstrated that anaerobic microsites develop even in ostensibly well-aerated upland soils, representing an unrecognised mechanism for carbon storage and greenhouse gas production (Keiluweit et al., 2017). As soil water content increases, oxygen diffusion decreases and anaerobic soil volumes gradually expand into areas with lower oxygen consumption rates, creating a delicate balance between oxygen consumption and replenishment (Schlüter et al., 2025). Temporal and depth-dependent variations in diffusivity observed in this study (Fig. 5a, b, c) directly influenced microbial dynamics, particularly in plant-associated treatments where root activity alters soil structure and gas transport pathways. During wetter periods, such as October, near-zero diffusivity values indicate oxygen limitations that likely slow aerobic microbial activity while promoting the development of anaerobic microsites. Water infiltration into pores reduces the volume and connectivity of air-filled pores, blocking pathways for atmospheric oxygen supply by diffusion (Du et al., 2023). Such microsites have been shown in other studies to enhance anaerobic respiration processes, contributing to increased emissions of reduced gases like N_2O and CH_4 in saturated soils (Linn and Doran, 1984; Tecon and Or, 2017). This occurs because increasing soil moisture reduces gaseous diffusion rates, directly affecting microbial physiological status by limiting the supply of electron acceptors like oxygen (Banerjee et al., 2016). In contrast, drier conditions in August and September improved gas diffusivity, enhancing oxygen penetration and enabling aerobic heterotrophs to dominate decomposition, consistent with findings from well-aerated peat and mineral soils (Hall et al., 2013; Werner et al., 2007).

The inverse moisture–diffusivity relationship we observed ($R^2 = 0.93$, $p < 0.0001$) accords with established transport theory (Jin and Jury, 1996; Moldrup et al., 2000) and the "bottleneck effect" of constrained pore connectivity (Cook et al., 2013). Although treatments did not differ significantly in this relationship ($F_{2,45} = 0.32$, $p > 0.05$), crop- and management-driven moisture regimes likely imposed heterogeneous redox and diffusional environments that modulate microbial processes and GHG fluxes (Ball, 2013), as reported for peat systems where oxygen penetration and water-table position govern redox cascades and CO_2/CH_4 production (Estop-Aragonés et al., 2016; Jaatinen et al., 2008). This spatial and temporal heterogeneity explains why denitrification activity is often concentrated in anoxic microsites and ephemeral events, presenting ongoing challenges for ecosystem-scale modelling (Schlüter et al., 2025).

The XGBoost regression model's success ($R^2 = 0.82$) in predicting CO_2 flux using microbial OTUs and soil physicochemical properties

represents a significant advancement in our understanding of the biological drivers of carbon flux. The identification of specific bacterial and fungal taxa (OUT-15_F, OTU_901, OTU_6_F, OTU_116_F, OUT_5115) as important predictors suggests potential microbial biomarkers for carbon cycling processes, is consistent with approaches proposed by Trivedi et al. (2016) and Nazaries et al. (2013). These findings indicate that microbial community composition, in combination with soil physicochemical properties, holds promise as a predictive biomarker for CO_2 flux in arable peat soils. Future research should focus on characterising these organisms' metabolic capabilities and ecological roles to better understand their contribution to CO_2 production (Morales and Holben, 2011; Žifčáková et al., 2016).

4.4. *Integrating microbial patterns with soil structure and implications for carbon loss in cultivated peat soils*

Given the critical influence of soil moisture on gas transport and microbial activity, effective water management is essential for mitigating greenhouse gas emissions from peatland soils (Evans et al., 2017; Regina et al., 2015). Although the moisture–diffusivity relationship was consistent across treatments, crop type and land management strongly influenced soil moisture dynamics, driving variability in microbial processes and carbon fluxes. Notably, higher CO_2 flux from bare soils, particularly early in the growing season, highlight the risks of leaving peat soils unvegetated and reinforce the importance of continuous vegetation cover for reducing carbon losses (Evans et al., 2017; Tiemeyer et al., 2016). In vegetated fields, root exudates from wheat and sugar beet likely enhanced microbial metabolism, promoting deeper decomposition (Fig. 5a, c).

Water table regulation remains central to controlling soil aeration and microbial activity (Regina et al., 2015; Renger et al., 2002). Our results show that even small shifts in soil moisture can trigger threshold responses in microbial respiration (Manzoni et al., 2012), underscoring the need for hydrological strategies tailored to crop types and seasonal conditions (Knox et al., 2015).

A key finding of this study is the tight coupling between soil structure, microbial community composition, and CO_2 dynamics. Microbial communities do not operate in isolation but are shaped by the soil's physical architecture, particularly porosity, connectivity, and bulk density, which regulate oxygen and carbon availability. Bare soil plots, with higher pore connectivity and diffusivity, supported microbial assemblages adapted to well-aerated conditions and showed elevated CO_2 efflux. In contrast, the more constrained pore structure of sugar beet plots limited diffusivity and CO_2 release but fostered distinct fungal communities, likely adapted to fluctuating redox conditions. Fungal communities were especially sensitive to bulk density and porosity, reflecting their hyphal capacity to explore air-filled pores, while bacterial communities showed subtler shifts aligned with structural changes. These patterns are consistent with previous studies linking microscale heterogeneity in oxygen and water dynamics to microbial assembly and function in peat soils (Fenner and Freeman, 2011; Urbanová and Bárta, 2014).

Understanding these soil–microbe–structure interactions is critical for improving greenhouse gas models. Carbon loss from peat is driven not only by temperature or microbial biomass but by the accessibility of oxygen and carbon substrates, processes governed by soil physical structure. By integrating XCT-derived structural data, microbial profiles, and in situ gas measurements, this study provides a framework for linking microscale habitat properties with ecosystem-scale carbon dynamics. Future research should build on this integrative approach to develop predictive models that incorporate physical constraints on microbial function for more accurate greenhouse gas accounting in managed peatlands.

5. Conclusion

This study demonstrates that soil structure, microbial community composition, and gas dynamics interact to control carbon cycling in cultivated peatlands. By combining XCT-derived pore metrics, in situ CO_2 measurements, and microbial community profiling, we identified seasonal gas diffusivity variation (Dp/D_0 ranging from 0.08 to 0.10 in dry periods to <0.01 during wet conditions) as the primary control on microbial function and CO_2 flux, with soil moisture explaining 93 % of this variation.

Bare soil plots exhibited ~30 % higher CO_2 concentrations and ~20 % lower fungal diversity compared to cropped soils, underscoring the importance of maintaining vegetation cover to moderate carbon loss. Conversely, wheat and sugar beet treatments supported more diverse microbial communities, particularly fungi such as *Mortierella*, but had lower CO_2 concentrations, likely reflecting the effects of restricted oxygen availability and plant–microbe interactions on microbial respiration. Fungal communities, dominated by *Sordariomycetes*, exhibited stronger sensitivity to land-use changes than bacterial communities, with sugar beet plots supporting the highest fungal diversity. Notably, microbial assemblages at 5 cm depth in sugar beet soils were distinct from other treatments, underscoring the strong influence of crop type on microbial community structure. Importantly, CO_2 concentrations remained relatively low across treatments despite the high carbon content of these soils, highlighting the critical role of air-filled porosity and gas diffusivity in regulating soil–atmosphere exchange. These findings indicate that microbial activity and carbon loss in drained peat are constrained not solely by microbial abundance or temperature but by the physical accessibility of oxygen and carbon substrates within the soil matrix.

Among the measured soil physical parameters, relative gas diffusivity (Dp/D_0), pore connectivity (Conn.D), porosity (φ), and bulk density emerged as key structural metrics regulating both microbial community composition and CO_2 flux across land-use treatments. To identify the biological drivers of CO_2 emissions, we employed an XGBoost machine learning model that explained 82 % of the variance in CO_2 using microbial OTU abundances and physicochemical variables. This approach identified specific microbial taxa—OTU_6_F (*Syncephalis* sp.), OTU_15_F (*Hypocreales* sp.), OTU_901 (*Vicinamibacterales*), OTU_116_F (*Microascales* sp.), and OTU_5115 (KD3-10)—alongside land-use treatment (bare soil) and soil temperature as the strongest predictors of CO_2 concentration. Collectively, these findings demonstrate the interconnected influence of soil structure, temperature, and microbial composition in driving carbon dynamics within cultivated peatlands. This integrated framework offers a promising route toward developing biological indicators of carbon cycling processes and provides critical insights for incorporating microbial-structural interactions into greenhouse gas models and sustainable peatland management strategies.

While this study provides mechanistic insights into soil–microbe–gas interactions, we acknowledge the lack of true field-scale replication and the focus on CO_2 alone without accounting for CH_4 and N_2O emissions as limitations. Future work incorporating multi-gas flux measurements and replicated designs will strengthen the predictive framework for greenhouse gas modelling in agricultural peatlands. We also recognise that extraction and PCR negative controls were not included during sequencing; however, all library preparation and sequencing were conducted under standard quality control procedures. Future studies will incorporate negative controls and cross-validation measures to further enhance data reliability. Overall, our findings highlight the value of integrating soil structural and microbial data to inform sustainable land management strategies aimed at reducing carbon losses and improving the resilience of cultivated peat systems.

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CRediT authorship contribution statement

Gavers K. Oppong: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **William Rickard:** Writing – review & editing, Visualization, Validation, Investigation, Formal analysis, Conceptualization. **Ursula Davis:** Writing – review & editing, Formal analysis. **Kamrun Suravi:** Writing – review & editing, Formal analysis. **Noel Clancy:** Writing – review & editing, Formal analysis. **Muhammad Ali:** Writing – review & editing, Formal analysis. **Asima Khan:** Writing – review & editing, Formal analysis. **Corentin Houpert:** Writing – review & editing, Formal analysis. **Xiaoxian Zhang:** Writing – review & editing, Supervision, Resources. **Ashiq Anjum:** Writing – review & editing, Supervision, Funding acquisition. **Stephen Wright:** Writing – review & editing, Project administration. **Pat Heslop-Harrison:** Writing – review & editing, Supervision, Resources. **Jörg Kaduk:** Writing – review & editing, Supervision, Resources. **Heiko Balzter:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Gavers Kwasi Oppong reports equipment, drugs, or supplies were provided by Rothamsted Research Sustainable Soils and Crops Department. If there are other authors, they 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 availability

Data will be made available on request.

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