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RESEARCH ARTICLE

Patterns and geographical drivers for the abundance of CO_2-assimilating bacteria, methanotrophs and CO-oxidizing bacteria in agricultural soils across eastern China

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Highlights

- Spatial factors govern carbon-cycling gene abundances in uplands, whereas biotic and substrate factors dominate in paddy soils.
- Strong correlations reveal an integrated "microbial carbon pump" linking CO_2, CH_4, and CO cycling.
- The high continental-scale abundance of *cbbL* and *coxL* genes suggests a previously underestimated microbial role in carbon trace gas cycling.

Abstract

Microorganisms carrying *cbbL*, *pmoA* and *coxL* genes play crucial roles in regulating soil-atmosphere exchanges of carbon trace gases (CO_2, CH_4, and CO). However, the geographical distribution patterns of these functional genes in agricultural ecosystems and their environmental drivers remain poorly understood. Here, we surveyed agricultural soils across four climate zones (tropical, subtropical, warm temperate, and mid-temperate) in eastern China to quantify the abundances of CO_2-assimilating bacteria (*cbbL* gene), methanotrophs (*pmoA* gene), and CO-oxidizing bacteria (*coxL* gene). We found significant ecosystem-specific patterns: the *cbbL* gene was more abundant in upland soils (averaging 9.46×10^9 copies g^{-1}) than in paddy soils (6.44×10^9 copies g^{-1}). In contrast, methanotrophs abundance was 1 to 3 orders of magnitude higher in paddy (averaging 1.17×10^8 copies g^{-1}) than in upland (5.78×10^6 copies g^{-1}) soils. The *coxL* gene maintained similar abundance levels across both soil types (averaging 6.12×10^8 *vs.* 5.91×10^8 copies g^{-1}). Structural equation models revealed that spatial factors primarily shaped *cbbL* and *pmoA* in uplands, whereas total bacterial abundance was the dominant predictor for all three genes in paddy soils. These results highlight distinct ecological controls on microbial functional groups and provide a predictive framework for how land use and climate change may regulate microbial mediation of carbon gas fluxes across a continental-scale transect in eastern China.

Keywords: paddy, upland, CO_2-assimilating bacteria, methanotrophs, CO-oxidizing bacteria, continental scale

1. Introduction

The carbon (C) cycle, fundamental to terrestrial ecosystem functioning (Crowther *et al.* 2016), is critically regulated by soil microorganisms. These microbes govern soil C fluxes, influencing both soil fertility and atmospheric concentrations of key carbon trace gases (CO_2, CH_4 and CO) (Crowther

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et al. 2019; Fan *et al.* 2021; Liu *et al.* 2023). The exchange of these gases between soil and atmosphere is driven by biogeochemical processes mediated by specific functional microbial groups (Trivedi *et al.* 2013; Delgado-Baquerizo *et al.* 2016). For example, autotrophic bacteria carrying the *cbbL* gene assimilate CO_2, thereby reducing atmospheric CO_2 levels and contributing to soil organic carbon (SOC) storage (Yuan *et al.* 2015; Liao *et al.* 2023). Methanotrophs harboring the *pmoA* gene oxidize CH_4, constituting the primary biological sink for atmospheric CH_4 and enhancing SOC accumulation in paddy soils (Nazaries *et al.* 2018; Zheng *et al.* 2024). Meanwhile, CO-oxidizing bacteria with the *coxL* gene directly consume atmospheric CO, influencing tropospheric chemistry (King and Weber 2007; Greening and Grinter 2022).

These microbial processes do not act in isolation but form a synergistic network: methanotrophs and CO oxidizers produce CO_2 that supports autotrophic CO_2 fixation (*via cbbL*), while energy derived from CO oxidation can facilitate CH_4 oxidation (*via pmoA*), establishing an efficient carbon reflux loop (Cordero *et al.* 2019; Bay *et al.* 2021). The functional complementarity — including cross-feeding of metabolites (e.g., DOC-stimulated mixotrophy) and resource-dependent synergies enhances soil carbon storage and atmospheric CO/CH_4 mitigation (Ortiz *et al.* 2021; Greening and Grinter 2022). Collectively, this "microbial carbon pump" regulates greenhouse gas dynamics; methanotrophs alone are estimated to reduce paddy CH_4 emissions by up to 70%, while helping maintain soil carbon resilience under climate change (Zheng *et al.* 2024). Therefore, quantifying the co-distribution of these microbial functional groups (*cbbL*, *pmoA*, and *coxL* carriers) and clarifying their environmental drivers is essential for accurately modeling C-trace gas dynamics (Singh *et al.* 2010; Xu *et al.* 2024), especially since their abundances are strongly correlated with actual gas fluxes (Wu *et al.* 2017b; Lafuente *et al.* 2019; Liao *et al.* 2023).

Despite numerous studies on individual groups or specific sites (Whalen and Reeburgh 2001; Yuan *et al.* 2015; Wu *et al.* 2017b), integrated assessments of these three functional groups across contrasting agricultural ecosystems at continental scales remain scarce (Lafuente *et al.* 2019; Xu *et al.* 2024). Crucially, these groups collectively regulate atmospheric C: *cbbL*-carriers sequester CO_2, *pmoA*-carriers mitigate CH_4, and *coxL*-carriers remove CO. Studying them in an integrated manner provides a holistic view of microbial regulation of climate-relevant C gases (Yuan *et al.* 2015; Nazaries *et al.* 2018). Therefore, elucidating the drivers of their abundance across environmental gradients is paramount for predicting terrestrial C-related greenhouse gas emissions under climate change.

Agricultural lands represent the largest human-managed ecosystems globally and play a vital role in food security. Among these, paddy and upland fields constitute two major yet contrasting systems, often coexisting adjacent to one another in key grain-producing regions such as eastern China (Xia *et al.* 2019; Chen *et al.* 2021). Their fundamental hydrological differences result in distinct environmental conditions that shape microbial communities in divergent ways (Reeve *et al.* 2010; Jiao *et al.* 2020; Zhao *et al.* 2020). Paddy fields, which comprise approximately 25% of China's farmland, experience periodic flooding (Tian *et al.* 2015), creating anaerobic conditions that promote CH_4 production. In contrast, upland systems are predominantly aerobic. Agricultural management practices (e.g., tillage, irrigation, and fertilization) further alter C and nutrient inputs as well as soil physical properties (Zheng *et al.* 2021), thereby influencing microbial community structure and function (Reeve *et al.* 2010; Jiao *et al.* 2020). While larger-scale studies identify climate (temperature, precipitation) and soil properties (e.g., pH and texture) as primary drivers of microbial distributions (Maestre *et al.* 2015; Jiao *et al.* 2020), the co-occurrence patterns and specific environmental controls of *cbbL*-, *pmoA*- and *coxL*-carrying microbes across contrasting agricultural ecosystems at broad geographical scales remain poorly understood (Xu *et al.* 2024).

Furthermore, the *coxL* gene falls into two major phylogenetic types: form I (OMP-type, prevalent in oligotrophic environments and associated with α-, β-, and γ-Proteobacteria, Actinobacteria, and Firmicutes) and form II (BMS-type, frequently dominant in terrestrial soils and associated with a narrower phylogeny of α-Proteobacteria) (King and Weber 2007; Wu *et al.* 2017). Previous research has indicated that CO-oxidizing bacteria are ubiquitous in diverse natural and agricultural soils (King and Crosby 2002; King and Weber 2007; Xu *et al.* 2024), but most molecular surveys have focused on the form-I (OMP) *coxL* gene (Quiza *et al.* 2014). As a result, the abundance patterns and environmental drivers of another major CO-oxidizing group, form-II (BMS) *coxL*-carrying bacteria, remain largely unexplored (Weber and King 2010; Wu *et al.* 2017a).

In this study, we investigated the distribution of CO_2-assimilating (*cbbL*), CH_4-oxdizing (*pmoA*) and CO-oxdizing (*coxL*, BMS) bacterial communities based on 240 pairs of adjacent upland and paddy soils spanning four climate zones (tropics, subtropics, warm temperate, and mid-temperate) across eastern China. We aimed to address the core question: At a continental scale, what are the key drivers controlling the abundances of these C cycling functional genes, and does their relative importance shift between upland and paddy ecosystems? Based on this question, we established two specific objectives: (1) to characterize the abundance patterns of three functional genes in both agricultural systems, and (2) to identify their key biotic and abiotic predictors. Given the contrasting redox and substrate regimes of upland versus paddy systems, we anticipated enrichment of aerobic CO_2 assimilation and CO oxidation in uplands and of methanotrophy in paddies (Zhao *et al.* 2020), and we expected spatial factors to exert stronger influence in uplands whereas community size (total bacteria) and substrate availability would be more influential in paddies.

2. Material and methods

2.1. Field survey and soil sampling

Soil samples were collected from four major climatic zones (tropics, subtropics, warm temperate zone and middle temperate zone) of eastern China represented by four major Soil Orders (Ferralsols, Alisols, Fluvisols and Phaeozems) (Zheng *et al.* 2021). To evaluate the abundance of three

C-cycling genes along the temperate gradient, 10 counties were selected in each climatic zone. And, six sampling sites were selected in each county, giving a total of 240 sites (Zheng *et al.* 2021). All these sites included pairs of adjacent paddy and upland over the past 20 years. The cropping systems in paddy fields were single-rice in both mid temperate and warm temperate, single- or double-rice in subtropics, and double- or triple-rice in tropics. The cropping systems in the upland fields were one season of crops in mid temperate, two seasons in warm temperate and subtropics, and two or three seasons in tropics, respectively, mainly including maize, soybean, wheat, canola, peanut, sweet potato, sugarcane (Zheng *et al.* 2021). Soil samples were collected during fallow seasons across climatic zones: specifically, during December 2016 to January 2017 in the subtropics, January 2017 in the warm temperate zone, April 2017 in the mid-temperate zone, and May 2017 in the tropics (Zheng *et al.* 2021). The surface (0–15 cm depth) soil samples were mixed by 6–8 surrounding soil cores and then transported to the laboratory in coolers with ice bags. The samples were then passed through a 2-mm mesh sieve, after all root residues and stones had been manually removed. Each soil sample was divided into three parts: (1) one part (5–10 g) stored at –80°C for DNA extraction, (2) one part (500 g) stored at 4°C to determine the microbial biomass, and (3) the remaining samples were air dried for soil physicochemical analyses.

2.2. Soil physicochemical analysis

Soil pH was measured in a 1:2.5 (v/v) soil: water suspension with a laboratory pH meter (Mettler-pH 320, Germany). Soil organic C (SOC) was determined by a wet digestion method using potassium dichromate (Nelson and Sommers 1982). Total nitrogen (TN) was measured using the Kjeldahl acid-digestion method (Bremner and Mulvaney 1982) followed by flow injection analysis (FOSS FIAstar 5000). Total phosphorus (TP) was quantified colorimetrically after alkaline oxidation-digestion (Bao 2000). Soil texture analysis was performed with a laser particle size analyzer (Malvern Instruments, UK).

Soil microbial biomass carbon (MBC) and soil microbial biomass nitrogen (MBN) were determined using a fumigation-extraction method based on the difference between carbon and nitrogen extracted with 0.5 mol L^{-1} K_2SO_4 (soil:extraction ratio=1:4) from chloroform-fumigated and unfumigated soil samples using universal conversion factors of 0.45 (Wu *et al.* 1990). The dissolved organic carbon (DOC) was determined using catalytic oxidation and non-dispersive infrared spectroscopy at 680°C (TOC-V CPH, Shimadzu, Japan).

2.3. DNA extraction and quantitative PCR of three C-cycling genes

Soil microbial genomic DNA was extracted from 0.3 g of freeze-dried soil sample using the PowerSoil Kit (MO BIO laboratories, Carlsbad, CA, USA) according to the manufacturer's instructions. The quality and quantity of the DNA dissolved in 30 μL sterilized H_2O were assessed by 1% agarose gel electrophoresis and ultraviolet absorption in a NanoDrop ND-1000 (Thermo Fisher Scientific, Waltham, MA, USA). The DNA extracts were stored at −80°C.

Quantification of the bacterial 16S rRNA gene, and the functional genes (*cbbL*, *coxL* and *pmoA*) involved in C cycling was performed by real-time PCR using the primers 341f/515r (López-Gutiérrez *et al.* 2004), K2f/V2r (Tolli and King 2005), BMSf/O/Br (King 2003) and A189f/mb661r (Kolb *et al.* 2003), respectively (Appendix A). The reaction mixtures containing 5 μL 2×SYBR Premix *Ex Taq* (TaKaRa Bio Inc., Shiga, Japan), 0.4 μL of each primer (10 μmol L^{-1}, Invitrogen, China), 3.2 μL nuclease-free water and 1 μL diluted soil DNA (1:10) amplified in an Roche LightCycler 480 II real-time PCR system (Roche, Rotkreuz, Switzerland). The thermal protocol for bacterial 16S rRNA gene was: 30 s at 95°C followed by 30 cycles of 10s at 95°C, 30 s at 60°C, and 30 s at 72°C. For bacterial *cbbL* genes was: 30 s at 95°C followed by 40 cycles of 10 s at 95°C, 40 s at 62°C, and 30 s at 72°C, followed by a dissociation stage of 95°C for 15 s, 60°C for 15 s, then a ramp up to 95°C. For *coxL* gene, the amplification protocol was 30 s at 95°C, followed by 40 cycles of 15 s at 95°C, 20 s at 62°C, and 20 s at 72°C. For *pmoA* genes, the amplification protocol was 94°C for 3 min, followed by 45 cycles of 94°C for 25 s, 65°C for 20 s, and 72°C for 45 s.

After each run, a dissociation stage was added and melting curves were recorded to discriminate between specific and nonspecific signals. A standard curve was generated using 10-fold serial dilutions of plasmids containing bacterial 16S rRNA, *cbbL*, *coxL* and *pmoA* genes inserts and was carried out in parallel with that for the soil functional genes. Copy numbers of the bacterial 16S rRNA, *cbbL*, *coxL* and *pmoA* genes in the reaction mixture were calculated automatically using Roche LightCycler 480 service software within the real-time PCR system, with reference to the standard curve generated within each run.

Amplification efficiencies ($E=10^{1/-slope}-1$) for bacterial 16S rRNA genes, *cbbL*, *coxL* and *pmoA* were 89.9, 96.2, 95.1, and 88.9%, respectively. All correlation coefficients (R^2) were over 0.99 with intercepts of 34.8–39.3.

2.4. Data analysis

Data of mean annual temperature (MAT) and the mean annual precipitation (MAP) (10 years from 2007 to 2016) were obtained from China Meteorogical Data Sharing Service System (http://cdc.cma.gov.cn/). MAT in the study area ranged from 4.1°C to 24.2°C, and MAP ranged from 555.6 to 1,955.0 mm.

Paired-sample *t*-test was performed to assess the differences of soil physicochemical properties, microbial biomass and the abundance of functional genes between upland and paddy in each climate. All tests used a significance level of P=0.05.

To explore the most important drivers of the abundance of C-cycling functional genes, a classification random forest analysis (RF) (Breiman 2001) was conducted. The total bacterial abundance (16S rRNA gene copies) was treated as a key biotic predictor variable in our models. We reasoned that it represents the overall carrying capacity of the environment, which exerts a top-down constraint on the absolute abundance of specific functional groups within the community. Data of environmental variables and functional

genes abundance were log10-transformed. These analyses were conducted using the Randomforest package (Liaw and Wiener 2002) for the R statistical software, version 4.3.1 (http://cran.r-project.org/). Predictors identified as significant in the RF were further incorporated into the structural equation modeling (SEM, Grace 2006). The fit of SEMs was evaluated using χ^2 values, *P*-values, a high comparative fit index (CFI), and the root mean square error of approximation (RMSEA) (Hooper *et al.* 2008). Based on model fit indices, the most effective predictors were ultimately retained. Due to collinearity issues between spatial distance metrics (longitude and latitude) and climatic indicators (MAT and MAP), only spatial distance metrics were ultimately retained for inclusion in the SEMs. And the direct and indirect effects of geographical location (latitude and longitude), soil properties (pH, clay content and SOC/DOC), and biotic variable (the total bacterial abundance) on the abundance of the *cbbL*, *coxL* and *pmoA* genes were evaluated. The SEMs were performed by using the Amos 21.0 software package (Small Waters Corporation, IL, USA).

3. Results

3.1. Soil physicochemical properties and microbial biomass

Across all climate zones, paddies contained higher SOC and TN than adjacent uplands (Table 1). The level of total soil P was similar in upland and paddy, except for subtropics where it was higher in upland than in paddy. Soil pH was generally higher in paddy than in upland, especially in subtropics and mid-temperate zones. Soil clay content was higher in upland than in paddy with an exception in warm temperate. In tropics and subtropics, upland soils exhibited markedly higher dissolved organic carbon (DOC) levels compared to paddy soils, while microbial biomass carbon (MBC) and nitrogen (MBN) concentrations were significantly greater in paddy systems.

3.2. Abundance of 16S rRNA, *cbbL*, *coxL* and *pmoA* genes

Soil bacterial abundance (16S rRNA gene) was consistently higher in paddy than in upland soils across all climate zones (Appendix B). However, the distribution of microbial functional genes for C-trace gases (*cbbL*, *coxL* and *pmoA*) showed distinct land-use patterns structured by climate (Fig. 1-A–C). The *cbbL* gene exhibited significantly higher abundance in upland soils (averaging 9.46×10^9 copies g^{-1}) compared to paddy systems (6.44×10^9 copies g^{-1}) (Fig. 1-A). Regionally, upland dominance was pronounced in tropical ($P<0.001$) and warm temperate zones ($P<0.05$), whereas subtropics displayed a reversed pattern. No significant differences were observed between land-use types in mid-temperate zone. Paddy soils maintained exceptional *pmoA* gene enrichment (averaging 1.17×10^8 copies g^{-1}) that consistently surpassed upland abundance (5.78×10^6 copies g^{-1}) (Fig. 1-B). Particularly in the subtropics and mid-temperate zones, the abundance of the *pmoA* gene in paddy soils was 1–3 orders of magnitude higher than that in upland soils ($P<0.001$). For the *coxL* gene, comparable average abundances were recorded in both land-use types (6.12×10^8 *vs*. 5.91×10^8 copies g^{-1} in upland and paddy soils, respectively) (Fig. 1-C).

3.3. Correlations among the abundance of *cbbL*, *coxL* and *pmoA* genes

Across the four climates, positive correlations among the abundance of the three functional genes occurred in both upland and paddy soils (Fig. 2-A–C). The abundances of *cbbL* gene were more strongly related with the *coxL* gene in both land uses (R^2=0.38 in upland; R^2=0.48 in paddy) than those with *pmoA* gene (R^2=0.25 in both upland and paddy) (Fig. 2-A and C). Relatively weaker correlations were observed between *pmoA* and *coxL* gene abundances (R^2=0.12 in upland; R^2=0.14 in paddy) (Fig. 2-B).

In upland, stronger correlations among the abundance of *cbbL* to *coxL*

Table 1 Basic soil physicochemical properties and environmental variables in upland and paddy soils across four climates

Variables	Tropics		Subtropics		Warm temperate		Mid-temperate	
	Upland	Paddy	Upland	Paddy	Upland	Paddy	Upland	Paddy
SOC (g kg^{-1})	14.42±4.80	25.38±8.04**	10.86±3.33	22.42±6.04**	10.74±3.93	12.4±3.52*	20.42±15.19	26.88±14.58*
Total N (g kg^{-1})	1.23±0.43	1.98±0.59**	1.05±0.30	2.02±0.54**	1.08±0.36	1.23±0.34*	1.34±0.34	1.94±0.93**
Total P (g kg^{-1})	1.04±0.65	0.98±0.58	0.80±0.31	0.65±0.19**	0.97±0.23	1±0.27	0.87±0.25	0.84±0.28
pH	5.25±0.7	5.35±0.41	5.17±0.68	5.35±0.70	7.13±0.97	7.23±0.61	5.61±0.56	6.72±0.67**
Clay (%)	16.38±8.89	7.27±4.12**	12.71±3.22	7.57±2.62**	6.76±1.95	7.8±2.99**	9.81±1.38	7.95±2.02
Silt (%)	66.89±8.98	70.3±6.54**	75.03±4.81	69.60±4.40**	66.11±7.84	64.67±9.94	70.77±3.52	65.2±6.64
Sand (%)	16.73±9.18	22.43±6.61**	12.31±6.30	22.82±5.65**	27.13±9.18	27.53±12.04	19.42±4.24	26.85±7.94
DOC (mg kg^{-1})	71.49±56.83	19.75±16.35**	84.19±48.32	45.12±30.25**	88.27±32.38	106.53±61.61*	39.23±8.75	37.65±13.37
MBC (mg kg^{-1})	245.64±174.18	517.87±251.96**	184.30±75.49	623.59±310.06**	285.53±148.78	311±174.63	168.92±54.70	202.47±101.72*
MBN (mg kg^{-1})	31.64±23.76	42.47±19.38*	35.30±20.31	62.41±25.44**	45.01±32.97	52.80±29.18	26.77±15.31	26.54±15.31
MAT (°C)	24.2±0.7	24.2±0.7	18.3±0.6	18.3±0.6	14.9±0.4	14.9±0.4	4.1±1.1	4.1±1.1
MAP (mm)	1,955.0±256.0	1,955.0±256.0	1,569.9±247.6	1,569.9±247.6	693.5±109.4	693.5±109.4	555.7±47.5	555.7±47.5

Data are mean±SD (n=60). The significant differences between upland and paddy soils based on paired *t*-test are denoted by asterisks (**, $P<0.01$; *, $P<0.05$).

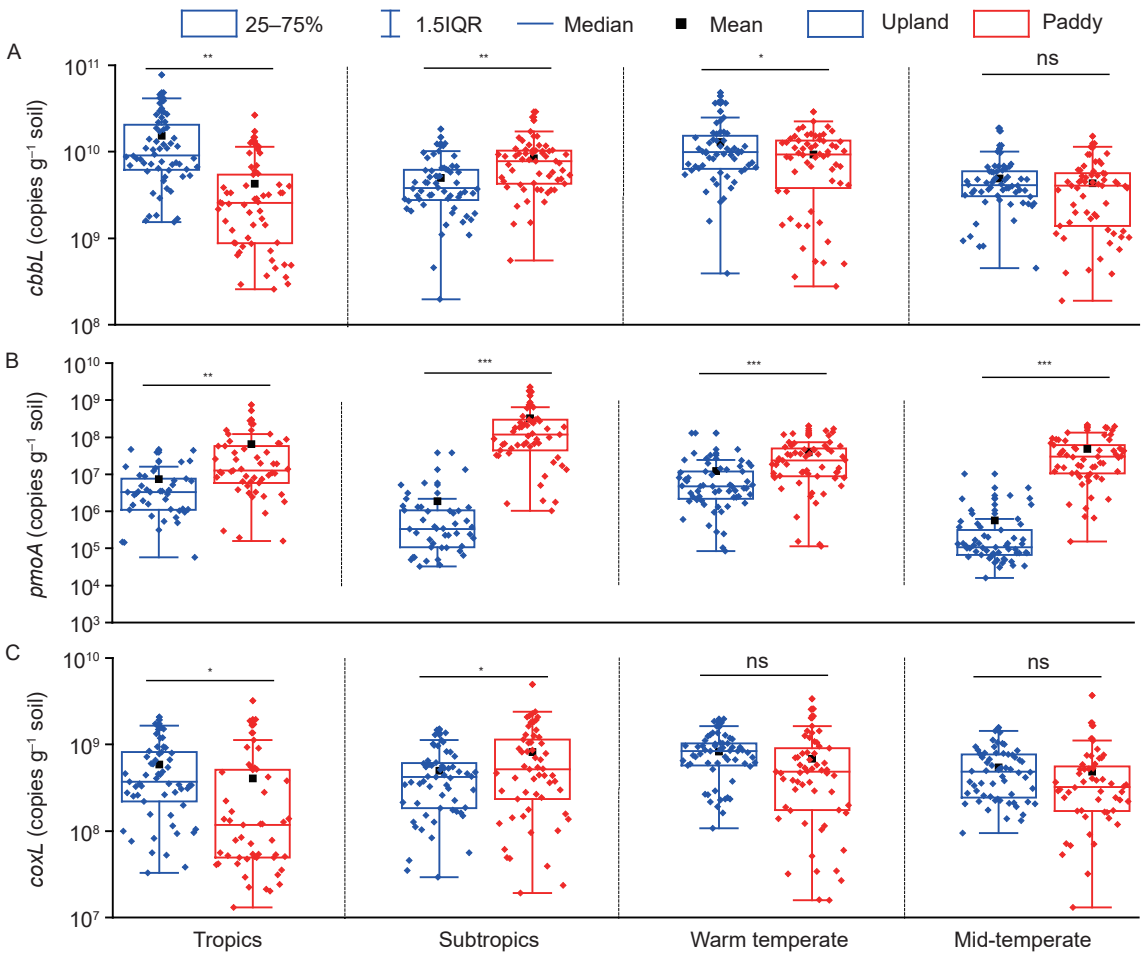


Fig. 1 Abundances of *cbbL*, *pmoA* and *coxL* gene in paddy and upland soils across eastern China. Significant differences between upland and paddy soils based on paired *t*-test are denoted by asterisks (***, $P<0.001$; **, $P<0.01$; *, $P<0.05$); ns, no significant difference.

were also found in each climatic zone (Appendix C). However, only weaker relationships of *cbbL* to *pmoA* and *pmoA* to *coxL* were found in tropics. In paddy, positive correlations among three functional genes were found in each climatic zone except the *cbbL* to *pmoA* in subtropics (Appendix C).

3.4. Environmental factors controlling abundances of *cbbL*, *coxL* and *pmoA* genes

Random forest analyses showed 12, 15 and 7 out of 18 predictors in upland significantly affected the abundance of *cbbL*, *pmoA* and *coxL*, respectively, and accounted for 32.36–48.11% of total variances (Fig. 3-A, C and E). For *cbbL* gene, total bacterial abundance was the dominant drivers, followed by latitude, clay, longitude, MAT and MAP (Fig. 3-A). Latitude, pH and MAT were the important drivers for the distribution of *pmoA* gene, followed by longitude, clay and bacteria (Fig. 3-C). The abundance of *coxL* gene was mainly driven by total bacterial abundance (Fig. 3-E). In paddy, 9, 8 and 7 out of 18 predictors significantly influenced the abundance of three C-cycle functional genes respectively (Fig. 3-B, D and F), explaining 23.56–43.26% of total variance, with total bacteria abundance being the universal key predictor governing all three genes.

SEMs were further used to identify the direct, indirect influences on the *cbbL*, *pmoA* and *coxL* genes (Fig. 4-A–F). In upland, the models explained 28, 48 and 23% of total variance for the abundance of *cbbL*, *pmoA* and *coxL*, respectively, whereas the corresponding values were 46, 21 and 28% for paddy. The main predictors for these gene abundances were different between paddy and upland, especially for *cbbL* and *pmoA* gene. For example, spatial coordinates of latitude and longitude had converse effects on these two gene abundances between upland and paddy (Fig. 5-A–D). Bacterial abundance had greater positive effects on all these three genes in paddy than upland. The significant correlations between bacterial abundance and the three functional gene abundances further corroborate this finding, with notably stronger associations observed in paddy soils compared to upland soils (Appendix D). Generally, clay exerted negative influences on the gene abundances in upland, whereas DOC had positive effects in paddy.

The spatial distances explained the greatest proportion of the variance in the abundance of *cbbL* and *pmoA* gene in upland, with minor contributions from clay and total bacteria abundance (Fig. 5-A and C). However, the relative

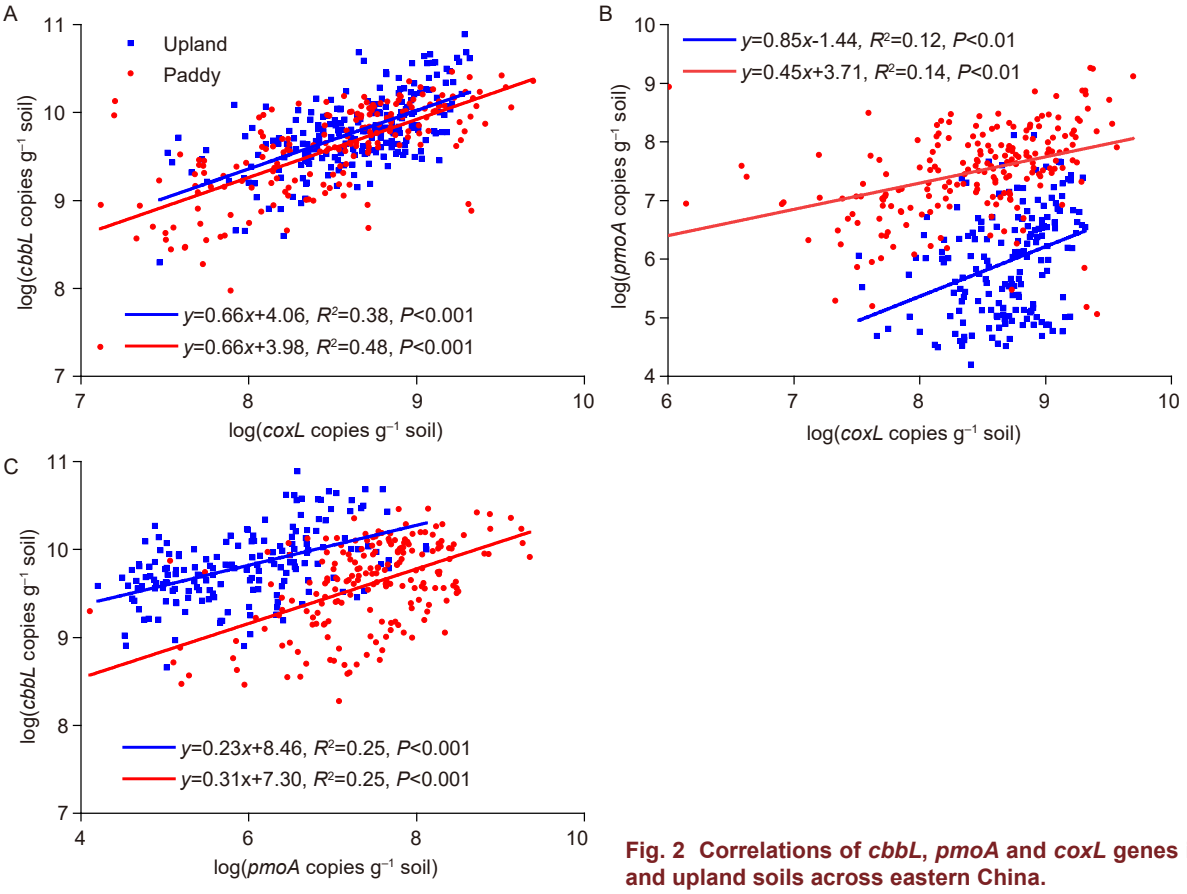


Fig. 2 Correlations of *cbbL*, *pmoA* and *coxL* genes in paddy and upland soils across eastern China.

importance of spatial distance decreased in paddies, even though we observed significant negative quadratic relationships between latitude and the abundance of both *cbbL* and *pmoA* gene in paddy soil (Appendixes E and F). Instead, the total bacteria explained the largest of proportion of variance for *cbbL* and *pmoA* genes (Fig. 5-B and D). For *coxL* gene, the contribution from total bacteria abundance was also higher in paddy than in upland soils (Fig. 5-C and F). Significantly negative quadratic relationships between *coxL* gene abundance and latitude/longitude as well as MAT were also observed in both upland and paddy (Appendix G).

4. Discussion

4.1. Land-use mediated ecological drivers of C-cycling functional genes

Our continental-scale analysis reveals macroscopic patterns in the abundance of carbon-cycling functional genes, underscoring the value of large-scale approaches in uncovering biogeographic patterns often obscured in local studies. While climate and soil properties are known to shape these microbial communities (Guo *et al.* 2015; Lafuente *et al.* 2019), our findings demonstrate a fundamental divergence in their primary drivers between upland and paddy ecosystems.

In upland systems, the spatial distance explained the largest proportion of variance in *cbbL* and *pmoA* gene abundances (Figs. 3 and 4). This strong spatial signal suggests pronounced dispersal limitation and potential historical contingency in shaping these microbial communities (Xiong *et al.* 2012). This pattern likely arises from limited microbial dispersal between isolated upland habitats and stronger environmental filtering under aerobic conditions (Li *et al.* 2024), aligning with the concept that geographical barriers and historical colonization significantly influence microbial biogeography in well-drained ecosystems (Martiny *et al.* 2006). These results confirm our second hypothesis that geographic filtering predominates in uplands.

In contrast, in paddy systems, the importance of spatial factors diminished, with total bacterial abundance and DOC emerged as the dominant predictors (Figs. 3 and 4). This shift indicates a substrate-driven community assembly under flooded conditions, promoting niche convergence. These patterns are consistent with reports that distinct phylogenetic lineages of CO_2-assimilating bacteria and methanotrophs dominate in upland versus paddy soils (Knief 2015; Liao *et al.* 2023), reflecting fundamental niche partitioning driven by oxygen availability and energy conservation strategies. Our multi-climate zone comparison demonstrates that climate-land use interactions override purely local effects in determining microbial functional distributions.

Integrated modeling (RF and SEM) further revealed that these microbial responses to agricultural management are mediated by metabolic constraints across climate zones. The dominance of *cbbL* (Calvin-cycle) and *coxL* (CO-oxidizing) genes in aerobic uplands, particularly in the tropics, indicates preferential selection for taxa adapted to fluctuating redox conditions (Yuan *et al.* 2012, 2013). Although MAT/MAP were excluded from SEM due to collinearity with longitude/latitude, their importance in RF (Fig. 3-A–F) confirms temperature-

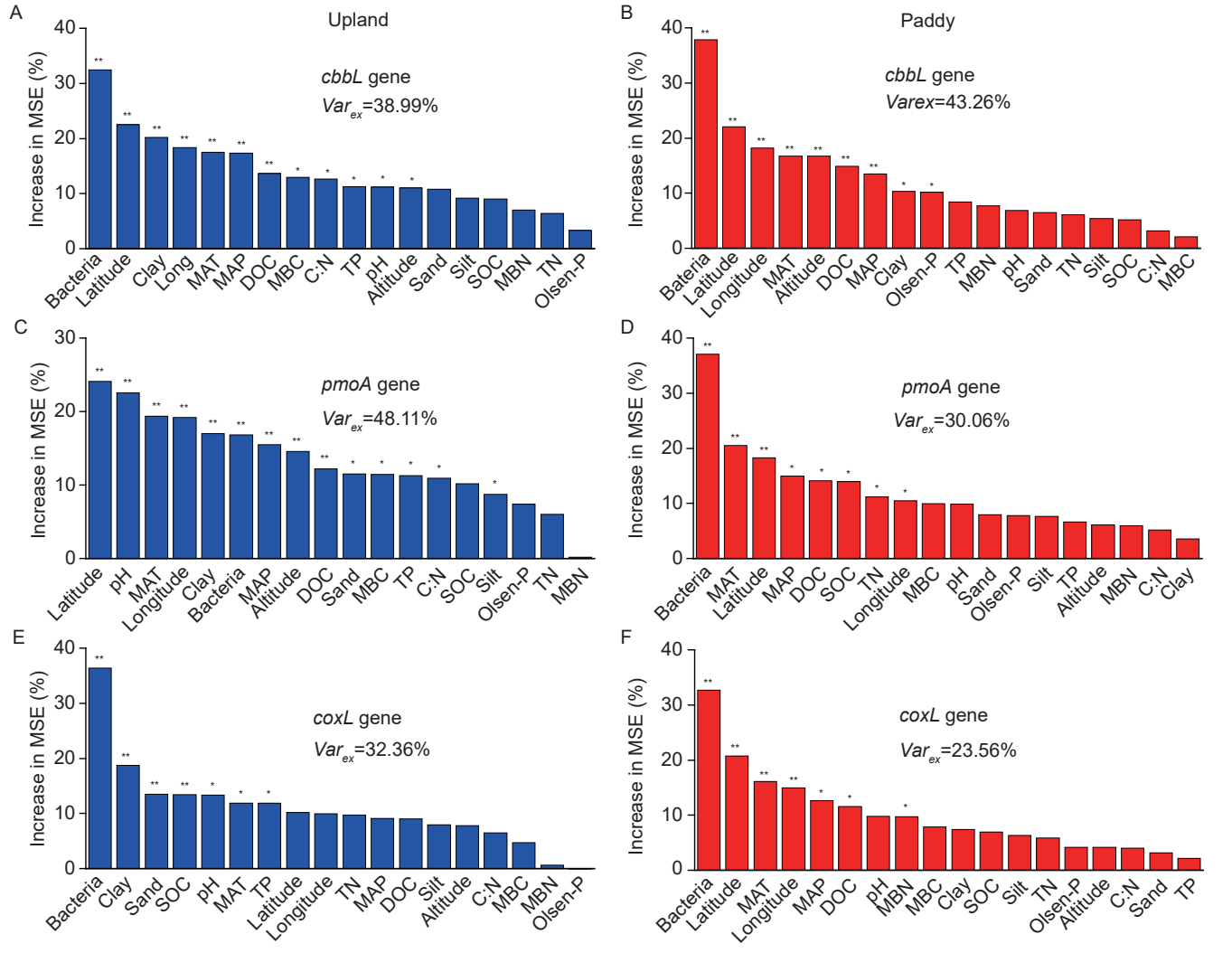


Fig. 3 Random forest mean predictor importance of environmental variables on the abundance of *cbbL*, *pmoA* and *coxL* genes among paddy and upland soils. This accuracy importance measure was computed for each tree and averaged over the forest (5,000 trees). Significant factors are donated by asterisks (**, P<0.01; *, P<0.05). Bacteria, total bacteria abundance; SOC, soil organic carbon; MAT, mean annual temperature; MAP, mean annual precipitation; TP, total phosphorus; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; DOC, dissolved inorganic carbon.

moisture co-regulation of aerobic processes (Xiao *et al.* 2014). The strong positive correlation between *cbbL* gene abundance and RubisCO activity observed in previous studies (Yuan *et al.* 2012; Xiao *et al.* 2014) suggests that soils with high *cbbL* gene abundance may support greater CO_2 fixation potential.

The *coxL* gene exhibited land-use responses parallel to those of *cbbL* across climate zones (Fig. 1-A and C), reflecting conserved microbial habitat adaptation strategies (King and Weber 2007; Xu *et al.* 2023). This convergent response implies coordinated ecological selection pressures, where both chemoautotrophic CO oxidizers (*coxL*) and Calvin-cycle autotrophs (*cbbL*) appear to favor aerobic upland conditions in the tropics, while shifting toward flooded paddy environments in subtropical regions. Such adaptations likely reflect metabolic trade-offs between oxygen tolerance, substrate availability, and energy conservation across temperature-moisture gradients (Xu *et al.* 2023).

Most strikingly, *pmoA* genes were consistently enriched by 1–3 orders of magnitude in paddy soils. This can be directly attributed to CH_4 supersaturation under flooded conditions (Bridgham *et al.* 2013), where methanogenic activity elevates porewater CH_4 concentrations far exceeding atmospheric levels (Eller and Frenzel 2001; Dlugokencky *et al.* 2011). Thus, paddy fields provide abundant substrate that sustains larger populations of methane-oxidizing bacteria (Zhao *et al.* 2020; Zheng *et al.* 2024), confirming our first hypothesis regarding the enrichment of methanotrophy in paddies.

4.2. Ecological linkages among *cbbL*, *pmoA* and *coxL* genes

The significant positive correlations among *cbbL*, *pmoA*, and *coxL* gene abundances (Fig. 2-A–C) suggest functional synergisms within microbial communities involved in the oxidation and assimilation of trace carbon gases, supporting the concept of a “microbial carbon pump”. The strong correlation between *cbbL* and *coxL* abundances indicates tight functional coupling between CO_2 fixation and CO

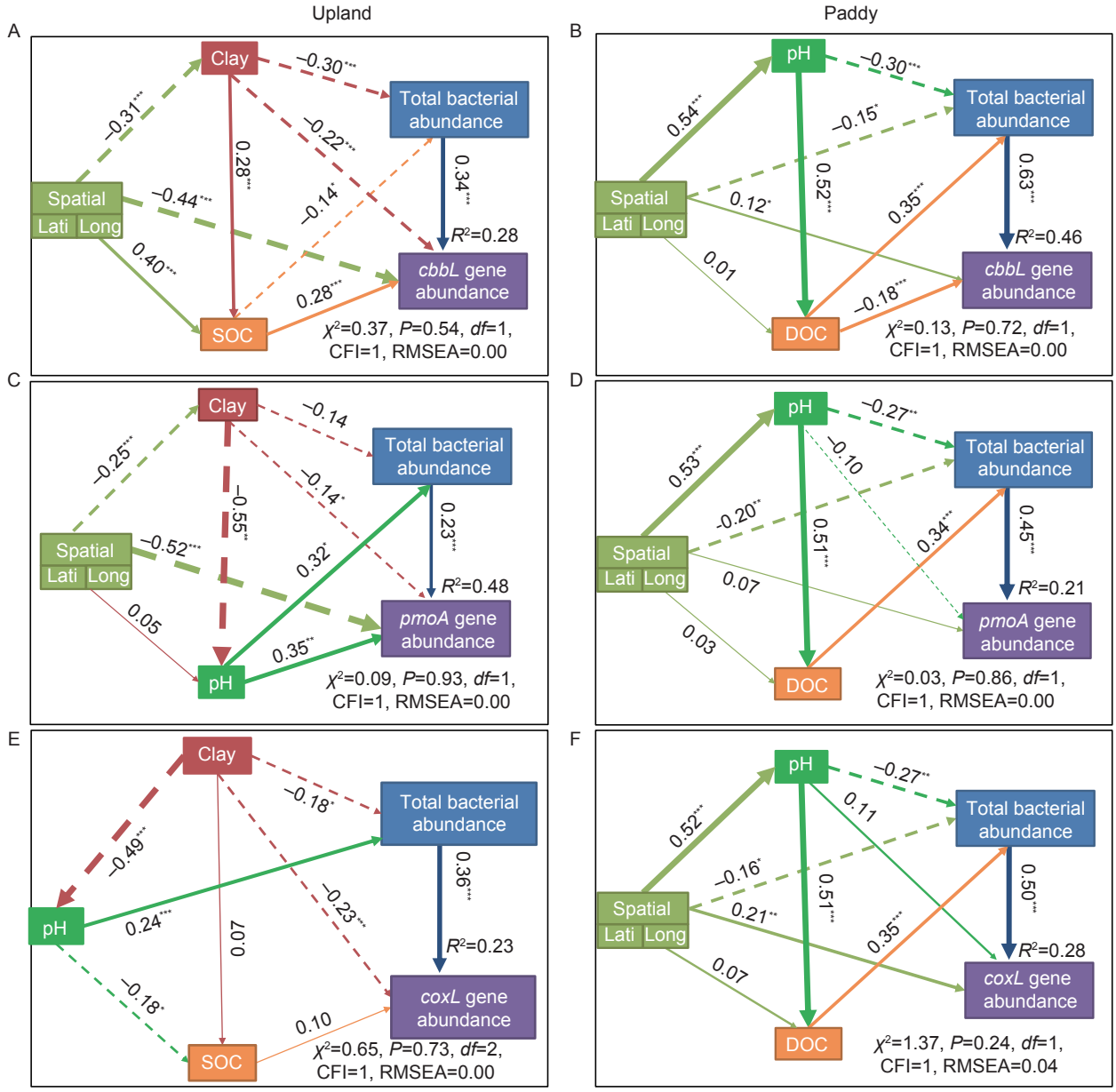


Fig. 4 Structural equation modeling showed the relationships of environmental factors to the abundance of functional genes in upland (A, C and E) and paddy (B, D and F) soils. The spatial coordinates of the study sites are given as latitude (Lati) and longitude (Long). Numbers adjacent to arrows are standardized path coefficients, analogous to relative regression weights, and indicative of the effect size of the relationship. Significances are denoted by asterisks (***, $P<0.001$; **, $P<0.01$; *, $P<0.05$). Solid and dashed arrows indicate positive and negative relationships, respectively. Arrow width indicated the strength of the relationship. The proportion of variance explained (R^2) appears alongside each endogenous variable in the model. Goodness-of-fit statistics for each model are shown in the lower right corner (*df*, degrees of freedom; RMSEA, root mean squared error of approximation).

oxidation (Cordero *et al.* 2019; Tveit *et al.* 2019; Bay *et al.* 2021). This is consistent with reports that many CO-oxidizing bacteria (e.g., *Bradyrhizobium*, *Burkholderia*) possess both *coxL* and *cbbL* genes, enabling simultaneous CO oxidation and CO_2 fixation *via* the Calvin cycle (King and Weber 2007). This metabolic integration allows energy derived from CO oxidation to support biomass synthesis (Cordero *et al.* 2019; Leung *et al.* 2024), explaining their co-occurrence.

Similarly, the significant positive correlation between *cbbL* and *pmoA* abundances (R^2=0.25, P<0.01, Fig. 2-C) points to ecological interactions between CO_2-fixing and CH_4-oxidizing microbes, potentially mediated through several mechanisms: (1) Cross-feeding synergy. Methanotrophs (*pmoA*-harboring) oxidize CH_4 to methanol, which may serve as a carbon source for *cbbL*-containing bacteria (Tveit *et al.* 2019). (2) Shared habitat preferences. Both functional types thrive under aerobic conditions (Tolli and King 2005; Knief 2015), leading to co-occurrence under similar redox gradients. (3) Dual-functional taxa. Some proteobacteria (e.g., *Methylocapsa*) possess both *pmoA* and *cbbL* genes (Tveit *et al.* 2019), enabling them to participate in both processes. These linkages underscore the interconnected

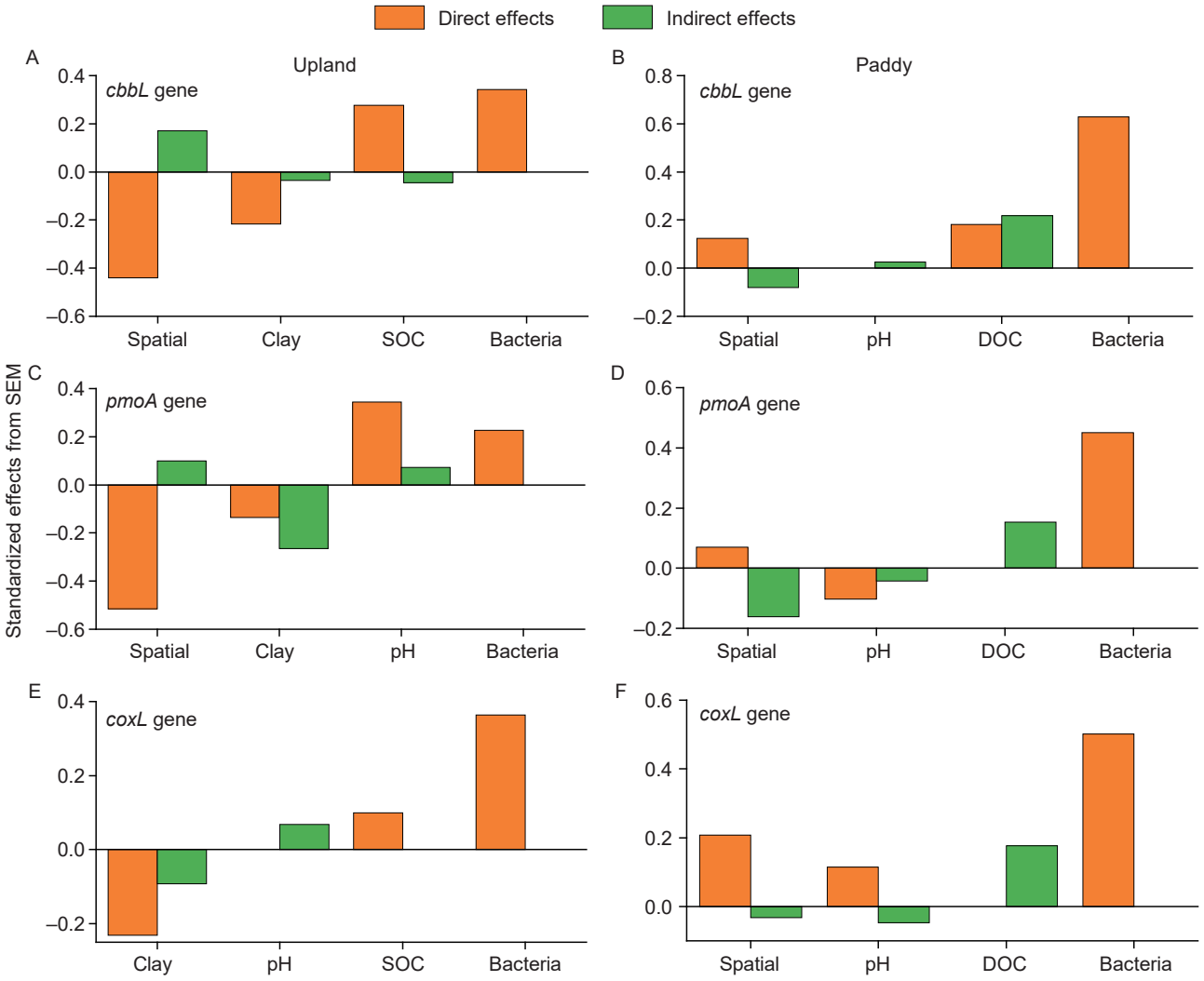


Fig. 5 Standardized direct and indirect effects derived from the structural equation modeling (SEM). Spatial, the first principal component (PC1) from a rincipal component analysis of latitude and longitude, representing the primary axis of geographic variation; SOC, soil organic carbon; DOC, dissolved inorganic carbon; MAT, mean annual temperature; Bacteria, total bacterial abundance.

nature of microbial carbon transformations in soil.

4.3. Uncertainties and research needs

This study provides the first continental-scale assessment of the co-distribution of these functionally linked microbial groups across contrasting agricultural ecosystems. The high abundances of *cbbL* and *coxL* genes observed across climates underscore the significant role of microbial CO_2 fixation and CO oxidation in agricultural carbon cycling (Liao *et al.* 2023; Xu *et al.* 2024). Our findings demonstrate that the integration of multi-climate zone sampling with paired upland-paddy comparisons offers a powerful framework for unraveling the complex interplay between microbial function, land use, and climate (Fig. 6).

Microbial metabolism of atmospheric trace gases represents a critical nexus between microbial ecology and global biogeochemistry (Bay *et al.* 2021; Greening and Grinter 2022). While our study reveals robust spatial and environmental relationships, key questions remain. Future research should focus on how microbial taxonomic and functional diversity *in situ* mediates gas assimilation rates, and how these processes respond to environmental perturbations, particularly under the escalating impacts of climate change on agricultural systems. The empirical relationships identified here provide a solid foundation for predicting the responses of these critical microbial functions to future environmental scenarios.

5. Conclusion

We present a continental-scale investigation of *cbbL*, *pmoA* and *coxL* genes across paired upland-paddy soils and identify ecosystem-specific controls. First, we demonstrate that *cbbL*, *pmoA*-, and *coxL*-associated microorganisms are ubiquitous in agricultural soils spanning diverse climate zones, underscoring the necessity of incorporating these functional groups into terrestrial biogeochemical models. Second, we provide robust empirical evidence that geographic factors (longitude and latitude), climatic variables (mean annual temperature and precipitation), and soil properties (e.g., SOC, DOC, pH, and clay content) serve as key predictors of

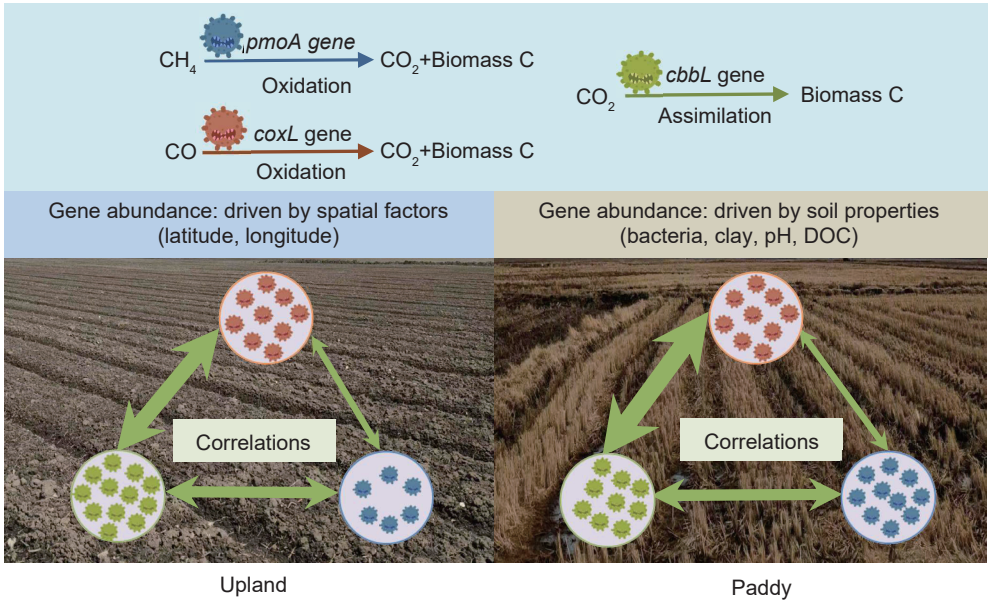


Fig. 6 Conceptual framework of drivers and processes governing C-trace gases microbial functional genes in contrasting agricultural ecosystems. The number of icons indicates gene abundance, and the thickness of the arrows indicates the intensity of correlations. DOC, dissolved organic carbon. In upland system, gene abundance is primarily driven by geographical factors (latitude and longitude). In paddy system, genes abundance is primarily driven by soil properties (e.g., bacterial abundance, clay, pH, and DOC).

the abundances of these functional genes. Notably, we found that CO_2-assimilating bacteria and methanotrophs in upland soils exhibit greater sensitivity to these environmental drivers compared to those in paddy systems. Finally, the consistently high abundance of *cbbL* and *coxL* genes in both upland and paddy soils across climatic gradients suggests that the contribution of microorganisms to the cycling of carbon trace gases may have been substantially underestimated in previous studies. These findings enhance our understanding of the large-scale spatial distribution and ecological drivers of microbial functional groups involved in carbon gas transformations, providing a critical foundation for predicting ecosystem-level responses to environmental change.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this manuscript, the authors used DeepSeek web version to assist in improving the clarity and readability of the language during the preparation of this manuscript. All content generated was carefully reviewed and revised by the authors as necessary, and the authors take full responsibility for the final content of the article.

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