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Land use change affects soil methane sink capacity of Brazilian biomes

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Abstract

Soils are the only biological sink for atmospheric Methane (CH_4), making microbial methane consumption a dynamic component of the global carbon cycle. However, land-use change toward agriculture can inhibit this process, partly due to the application of NH_4^+-based fertilizers. To assess whether this effect contributes to reductions in CH_4 uptake following land-use change in Brazilian biomes, we incubated soils from natural and cultivated areas across four endangered biomes: Caatinga, Cerrado, Pampas, and Atlantic Forest. Among soils exhibiting net CH_4 uptake, natural soils oxidized an average of 11.9 µg C kg^{-1} soil day^{-1}. Ammonium sulfate addition reduced CH_4 oxidation by 33% in pristine soils, whereas soils from agricultural fields showed no detectable methane uptake. With the exception of the Caatinga biome, pristine soils consumed atmospheric CH_4 and harbored higher abundances of methanotrophic bacteria compared to managed soils. Our findings indicate that nitrogen addition, at levels typical of NH_4^+-based fertilization, had a less pronounced effect on CH_4 uptake than land-use change itself, underscoring the importance of conserving natural ecosystems to support the CH_4 cycle. Furthermore, soil nutrient availability, particularly micronutrients, emerged as a potential regulator of methanotrophy, capable of either stimulating or inhibiting microbial methane consumption. In the context of accelerated climate change in the tropics and globally, it is imperative to rethink agricultural practices, biomass production models, and land-use and fertilization strategies to minimize potential increases in greenhouse gas emissions.

Keywords Caatinga, Cerrado, Atlantic forest, Pampas, Greenhouse gases, Methanotrophy

1 Introduction

Atmospheric concentrations of carbon dioxide (CO_2), methane (CH_4) and nitrous oxide N_2O have been rising since the 18th century, marking the onset of the industrial era, with CH_4 being the most rapidly increasing: from 719 ppb in 1750 to 1895 ppb in 2021 [1, 2]. Currently, about 22% of global warming is attributed to atmospheric CH_4 [2]. Soils act as the only biological sink for atmospheric CH_4, although this biological sink represents only a relatively small fraction of the total global CH_4 sink, accounting for approximately

31 Tg CH_4 yr^{-1} uptake [3, 4]. Despite its limited contribution in global terms, the biological sink remains relevant because changes in soil CH_4 uptake can reflect shifts in overall soil microbial activity, underscoring the importance of understanding the microbial processes that regulate CH_4 oxidation.

An important driver of methane-cycling microbes and CH_4 emissions is agricultural management and the associated vegetation cover [5]. The conversion of natural ecosystems into agricultural land has been associated with increased CH_4 emissions [5, 6]. CH_4 fluxes are determined by the balance between production and oxidation, mediated by methanogens under anoxic conditions and methanotrophs under oxic conditions [7]. Changes in edaphic conditions and environmental disturbances can also alter the rates of CH_4 production and consumption [8].

In Brazil, increasing anthropogenic pressure and the demand for biomass have led to the progressive loss of natural areas across biomes such as the Amazon Rainforest, Atlantic Forest, Cerrado, Pampas, and Caatinga, which have been converted into agricultural landscapes with intensive use of mineral fertilizers [9–13]. The effects of inorganic nitrogen (e.g., ammonium (NH_4^+) and nitrate (NO_3^-)) are known to regulate soil CH_4 oxidation through multiple mechanisms [14], and nitrogen addition has been shown to negatively affect both bacterial and fungal diversity [15]. The intensity of these impacts depends on the specific ecosystem, management practices, soil properties, pH, temperature, and the amount of nitrogen applied [15, 16]. Additionally, the toxicity of nitrite (NO_2^-), nitric oxide (NO) end nitrous oxide (N2O), produced during NH_4^+ oxidation, to methane-oxidizing microbial communities is well established and may further suppress CH_4 uptake [17].

Historically, the Atlantic Forest originally covered 150 million hectares, but it has undergone massive conversion since the beginning of the industrial era [18]. Other biomes are at the agricultural frontier, where advancements in crop breeding and agronomic techniques have made agriculture viable and competitive even under challenging climatic and soil conditions [19, 20]. Much of the research and public concern regarding land-use change has focused on the Amazon Rainforest [21], yet other biomes are also under significant pressure [19, 20, 22]. For instance, the Cerrado and Caatinga lost 26.6 and 9.0 million hectares of natural vegetation, respectively, between 1990 and 2010 [19]. These values represent approximately 14–15% (Cerrado) and 12% (Caatinga) of all deforestation recorded nationally during that period, indicating that their contribution to total land-cover loss is substantial.

Similar to the Atlantic Forest, the Cerrado is a biodiversity hotspot, originally occupying around 200 million hectares in Brazil [22]. The Caatinga, an exclusively Brazilian biome, covers approximately 73.5 million hectares and is characterized by semiarid climate and xerophytic vegetation [23]. Despite its ecological uniqueness and extent, the Caatinga has received little scientific attention [24]. The Pampas represent Brazil's subtropical native grasslands, covering about 13.7 million hectares, of which nearly 25% had been converted to cropland by the early 21 st century [25]. Assessing the impacts of land-use change on ecosystem services is essential to inform policies that balance conservation and production in natural and managed landscapes [26].

Among the most uncertain outcomes of converting natural ecosystems into agroecosystems is the net balance of carbon and greenhouse gases. For instance, land-use change can enhance soil carbon stocks in well-managed systems, particularly in soils

under perennial crops [27, 28]. Conversely, agriculture may reduce soil CH_4 uptake capacity [29, 30]. However, the cause–effect relationship between soil management and CH_4 cycling remains unclear. Levine et al. (2011), for example, demonstrated a link between microbial diversity, agricultural history, and CH_4 uptake [30]. Reduced CH_4 uptake in agricultural soils may be due to nitrogen addition, as NH_4^+ and CH_4 oxidation are mediated by the same enzyme, methane monooxygenase (MMO), in methane-oxidizing bacteria (MOB), despite no energy gain from NH_4^+ oxidation [17]. In fact, NH_4^+ competes with CH_4 for the enzyme active site, potentially inhibiting CH_4 oxidation [17]. Intriguingly, Goldman et al. (1995) observed a strong positive correlation between natural soil NH_4^+ and CH_4 uptake at NH_4^+ levels below those typically applied in agricultural fields, and no microbial group is currently known to facilitate simultaneous beneficial oxidation of both NH_4^+ and CH_4 [31].

Considering the undergoing changes in the Brazilian biomes, we hypothesize that natural soils have a higher capacity to oxidize CH_4, but that land-use change, and NH_4^+-based fertilizer application reduce this capacity. To test this hypothesis, we investigated soils from four Brazilian biomes using a paired design comparing adjacent natural and agricultural sites (Fig. 1). By law, a fraction of the agricultural properties in Brazil is kept undisturbed as reserve. Usually, this fraction is distributed in fragments along the cropping area in the property. Therefore, the sampling points for the natural and agricultural sites were just few steps away from each other, minimizing the spatial variability of the

Fig. 1 Distribution of paired natural and adjacent cultivated areas where soils were sampled. Geographic coordinates for each site are provided in the Supplementary Material (Table S1)

soil. We also applied ammonium sulfate to test the effect of NH_4^+ addition on CH_4 oxidation. Understanding the impacts of land-use change on CH_4 cycling is crucial for evaluating ecosystem service trade-offs and guiding sustainable management.

2 Methods

2.1 Experimental design

Soils were sampled from four Brazilian biomes, Atlantic Forest, Cerrado, Caatinga, and Pampas, in paired natural and adjacent cultivated areas (Fig. 1; Table S1, Supplemental Material). Regardless of crop type, all cultivated sites included in the study received fertilizer at least once per year, as a criterion for inclusion in the experimental design. In total, 11 sites met this criterion: three with perennial crops, two with semi-perennial crops (sugarcane), and six with annual or rotational crops. The experimental design comprised four treatments: natural soil, natural soil with nitrogen amendment, cultivated soil, and cultivated soil with nitrogen amendment. This design allows us to test whether land use, nitrogen amendment, or their interaction affects soil CH_4 uptake.

2.2 Soil sampling and processing

Sampling was conducted in autumn 2016, after crop harvest or during crop senescence, in order to avoid acute or residual effects of fertilizer application. At each site, composite samples of approximately 20 kg of soil were collected using hand augers (0–20 cm depth). Samples were transported to the laboratory, homogenized, air-dried and sieved (2 mm). For chemical analyses, subsamples of approximately 4 kg of soil were used, following the standard requirements of the Agronomic Institute of Campinas protocol for routine soil analysis. Soil available P, Ca^{2+}, Mg^{2+}, Al^{3+}, pH, and micronutrients were determined following the procedures described by van Raij et al. (2001) [32]. Inorganic nitrogen was measured colorimetrically in 2 M KCl extracts, using the methods of Norman et al. (1985) for NO_3^- and Krom (1980) for NH_4^+ [33, 34]. Total soil organic C and N were quantified using an elemental analyzer (PerkinElmer CHN 2400, Waltham, USA). Soil texture and chemical parameters are presented in the Supplementary Material (Table S2).

Microcosms (n = 4 per treatment) for gas measurements were assembled as described by Pitombo et al. (2018) and maintained in a climate-controlled room at 25 ± 2 °C [35]. Soil density was used to calculate the dry soil mass required to fill each microcosm with 300 mL of bulk soil. A one-week pre-incubation period at 40% water-filled pore space (WFPS) was applied to allow microbial community stabilization. For treatments receiving nitrogen, soils were amended with an $(NH_4)_2SO_4$ solution to achieve a concentration of 100 mg N kg^{-1} soil, consistent with typical levels found in cropped soils following fertilization and commonly used in microcosm experiments. As noted by Pitombo et al. (2018), this amount is equivalent to approximately 50 kg N ha^{-1} [35].

After pre-incubation, and for all treatments, WFPS was adjusted to 45%, which approximates the optimal condition for soil CH_4 oxidation [36]. During both pre-incubation and the gas sampling phase, 5 mg of carbon, in the form of an artificial root exudate solution without nitrogen (van Zwieten et al., 2014), was added daily to each microcosm to sustain basal soil respiration [37]. Soil moisture was subsequently maintained by adjusting the water content based on the weight of the microcosms.

2.3 Methane fluxes

After the pre-incubation period, CH_4 fluxes were measured daily over a period of ten days. Microcosms were closed only during sampling to avoid gas saturation. Headspace gas samples were collected at 1, 30, 60, and 90 min after closure using 20 mL syringes. CH_4 concentrations were determined by gas chromatography (GC-2014, Shimadzu, Kyoto, Japan) equipped with a flame ionization detector. The entire sample volume (20 mL) was injected directly into the chromatograph inlet, which included a sample loop to standardize the volume analyzed.

The instrument was calibrated daily using three certified standards (0.92, 1.81, and 3.58 ppm), and the limit of quantification for CH_4 was 0.1 ppm. Gas fluxes were calculated by fitting linear regressions of CH_4 concentration over time. Further details regarding sampling procedures, quality control, and flux calculations can be found in Pitombo et al. (2018) [35].

2.4 Soil DNA extraction and Real-Time PCR

After the gas flux measurement period, soil samples from the microcosms were frozen at − 20 °C for molecular analyses. DNA was extracted from 250 mg of soil using the PowerSoil DNA Isolation Kit (MoBio Laboratories, Carlsbad, USA) following the manufacturer's protocol. DNA quantity and quality were verified on a 2% agarose gel and with a Synergy HTX microplate reader (BioTek Inc., Winooski, VT, USA) by measuring absorbance at 230, 260, 280, and 320 nm.

The abundance of the particulate methane monooxygenase gene (pmoA), which encodes a key enzyme in both type I and type II methanotrophs, was quantified by quantitative real-time PCR (qPCR). The primer pair pmof1 (5'-AACTTCTGGGGNTGGAC-3') and pmor (5'-RCNACGTCNTTACCGAA-3'), originally developed by Cheng et al. (1999) and modified by Stoecker et al. (2006) to increase the degeneracy of the forward primer, was used to amplify pmoA [38, 39]. This primer set targets both type I and type II methanotrophs and was chosen to evaluate the overall effect of land-use change on methanotroph abundance.

The qPCR reactions were performed on a QuantStudio 3 Real-Time PCR System (Applied Biosystems, Foster City, CA, USA) in a total reaction volume of 10 µL, using SYBR® Green JumpStart™ Taq ReadyMix (Sigma-Aldrich, St. Louis, MO, USA) supplemented with the appropriate reference dye. The annealing temperature was set at 58 °C, data were acquired during the extension step at 72 °C, and melting curve analysis was conducted to verify product specificity.

A pool of sequenced pmoA amplicons from environmental samples was used as the standard for gene quantification. The number of amplicons per µL in the standard was determined by fluorescence-based quantification using the Quant-iT™ dsDNA Assay Kit (Invitrogen, Carlsbad, CA, USA). Standards were analyzed in triplicate, while sample reactions were run in two technical replicates, in addition to the experimental replication ($n = 4$).

2.5 Statistical analyses

Analysis of variance (ANOVA), followed by Tukey's post hoc test, was used to assess both main effects and pairwise differences in CH_4 fluxes across land-use types and nitrogen addition treatments. The same statistical approach was applied to test the effect of

land use on the abundance of the methane monooxygenase-encoding gene. To explore whether biomes or soil parameters drove differences in CH_4 uptake and gene abundances, we performed a non-metric multidimensional scaling (NMDS) ordination based on Euclidean dissimilarities of normalized data.

Subsequently, Generalized Linear Mixed Models (GLMMs; Bolker et al., 2009) were used to evaluate the influence of soil parameters on CH_4 oxidation rates [40]. The global model,, which included all potential explanatory variables, was fitted using the lme4 R package (version 1.1–10; Bates et al., 2015), with replicate included as a random effect [41]. Model selection was based on the Akaike Information Criterion (AIC), ranking all model combinations using the MuMIn R package (version 1.15.6; Barton, 2016) [42]. Coefficients of determination (R^2) were calculated following Johnson (2014) [43]. To facilitate interpretation of effect sizes, all data were normalized (scaled between 0 and 1) prior to analysis.

3 Results

3.1 Methane flux

The results of the incubation experiment are presented in Fig. 2. Overall, land-use change significantly inhibited soil CH_4 oxidation ($p < 0.001$). This effect was evident in

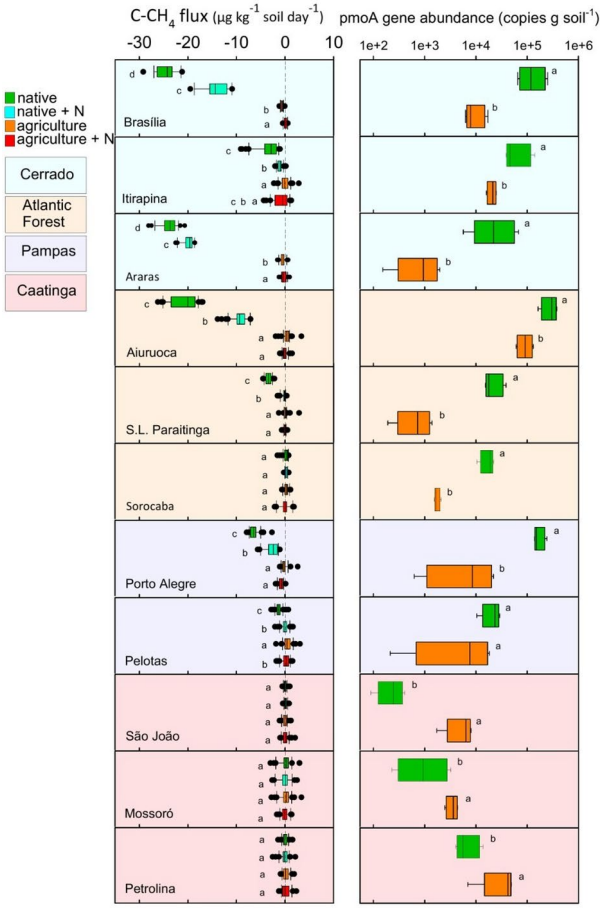

Fig. 2 CH_4 fluxes (left panel) and particulate methane monooxygenase gene abundances (right panel) in soils from cropped areas and native vegetation, with and without nitrogen addition. Different letters indicate statistically significant differences between treatments ($p < 0.05$). Each boxplot represents the mean of 40 gas flux measurements (4 replicates × 10 days)

the pairwise comparisons (Fig. 2), with the exception of soils from the Caatinga and one site in the Atlantic Forest, which did not exhibit detectable CH_4 oxidation under either native or cropped conditions (Fig. 2). Soils under native vegetation showed a mean CH_4 uptake of 7.3 μg C kg^{-1} soil day^{-1}. When considering only soils that displayed net CH_4 uptake, the average oxidation rate increased to 11.9 μg C kg^{-1} soil day^{-1}. The highest CH_4 oxidation rate observed was 28 μg C kg^{-1} soil day^{-1} at the Brasília site (Cerrado biome; Fig. 2). In these conditions, CH_4 concentrations in the microcosm headspace decreased to approximately 0.7 ppm over the 90 min the microcosms remained closed for gas sampling.

Nitrogen addition significantly reduced CH_4 oxidation in soils from native sites ($p = 0.007$). In soils that initially exhibited significant CH_4 uptake, the mean oxidation rate decreased to 7.98 μg C kg^{-1} soil day^{-1} after N addition, corresponding to a 33% inhibition. Furthermore, inhibition was statistically significant in all pairwise comparisons, ranging from 17% at the Araras site to 100% at the Pelotas site (Fig. 2). In contrast, N addition had no statistically significant effect on CH_4 fluxes from cropped soils, where mean fluxes were − 0.2 and − 0.4 μg C kg^{-1} soil day^{-1} without and with N addition, respectively.

3.2 Methanotrophs abundance

Land-use change reduced the abundance of methanotrophs in all soils that exhibited active CH_4 oxidation, except at one site in the Pampa biome (Fig. 2). Interestingly, in the Caatinga biome, cropped soils showed higher methanotroph abundance compared to soils under native vegetation (Fig. 2).

3.3 Factors driving CH_4 uptake

Non-metric multidimensional scaling (NMDS) of methane monooxygenase gene abundance and CH_4 oxidation rates, along with all measured soil parameters, revealed no clear grouping by biome or soil parameter (Fig. 3). However, the analysis suggested a potential influence of sodium (Na) on the absence of CH_4 uptake and low methanotroph abundance observed in soils from the Caatinga, as these were the only soils containing available Na. Other soils positioned near Caatinga samples in the NMDS plot are likely influenced by different factors, such as soil carbon (C), total nitrogen (N), ammonium (NH_4^+), and copper (Cu) (Fig. 3).

Given the lack of distinct grouping in the NMDS, we applied generalized linear mixed models (GLMMs) to identify soil parameters most strongly associated with CH_4 oxidation. The global and best-fit models are summarized in Table 1. According to the normalized coefficients, the best model indicated that low pH, higher soil carbon, and greater availability of iron (Fe) and copper (Cu) were the strongest positive drivers of CH_4 oxidation rates. Conversely, higher levels of available aluminum (Al), manganese (Mn), and zinc (Zn) appeared to inhibit CH_4 oxidation.

4 Discussion

Our results demonstrate that converting natural tropical soils into croplands significantly suppresses methane oxidation activity. Nitrogen addition also reduced CH_4 oxidation rates, though not as strongly as land-use change. The differences in methanotrophic bacterial abundance between land uses highlight the dominant effect of land-use change

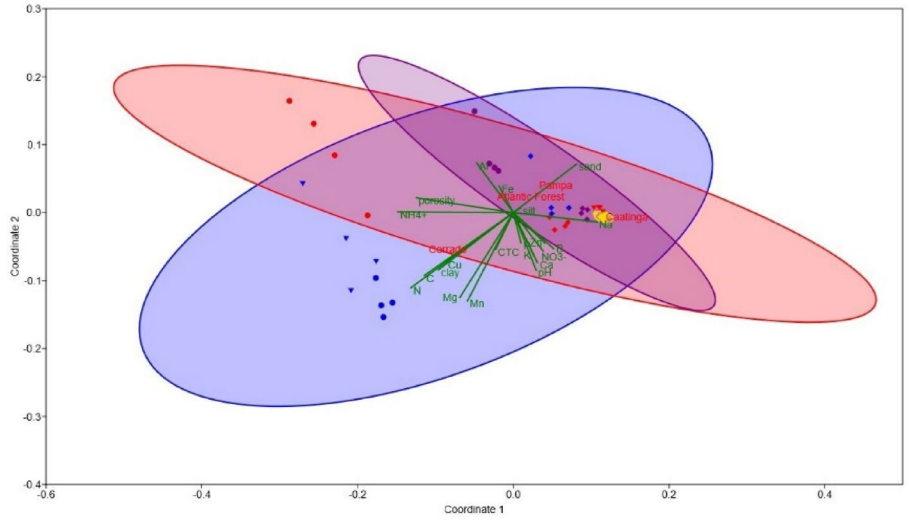

Fig. 3 Non-metric multidimensional scaling (NMDS) of pmoA gene abundance and CH_4 oxidation rates in relation to soil parameters. Ellipses (95% confidence intervals) indicate biomes: blue = Cerrado, red = Atlantic Forest, purple = Pampa, yellow = Caatinga

Table 1 Summary of the global and best-fit generalized linear mixed models identifying soil parameters associated with CH_4 uptake capacity. Positive β values indicate that the parameter contributes positively to CH_4 uptake, whereas negative β values indicate Inhibition of CH_4 oxidation. NS denotes parameters that are not statistically significant predictors ($p \geq 0.05$) but improve the model likelihood in the best-fit model. $p < 0.05$

Parameters	Global model	Best model
Intercept	0.095^{β}	0.150
Soil C	3.968	4.770*
P	5.503	0.116^{ns}
Fe	3.085	7.439*
Mn	− 10.582	− 8.260*
Zn	− 5.002	− 2.432*
Cu	9.178*	8.537*
Al	− 11.469*	− 11.375*
$N\text{-}NH_4^+$	1.729	–
$N\text{-}NO_3^-$	3.522	–
Porosity	0.355	–
pH	− 4.307	− 3.146
Log pmoA	0.072	–
AIC	− 16.3	− 23.3
r^2	0.954	0.951

on atmospheric methane consumption, which appears to be more pronounced in tropical systems than in temperate ecosystems. For instances, in Northern Europe the conversion to agriculture reduced by 60% the CH_4 oxidation in soils while we observed no significant methanotrophy activity [44].

The main exception was observed in the Caatinga biome, where soils did not show consistent methanotrophy, irrespective of land use (Fig. 2). Similar results were reported by Ribeiro et al. (2016) in in situ measurements in natural Caatinga [45]. Although semiarid regions cover about 18% of the Earth's surface and, together with arid regions, could represent an important CH_4 sink [46], our results suggest that Caatinga soils neither uptake nor emit methane significantly. This could be attributed to their low carbon

stocks and likely low dissolved organic carbon (DOC), an important substrate positively associated with CH_4 emissions [47], and to low nutrient availability that limits primary production [48]. Furthermore, the Caatinga's uneven rainfall and frequent negative water balances may further constrain microbial activity [48].

Although methanotrophy is most intense in the top 10 cm of soil, it also occurs throughout the soil profile [49–51]. Therefore, extrapolating our microcosm data to field conditions must be done cautiously. Field measurements from three of our study sites have reported comparable findings. For example, at São Luiz do Paraitinga, Carmo et al. (2012) recorded annual CH_4 uptake of ~ 5 kg C-CH_4 ha^{-1} yr^{-1}, whereas our microcosm experiments at the same site showed CH_4 uptake three times lower than the average across all soils [7]. Carmo et al. (2012) also noted reductions in CH_4 uptake during late spring, associated with elevated soil NH_4^+ levels (~ 40 mg kg^{-1}) [7]. Tate (2015) suggested that soils oxidizing ~ 8 kg C-CH_4 ha^{-1} yr^{-1} are strong methane sinks [52], indicating that soils from Aiuruoca, Brasília, and Araras could be even stronger sinks. Remarkably, forest soils in China oxidized ~ 1.2 µg C-CH_4 kg^{-1} day^{-1} in laboratory studies [53], ~ 20-fold lower than the highest rates observed in our study. Similarly, Nishisaka et al. (2019) reported negligible CH_4 fluxes at Sorocaba under native vegetation [54], corroborating our microcosm results (Fig. 3). Comparable patterns were observed annually in cropped soils at Sorocaba and Araras [28, 55].

Our models identified soil carbon, pH, and available iron (Fe) as relevant factors influencing CH_4 uptake (Table 1), with pH showing a negative correlation. Although porosity regulates gas diffusion [56], it did not emerge as a significant predictor in our models. Instead, soil organic matter, represented by soil organic carbon, appeared critical for methanotrophy. Labile carbon is essential for maintaining methanotroph populations, and enrichment with organic carbon can restore methanotrophic communities in degraded soils [6]. The addition of organic residues has also been shown to stimulate CH_4 uptake, possibly by improving soil aggregate structure [57, 58], which is important for restoring degraded ecosystems.

Soil compaction, a known consequence of agriculture [59], may also contribute to the observed reduction in CH_4 uptake, as it reduces porosity and impedes gas exchange [60]. Nitrogen addition further inhibits methanotrophy, though its effect was less pronounced than that of land-use change. Methanotrophs are oligotrophic organisms sensitive to nutrient enrichment, which can shift microbial communities toward copiotrophic taxa after fertilization [61, 62]. Similarly, increased pH to enhance crop productivity can also enhance microbial diversity [63, 64], potentially increasing competition and reducing high-affinity methanotrophs [65]. In intensively managed systems, methanotrophs may also be disadvantaged due to competition for space, nutrients, inhibition by secondary metabolites, or predation [66–68].

Micronutrients also influence methanotrophy in mechanistic ways. Our results indicated that available zinc (Zn) inhibited CH_4 oxidation, consistent with its ability to interfere with methane monooxygenase (MMO) by displacing essential metal cofactors and altering enzyme conformation [69]. Conversely, copper (Cu), the central component of the particulate methane monooxygenase (pMMO), enhances methanotrophy by promoting pMMO expression and supporting its catalytic activity [70, 71]. Iron (Fe^{3+}), as demonstrated in studies referenced in [72], contributes indirectly to CH_4 oxidation by participating in electron transfer chains and redox cycling required for MMO function,

including the activity of cytochromes involved in methanotroph respiration [72–74]. Sodium (Na) appeared particularly relevant in Caatinga soils, which uniquely contained available sodium, potentially contributing to the observed lack of methanotrophy. Transient environmental conditions, such as organic byproduct addition or drought–rewetting cycles, can shift methanotrophic community composition [75, 76], possibly explaining why methanotroph abundance did not fully account for variation in CH_4 oxidation (Table 1). Dormant microbial seed banks [77] may also contribute to the observed patterns. Nonetheless, soils with higher methane monooxygenase gene copy numbers tended to show higher CH_4 oxidation rates (Fig. 2), suggesting a functional link between methanotroph abundance and activity.

We estimate that soils with ~ 10^5 gene copies g^{-1}, oxidizing ~ 12 ng C-CH_4 day^{-1} g^{-1} soil, sustain ~ 100 ng of methanotroph biomass, assuming ~ 1 pg dry mass per cell [78]. This biomass–activity ratio is compatible with the maintenance of methanotroph communities at atmospheric CH_4 levels [79], and our observed rates exceed theoretical minimums required for sustaining high-affinity methanotrophs, such as the USCα cluster [80]. Indeed, in the Brasília microcosms, CH_4 concentration dropped to ~ 0.7 ppm in just 90 min, much faster than rates observed in pure cultures [81].

Interestingly, methanotroph abundance increased in Caatinga soils after land-use change, contrary to patterns observed elsewhere (Fig. 2). This may reflect increased productivity and microbial biomass under cropping in this adverse environment, but the abundance remained below the threshold for detectable methanotrophy. The presence of facultative methanotrophs, capable of using multi-carbon substrates such as acetate or ethanol [82], may explain the observed patterns.

5 Conclusion

Our findings indicate that tropical upland soils under native vegetation are consistent methane sinks, whereas soils under agriculture tend to be neutral or even sources of CH_4. Land-use change substantially reduces methanotroph abundance and methane oxidation, while nitrogen addition has a comparatively smaller effect. Soils enriched in micronutrients exhibited the highest methanotrophy and methanotroph abundance. Notably, Caatinga soils did not uptake CH_4, underscoring the need to reassess ecosystem services in drylands. Although specific factors such as nitrogen, compaction, or facultative methanotrophs play roles, the resilience of methanotrophy depends on the complex interplay of biotic and abiotic factors. In the context of global climate change, rethinking agricultural practices and land-use policies, particularly in tropical regions, is imperative to mitigate greenhouse gas emissions and preserve ecosystem functions.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1007/s44378-026-00164-6.

Supplementary Material 1.

Acknowledgements
The authors are grateful to FAPESP grant number (12/50694-6), CAPES for the Master's scholarship granted to HDQ and to CNPq for the Postdoc scholarship granted to LMP (151572/2018-6) and for the Productivity Grant to RHT (305987/2025-9).

Author contributions
L.M.P. designed the project, supervised the experiment, performed statistical analyses, wrote and revised the manuscript.H.D.Q. carried out the experiment, analyzed the data, contributed to writing and revising the

manuscript.R.H.T. performed statistical analyses, contributed to writing and revising the manuscript.D.S., C.F.A.T.-G. and C.B. provided soil samples, evaluated the collected data, and revised the manuscript.P.L.E.B. provided critical review.J.B.C. supervised the project, supervised the experiments, and revised the data.All authors reviewed and approved the final version of the manuscript.

Funding
São Paulo Research Foudation - FAPESP (grant 12/50694-6). Coordination for the Improvement of Higher Education Personnel - CAPES (Master's scholarship to HDQ). National Council for Scientific and Technological Development - CNPq - Postdoctoral fellowship to LMP (151572/2018-6) and Productivity Grant to RHT (305987/2025-9).

Data availability
The datasets generated and/or analyzed during the current study are available in the SciDB repository, [https://www.scidb.cn/en/anonymous/TkYzaVF2]. The data include methane (CH_4) flux measurements, soil physicochemical properties (e.g., organic carbon, nitrogen, texture, nutrients, pH, WFPS), and biological data (presence or absence of the pmoA gene, encoding methane monooxygenase from methanotrophs) collected from Brazilian biomes (Cerrado, Atlantic Forest, Caatinga, Pampas, Amazon) in 2016. The data are provided in a CSV file with accompanying metadata following standard documentation practices. Additional details on data collection and processing, including molecular analyses for pmoA, are available in the supplementary materials and the methods section of this manuscript. The data are freely accessible for reuse under a CC0 license, with citation recommended.

Declarations

Ethics approval and consent to participate
Not applicable.

Author's statement on the use of generative AI tools
The authors used OpenAI's GPT (ChatGPT) to assist in improving the clarity, grammar, and flow of the English text in sections of this manuscript. All intellectual content, study design, data analysis, interpretation, and scientific conclusions were conceived, executed, and validated solely by the authors. The authors reviewed and approved all edits made to ensure accuracy and appropriateness of the scientific content.

Ethical responsibilities of authors
All authors have read, understood, and have complied as applicable with the statement on "Ethical responsibilities of Authors" as found in the Instructions for Authors.

Competing interests
The authors declare no competing interests.

Received: 6 September 2025 / Accepted: 19 January 2026
Published online: 26 January 2026

References

1. Intergovernmental Panel on Climate Change. Climate change 2021: The physical science basis. Contribution of Working Group I to the sixth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press; 2021.
2. Lan X, Thoning KW, Dlugokencky EJ. Trends in globally averaged CH4, N2O, and SF6 determined from NOAA Global Monitoring Laboratory measurements. Glob Monitor Lab. 2022. https://doi.org/10.15138/P8XG-AA10.
3. Curry CL. Modeling the soil consumption of atmospheric methane at the global scale. Glob Biogeochem Cycles. 2007. https://doi.org/10.1029/2006GB002818.
4. Kirschke S, Bousquet P, Ciais P, Saunois M, Canadell JG, Dlugokencky EJ, Bergamaschi P, Bergmann D, Blake DR, Bruhwiler L, Cameron-Smith P, Castaldi S, Chevallier F, Feng L, Fraser A, Heimann M, Hodson EL, Houweling S, Josse B, Zeng G. Three decades of global methane sources and sinks. Nat Geosci. 2013;6(11):813–23. https://doi.org/10.1038/ngeo1955.
5. Venturini AM, Dias NMS, Gontijo JB, Yoshiura CA, Paula FS, Meyer KM, Nakamura FM, da França AG, Borges CD, Barlow J, Berenguer E, Nüsslein K, Rodrigues JLM, Bohannan BJM, Tsai SM. Increased soil moisture intensifies the impacts of forest-to-pasture conversion on methane emissions and methane-cycling communities in the Eastern Amazon. Environ Res. 2022. https://doi.org/10.1016/j.envres.2022.113139. 212(Pt. A), Article 113139.
6. Carmo JB, do deS, Neto ER, Duarte-Neto PJ, Ometto JPHB, Martinelli LA. Conversion of the coastal Atlantic forest to pasture: consequences for the nitrogen cycle and soil greenhouse gas emissions. Agric Ecosyst Environ. 2012;148:37–43. https://doi.org/10.1016/j.agee.2011.11.010.
7. Kaupper T, Mendes LW, Poehlein A, Frohlof D, Rohrbach S, Horn MA, Ho A. The methane-driven interaction network in terrestrial methane hotspots. Environ Microbiome. 2022. https://doi.org/10.1186/s40793-022-00409-1., 17, Article 15.
8. Bodelier PLE, Pérez G, Veraart AJ, Krause S. Methanotroph ecology, environmental distribution and functioning. In: Lee EY, editor. Methanotrophs: Microbiology fundamentals and biotechnological applications. New York: Springer; 2019. p. 1–38.
9. Silva AA, Braga MQ, Ferreira J, dos Santos VJ, do Carmo Alves S, de Oliveira JC, Calijuri ML. Anthropic activities and the legal amazon: estimative of impacts on forest and regional climate for 2030. Remote Sens Applications: Soc Environ. 2020;18:Article100304. https://doi.org/10.1016/j.rsase.2020.100304.
10. Cirne-Silva T, Carvalho W, Terra MCNS, de Souza CR, Santos ABM, Robinson SJB, dos Santos RM. Environmental heterogeneity caused by anthropogenic disturbance drives forest structure and dynamics in Brazilian Atlantic forest. J Trop for Sci. 2020;32(2):125–35. https://www.jstor.org/stable/26921956.
11. Segura-Garcia C, Bauman D, Arruda VL, Alencar A, Menor IO. Human land occupation regulates the effect of the climate on the burned area of the Cerrado biome. Copernicus Meetings. 2024. https://doi.org/10.5194/egusphere-egu24-10377.

12. Galarza RDM, Mulazzani RP, Boeno D, Gubiani PI. Changes in physical and hydraulic properties in sandy soils of the Pampa biome under different uses. Revista Brasileira De Ciência Do Solo. 2023;47:e0230032. https://doi.org/10.36783/18069657.rbcs20230032.
13. Macedo RS, Moro L, Lambais ÉO, Lambais GR, Bakker APD. Effects of degradation on soil attributes under Caatinga in the Brazilian semi-arid. Rev Arvore. 2023;47:e4702. https://doi.org/10.1590/1806-908820230000002.
14. Kang H, Lee J, Zhou X, Kim J, Yang YR. The effects of N enrichment on microbial cycling of non-CO2 greenhouse gases in soils: a review and a meta-analysis. Microb Ecol. 2022;84(4):945–57. https://doi.org/10.1007/s00248-021-01911-8.
15. Lu M, Zhou XH, Luo YQ, Yang YH, Fang CM, Chen JK, et al. Minor stimulation of soil carbon storage by nitrogen addition: a meta-analysis. Agric Ecosyst Environ. 2011;140:234–44. https://doi.org/10.1016/j.agee.2010.12.010.
16. Lee J, Oh Y, Lee ST, Seo YO, Yun J, Yang YR, Kim J, Zhuang QL, Kang H. Soil organic carbon is a key determinant of CH4 sink in global forest soils. Nat Commun. 2023;14:3110. https://doi.org/10.1038/s41467-023-38905-8.
17. Bodelier PLE. Interactions between nitrogenous fertilizers and methane cycling in wetland and upland soils. Curr Opin Environ Sustain. 2011;3:379–88. https://doi.org/10.1016/j.cosust.2011.06.002.
18. Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM. The Brazilian Atlantic forest: how much is left, and how is the remaining forest distributed? Implications for conservation. Biol Conserv. 2009;142:1141–53. https://doi.org/10.1016/j.biocon.2009.02.021.
19. Beuchle R, Grecchi RC, Shimabukuro YE, Seliger R, Eva HD, Sano E, Achard F. Land cover changes in the Brazilian Cerrado and Caatinga biomes from 1990 to 2010 based on a systematic remote sensing sampling approach. Appl Geogr. 2015;58:116–27. https://doi.org/10.1016/j.apgeog.2015.01.017.
20. Lapola DM, Martinelli LA, Peres CA, Ometto JPHB, Ferreira ME, Nobre CA, et al. Pervasive transition of the Brazilian land-use system. Nat Clim Chang. 2014;4:27–35. https://doi.org/10.1038/nclimate2056.
21. Aleixandre-Benavent R, Aleixandre-Tudó JL, Castelló-Cogollos L, Aleixandre JL. Trends in global research in deforestation: a bibliometric analysis. Land Use Policy. 2018;72:293–302. https://doi.org/10.1016/j.landusepol.2017.12.060.
22. Strassburg BBN, Brooks T, Feltran-Barbieri R, Iribarrem A, Crouzeilles R, Loyola R, et al. Moment of truth for the Cerrado hotspot. Nature Ecology & Evolution. 2017;1:99. https://doi.org/10.1038/s41559-017-0099.
23. Leal IR, da Silva JMC, Tabarelli M, Lacher TE Jr. Changing the course of biodiversity conservation in the Caatinga of northeastern Brazil. Conserv Biol. 2005;19(3):701–6. https://doi.org/10.1111/j.1523-1739.2005.00703.x.
24. Santos JC, Leal IR, Almeida-Cortez JS, Fernandes GW, Tabarelli M. Caatinga: the scientific negligence experienced by a dry tropical forest. Trop Conserv Sci. 2011;4:276–86. https://doi.org/10.1177/194008291100400306.
25. Overbeck GE, Müller SC, Fidelis A, Pfadenhauer J, Pillar VD, Blanco CC, et al. Brazil's neglected biome: the South Brazilian Campos. Perspect Plant Ecol Evol Syst. 2007;9:101–16. https://doi.org/10.1016/j.ppees.2007.07.005.
26. Adhikari K, Hartemink AE. Linking soils to ecosystem services: a global review. Geoderma. 2016;262:101–11. https://doi.org/10.1016/j.geoderma.2015.08.009.
27. Guo LB, Gifford RM. Soil carbon stocks and land use change: a meta-analysis. Glob Change Biol. 2002;8(3):345–60. https://doi.org/10.1046/j.1354-1013.2002.00486.x.
28. Escanhoela ASB, Pitombo LM, Brandani CB, Navarrete AA, Bento CB, do Carmo JB. Organic management increases soil nitrogen but not carbon content in a tropical citrus orchard with pronounced N2O emissions. J Environ Manage. 2019;234:13–20. https://doi.org/10.1016/j.jenvman.2018.11.109.
29. Powlson DS, Goulding KWT, Willison TW, Webster CP, Hütsch BW. The effect of agriculture on methane oxidation in soil. Nutr Cycl Agroecosyst. 1997;49:59–70. https://doi.org/10.1023/A:1009704226554.
30. Levine UY, Teal TK, Robertson GP, Schmidt TM. Agriculture's impact on microbial diversity and associated fluxes of carbon dioxide and methane. ISME J. 2011;5:1683–91. https://doi.org/10.1038/ismej.2011.40.
31. Goldman MB, Groffman PM, Pouyat RV, McDonnell MJ, Pickett STA. CH4 uptake and N availability in forest soils along an urban to rural gradient. Soil Biol Biochem. 1995;27(2):281–6. https://doi.org/10.1016/0038-0717(94)00185-4.
32. van Raij B, Andrade JC, Cantarella H, Quaggio JA. Análise química para avaliação da fertilidade de solos tropicais. Instituto Agronômico; 2001.
33. Norman RJ, Edberg JC, Stucki JW. Determination of nitrate in soil extracts by dual-wavelength ultraviolet spectrophotometry. Soil Sci Soc Am J. 1985;49:1182–5. https://doi.org/10.2136/sssaj1985.03615995004900050022x.
34. Krom MD. Spectrophotometric determination of ammonia: a study of a modified Berthelot reaction using salicylate and dichloroisocyanurate. Analyst. 1980;105(989):305–16. https://doi.org/10.1039/AN9800500305.
35. Pitombo LM, Ramos JC, Quevedo HD, do Carmo KP, Paiva JMF, Pereira EA, et al. Methodology for soil respirometric assays: step by step and guidelines to measure fluxes of trace gases using microcosms. MethodsX. 2018;5:656–68. https://doi.org/10.1016/j.mex.2018.06.008.
36. del Grosso SJ, Parton WJ, Mosier AR, Ojima DS, Potter CS, Borken W, et al. General CH4 oxidation model and comparisons of CH4 oxidation in natural and managed systems. Glob Biogeochem Cycles. 2000;14(4):999–1019. https://doi.org/10.1029/1999GB001226.
37. van Zwieten L, Singh BP, Kimber SWL, Murphy DV, Macdonald LM, Rust J, et al. An incubation study investigating the mechanisms that impact N2O flux from soil following biochar application. Agric Ecosyst Environ. 2014;191:53–62. https://doi.org/10.1016/j.agee.2014.02.030.
38. Cheng YS, Halsey JL, Fode KA, Remsen CC, Collins ML. Detection of methanotrophs in groundwater by PCR. Appl Environ Microbiol. 1999;65(2):648–51. https://doi.org/10.1128/AEM.65.2.648-651.1999.
39. Stoecker K, Bendinger B, Schöning B, Nielsen PH, Nielsen JL, Baranyi C, Toenshoff ER, Daims H, Wagner M. Cohn's crenothrix is a filamentous methane oxidizer with an unusual methane monooxygenase. Proc Natl Acad Sci. 2006;103:2363–7. https://doi.org/10.1073/pnas.0506361103.
40. Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, et al. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol. 2009;24(3):127–35. https://doi.org/10.1016/j.tree.2008.10.008.
41. Bates D, Mächler M, Bolker B, Walker S. Fitting linear mixed-effects models using lme4. J Stat Softw. 2015;67(1):1–48. https://doi.org/10.18637/jss.v067.i01.
42. Barton K. 2016. MuMIn: Multi-model inference (Version 1.15.6) [Computer software]. CRAN. https://CRAN.R-project.org/package=MuMIn. Accessed 24 May 2019.
43. Johnson PCD. Extension of Nakagawa & schielzeth's R2GLMM to random slopes models. Methods Ecol Evol. 2014;5(9):944–6. https://doi.org/10.1111/2041-210X.12225.

44. Dobbie KE, Smith KA, Prieme´ A, Christensen S, Degorska A, Orlanski P. Effect of land use on the rate of methane uptake by surface soils in Northern Europe. Atmos Environ. 1996;30(7):1005–11. https://doi.org/10.1016/1352-2310(95)00416-5.
45. Ribeiro K, Sousa-Neto ER, Carvalho JA, Lima JRS, Menezes RSC, Duarte-Neto PJ, et al. Land cover changes and greenhouse gas emissions in two different soil covers in the Brazilian Caatinga. Sci Total Environ. 2016;571:1048–57. https://doi.org/10.1016/j.scitotenv.2016.07.095.
46. Galbally IE, Kirstine WV, Meyer CPM, Wang YP. Soil-atmosphere trace gas exchange in semiarid and arid zones. J Environ Qual. 2008;37(2):599–607. https://doi.org/10.2134/jeq2006.0445.
47. Wang Y, Hu Z, Shen L, Liu C, Islam ARMT, Wu Z, et al. The process of methanogenesis in paddy fields under different elevated CO2 concentrations. Sci Total Environ. 2021;773:145629. https://doi.org/10.1016/j.scitotenv.2021.145629.
48. Menezes RSC, Sampaio EVSB, Giongo V, Pérez-Marin AM. Biogeochemical cycling in terrestrial ecosystems of the Caatinga biome. Braz J Biol. 2012;72(3):643–53. https://doi.org/10.1590/S1519-69842012000400004.
49. Hütsch BW. Tillage and land use effects on methane oxidation rates and their vertical profiles in soil. Biol Fertil Soils. 1998;27(4):284–92. https://doi.org/10.1007/s003740050435.
50. Koschorreck M, Conrad R. Oxidation of atmospheric methane in soil: measurements in the field, in soil cores and in soil samples. Glob Biogeochem Cycles. 1993;7(1):109–21. https://doi.org/10.1029/92GB02814.
51. Price SJ, Sherlock RR, Kelliher FM, McSeveny TM, Tate KR, Condron LM. Pristine new Zealand forest soil is a strong methane sink. Glob Change Biol. 2004;10:16–26. https://doi.org/10.1046/j.1529-8817.2003.00710.x.
52. Tate KR. Soil methane oxidation and land-use change: from process to mitigation. Soil Biol Biochem. 2015;80:260–72. https://doi.org/10.1016/j.soilbio.2014.10.010.
53. Zeng L, Tian J, Chen H, Wu N, Yan Z, Du L, Shen L. Changes in methane oxidation activity and methanotrophic community composition in saline alkaline soils. Front Microbiol. 2019. https://doi.org/10.3389/fmicb.2019.00924.
54. Nishisaka CS, Youngerman C, Meredith LK, Carmo JB, Navarrete A. Differences in N2O Fluxes and Denitrification Gene Abundance in the Wet and Dry Seasons Through Soil and Plant Residue Characteristics of Tropical Tree Crops. Front Environ Sci. 2019. https://doi.org/10.3389/fenvs.2019.00011.
55. Pitombo LM, Cantarella H, Packer APC, Ramos JC, Carmo JB. Straw preservation reduced total N2O emissions from a sugarcane field. Soil Use Manag. 2017;33:583–94. https://doi.org/10.1111/sum.12384.
56. Striegl RG. Diffusional limits to the consumption of atmospheric methane by soils. Chemosphere. 1993;26:715–20. https://doi.org/10.1016/0045-6535(93)90455-E.
57. Ho A, Reim A, Kim SY, Meima-Franke M, Termorshuizen A, de Boer W, et al. Unexpected stimulation of soil methane uptake as emergent property of agricultural soils following bio-based residue application. Glob Change Biol. 2015;21(10):3864–79. https://doi.org/10.1111/gcb.12974.
58. Van den Bergh SG, Chardon I, Leite MFA, Korthals GW, Mayer J, Cougnon M, et al. Soil aggregate stability governs field greenhouse gas fluxes in agricultural soils. Soil Biol Biochem. 2024;191:109354. https://doi.org/10.1016/j.soilbio.2024.109354.
59. Soane BD, van Ouwerkerk C. Soil compaction problems in world agriculture. In: Soane BD, van Ouwerkerk C, editors. Soil compaction in crop production. Amsterdam: Elsevier; 1994.
60. Sitaula BK, Hansen S, Sitaula JIB, Bakken LR. Methane oxidation potentials and fluxes in agricultural soil: effects of fertilisation and soil compaction. Biogeochemistry. 2000;48:323–39. https://doi.org/10.1023/A:1006262404600.
61. Dörr N, Glaser B, Kolb S. Methanotrophic communities in Brazilian Ferralsols from naturally forested, afforested, and agricultural sites. Appl Environ Microbiol. 2010;76(5):1307–10. https://doi.org/10.1128/AEM.02282-09.
62. Li S, Yang S, Wei X, Zhao N, Li Y, Liu A, Du Z, Zhang Q, Luo T, Liu J, Wang S. Reduced trace gas oxidizers as a response to organic carbon availability linked to oligotrophs in desert fertile Islands. ISME J. 2023;17:1257–66. https://doi.org/10.1038/s41396-023-01437-6.
63. Lauber CL, Hamady M, Knight R, Fierer N. Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. Appl Environ Microbiol. 2009;75(15):5111–20. https://doi.org/10.1128/AEM.00335-09.
64. Mendes LW, Tsai SM, Navarrete AA, de Hollanr M, van Veen JA, Kuramae EE. Soil-borne microbiome: linking diversity to function. Microb Ecol. 2015;70:255–65. https://doi.org/10.1007/s00248-014-0559-2.
65. Ho A, Kerckhof F-M, Luke C, Reim A, Krause S, Boon N, Bodelier PLE. Conceptualizing functional traits and ecological characteristics of methane-oxidizing bacteria as life strategies. Environ Microbiol Rep. 2013;5(3):335–45. https://doi.org/10.1111/j.1758-2229.2012.00370.x.
66. Hibbing ME, Fuqua C, Parsek MR, Peterson SB. Bacterial competition: surviving and thriving in the microbial jungle. Nat Rev Microbiol. 2010;8(1):15–25. https://doi.org/10.1038/nrmicro2259.
67. Thakur MP, Del Real IM, Cesarz S, Steinauer K, Reich PB, Hobbie S, et al. Soil microbial, nematode, and enzymatic responses to elevated CO2, N fertilization, warming, and reduced precipitation. Soil Biol Biochem. 2019;135:184–93. https://doi.org/10.1016/j.soilbio.2019.04.020.
68. Murase J, Frenzel P. Selective grazing of methanotrophs by protozoa in a rice field soil. FEMS Microbiol Ecol. 2008;65:408–14. https://doi.org/10.1111/j.1574-6941.2008.00511.x.
69. Sirajuddin S, Barupala D, Helling S, Marcus K, Stemmler TL, Rosenzweig AC. Effects of zinc on particulate methane monooxygenase activity and structure. J Biol Chem. 2014;289:21782–94. https://doi.org/10.1074/jbc.M114.581363.
70. Ho A, Lüke C, Reim A, Frenzel P. Selective stimulation in a natural community of methane oxidizing bacteria: effects of copper on PmoA transcription and activity. Soil Biol Biochem. 2013;65:211–6. https://doi.org/10.1016/j.soilbio.2013.05.027.
71. Ross MO, MacMillan F, Wang J, Nisthal A, Lawton TJ, Olafson BD, Mayo SL, Rosenzweig AC, Hoffman BM. Particulate methane monooxygenase contains only mononuclear copper centers. Science. 2019;364:566–70. https://doi.org/10.1126/science.aav2572.
72. Murrell JC, McDonald IR, Gilbert B. Regulation of expression of methane monooxygenases by copper ions. Trends Microbiol. 2000;8(5):221–5. https://doi.org/10.1016/S0966-842X(00)01739-X.
73. Fan L, Schneider D, Dippold MA, Poehlein A, Wu W, Gui H, et al. Active metabolic pathways of anaerobic methane oxidation in paddy soils. Soil Biol Biochem. 2021;156:108215. https://doi.org/10.1016/j.soilbio.2021.108215.
74. Chen KH, Feng J, Bodelier PL, Yang Z, Huang Q, Delgado-Baquerizo M, et al. Metabolic coupling between soil aerobic methanotrophs and denitrifiers in rice paddy fields. Nat Commun. 2024;15(1):3471. https://doi.org/10.1038/s41467-024-47827-y.

75. Ho A, Lee HJ, Reumer M, Meima-Franke M, Raaijmakers C, Zweers H, et al. Unexpected role of canonical aerobic methanotrophs in upland agricultural soils. Soil Biol Biochem. 2019;131:1–8. https://doi.org/10.1016/j.soilbio.2018.12.020.
76. Cai Y, Zheng Y, Bodelier PLE, Conrad R, Jia Z. Conventional methanotrophs are responsible for atmospheric methane oxidation in paddy soils. Nat Commun. 2016;7:11728. https://doi.org/10.1038/ncomms11728.
77. Lennon JT, Jones SE. Microbial seed banks: the ecological and evolutionary implications of dormancy. Nat Rev Microbiol. 2011;9:119–30. https://doi.org/10.1038/nrmicro2504.
78. Sender R, Fuchs S, Milo R. Revised estimates for the number of human and bacteria cells in the body. PLoS Biol. 2016;14(8):e1002533. https://doi.org/10.1371/journal.pbio.1002533.
79. Kolb S, Knief C, Dunfield PF, Conrad R. Abundance and activity of uncultured methanotrophic bacteria involved in the consumption of atmospheric methane in two forest soils. Environ Microbiol. 2005;7(8):1150–61. https://doi.org/10.1111/j.1462-2920.2005.00791.x.
80. Kolb S. The quest for atmospheric methane oxidizers in forest soils. Environ Microbiol Rep. 2009;1(6):336–46. https://doi.org/10.1111/j.1758-2229.2009.00047.x.
81. Tveit AT, Hestnes AG, Robinson SL, Schintlmeister A, Dedysh SN, Jehmlich N, et al. Widespread soil bacterium that oxidizes atmospheric methane. Proc Natl Acad Sci U S A. 2019;116:8515–24. https://doi.org/10.1073/pnas.1817812116.
82. Farhan Ul Haque M, Xu HJ, Murrell JC, Crombie A. Facultative methanotrophs—diversity, genetics, molecular ecology and biotechnological potential: a mini-review. Microbiology. 2020;166(10):894–908. https://doi.org/10.1099/mic.0.000977.

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