

Response to comments by [Reviewer #1](#) (Fatemeh Ajallooeian)

General comment:

Genuinely one of the better manuscripts I've reviewed in a while. The dataset is thorough, pairing lipid biomarkers with 16S sequencing and functional gene searches gives real weight to the microbial source interpretations rather than leaving them speculative. Writing is careful throughout, and the authors are upfront about where the evidence is solid vs where they're extrapolating, the Halamka discussion and the Gmm homolog caveat in 4.2 are good examples. Analysis is rigorous, and most of my pushback is just asking for caveats they clearly already know about to be stated more explicitly, not real problems with the approach. Figures are clear and well built, the ternary plot and MI comparisons in Fig. 5 put this dataset nicely in context against marine systems. Overall a genuinely novel contribution to a real gap in the terrestrial GDGT literature, just needs a handful of minor clarifications before it's ready.

[We would like to thank the reviewer for all the insightful comments and the positive assessment of the novelty and significance of our research. We have addressed all the issues listed below and have revised the manuscript accordingly. A point-by-point reply to the reviewer's comment is provided below and is colored blue. The text that would be added to the revised manuscript is shown in orange.](#)

Detailed comments:

Introduction:

Lines 88-99: the ob/sb-GDGT and O₂ depletion relationship is drawn from marine studies and then applied to the permafrost soil context without acknowledging that this is an extrapolation. Marine water column/sediment redox chemistry differs considerably from soil redox. As currently written, the mechanism reads as already established, when in fact its transferability to terrestrial systems is arguably what this

study is testing. I'd recommend adding a sentence explicitly noting that this link has not previously been demonstrated outside marine settings.

Thank you for pointing out this ambiguity. In a revised manuscript, we have now stated that the association between sb/ob-GDGTs and oxygen depletion has been established mainly in marine settings, whereas its applicability to terrestrial permafrost soils remains untested (Lines 101-103 in the revised main text), as follows:

However, this association has so far been established primarily in marine settings, and whether it also applies to terrestrial environments, where redox conditions are governed by distinct hydrological and biogeochemical processes, remains unclear.

The rationale for combining lipid MS with 16S sequencing is also not made explicit throughout the introduction. I agree as the authors themselves note too that Acidobacteria alone don't account for the full range of known brGDGT producers, this is the natural justification for the 16S component, but it should be stated directly rather than left implicit in my opinion. A 1-2 sentence statement clearly mentioning this should suffice.

Thank you for this helpful suggestion. In the revised manuscript (Lines 88-93), we now explicitly state that 16S rRNA gene sequencing provides microbial community composition, allowing us to examine broader community associations with lipid distributions.

These uncertainties limit the extent to which lipid distributions alone can constrain their biological sources and highlight the value of complementary information on microbial communities. Pairing lipid analysis with 16S rRNA gene sequencing provides such complementary information and has recently been applied to explore potential associations between tetraether lipid distributions and microbial taxa (De Mey-Śnieżyńska et al., 2026; Zeng et al., 2023; Ajallooeian et al., 2025).

Lines 100-110: this paragraph builds a chain on why there are proxy complications for application of brGDGTs in permafrost, but then it shifts to ob/sb-GDGTs specifically, it is somewhat unclear whether you're claiming brGDGT proxies are unreliable in saturated soils or ob/sb GDGTs are the opportunity for a new proxy here? Or both? I would try to reframe and tie this together.

In the revised main text, we have reframed this paragraph to clarify this proxy complication and the potential proxy opportunity, while emphasizing that the latter remains to be tested in terrestrial environments (Lines 111-125), as follows:

Soil hydrology in these permafrost environments is regulated by precipitation, seasonal snowmelt, freeze-thaw processes, and the presence and thickness of the active layer, resulting in pronounced spatial variation in soil water content (SWC). Hydrological variations associated with SWC can, in turn, alter soil oxygen availability and redox conditions. In particular, elevated SWC restricts oxygen diffusion through soil pores, promoting microoxic to anoxic conditions that can restructure microbial communities and associated biogeochemical processes (Marschner, 2021; Pett-Ridge and Firestone, 2005). Such hydrologically induced changes in redox conditions and microbial community composition may alter the sources and distributions of br-GDGTs, thereby complicating their application as paleoclimate proxies in water-saturated soils (Liang et al., 2023; Raberg et al., 2024; Tang et al., 2024). At the same time, previous observations that the distributions of sb/ob-GDGTs vary with oxygen availability in marine environments (Liu et al., 2014; Zeng et al., 2023), raising the possibility that these lipids may also respond to hydrologically mediated redox gradients in terrestrial soils.

Methods:

Cores were collected in a single field season (July-Aug 2018). Since the whole premise here is that SWC-driven redox variation shapes lipid distributions, one summer

snapshot can't really tell a stable moisture/redox gradient apart from seasonal or year to year variability. This doesn't need fixing, but should be flagged as a limitation in my opinion.

Thank you for this important comment. We agree that, because all soil cores were collected during a single field campaign, our dataset cannot fully distinguish persistent spatial gradients in soil moisture and redox conditions from seasonal or interannual variability.

Previous studies from the Qinghai-Tibetan Plateau suggest that permafrost can exert a hydrological buffering effect on soil water content. Long-term observations have shown smaller interannual variations in soil water content at permafrost sites than at permafrost-free sites, particularly where the active layer is relatively shallow (Liu et al., 2021). Permafrost can restrict vertical drainage, maintain relatively high water contents in the active layer, and regulate soil moisture through seasonal freezing and thawing. In addition, pronounced depth-dependent hydrological and hydrochemical gradients have been documented in permafrost soil profiles, with soil moisture, active-layer thickness, and freeze-thaw processes acting as important controls (Wang et al., 2018). We have now explicitly acknowledged this temporal limitation in the revised manuscript (Lines 276-278):

Nevertheless, the soil cores were collected during a single summer campaign, some seasonal or interannual variability in SWC and associated redox conditions cannot be excluded.

Lines 227-230: ASV-level networks use r -value >0.7 and genus-level use r -value >0.6 , but then line 230 says genera were selected for BLAST using r -value > 0.7 , I would clear this up to avoid confusion.

The two correlation thresholds were used for different purposes. The genus-level correlation network was constructed and visualized using ($|r| > 0.6$), whereas a stricter threshold of ($|r| > 0.7$) was subsequently applied to select a subset of strongly correlated

genera for the downstream BLASTp analysis. We explained these two steps explicitly in revised manuscript (Lines 250-252):

From the genus-level correlation network constructed using a threshold of $|r| > 0.6$, we further selected genera showing stronger correlations ($|r| > 0.7$) with branched GDGTs for downstream BLASTp analysis.

and also clarified this selection criterion in the caption of Table S5 as follows:

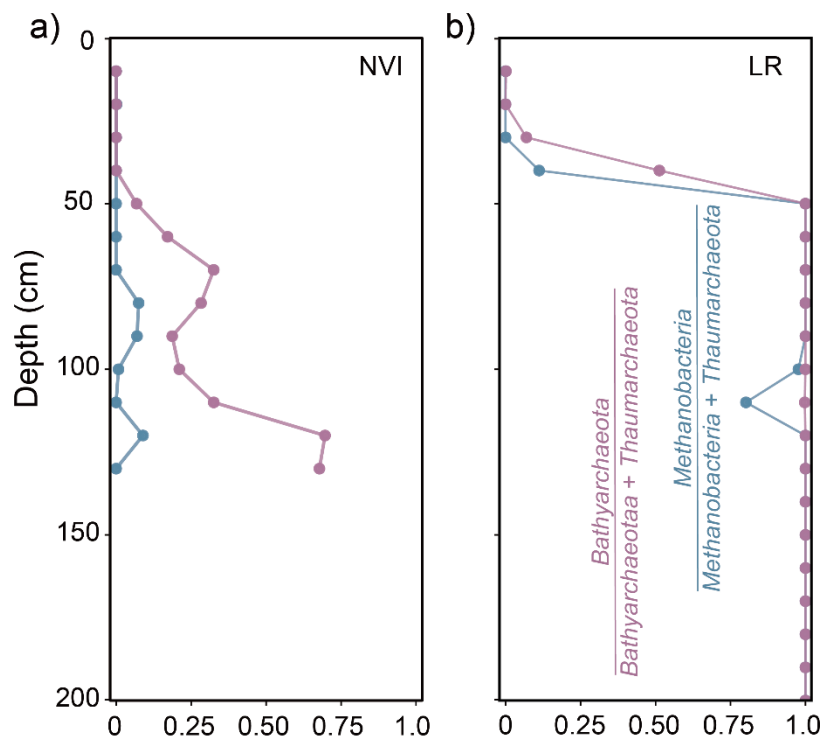
Table S5. Putative GDGT-related protein homologs searched in bacterial taxa positively or negatively correlated with br/sb/ob-GDGT ($|r| > 0.7$).

Results:

Line 318-322: The Methanobacteria/(Methanobacteria+Thaumarchaeota) ratio is framed as "more direct evidence" of redox conditions, but it only accounts for two of the anaerobic archaeal groups you've already brought into the discussion, Bathyarchaeota are mentioned two sentences earlier as another GDGT-0-producing anaerobic lineage in watersaturated soils, but aren't included in this ratio. Is there a reason for it? If Bathyarchaeota make up a meaningful share of the archaeal community at either site, leaving them out could skew how an anaerobic dominant ratio makes a sample look.

Thank you for pointing this out. Methanobacteria, Bathyarchaeota, and Thaumarchaeota together accounted for 92–100% and 62–100% of the archaeal communities in the NVI and LR profiles, respectively. These archaeal groups differ markedly in their ecological distributions and redox preferences. Bathyarchaeota occupy a relatively broad ecological niche, occurring from suboxic, sulfide-depleted shallow sediments to deeper anoxic layers, whereas Methanobacteria are generally restricted to strictly anaerobic environments.

Because both Methanobacteria and Bathyarchaeota have the potential to contribute to GDGT-0 production (Zheng et al., 2019), we also calculated the Bathyarchaeota/(Bathyarchaeota + Thaumarchaeota) ratio in below figure:



The two ratios exhibited broadly similar depth-dependent patterns in both sediment profiles. However, the Bathyarchaeota-based ratio began to increase at shallower depths than the Methanobacteria-based ratio, which is consistent with the broader redox tolerance of Bathyarchaeota.

We therefore initially evaluated the Methanobacteria/(Methanobacteria + Thaumarchaeota) ratio as a community-based indicator of soil redox conditions and revised manuscript (Line 344):

which provides an additional community-based indicator of soil redox conditions.

Line 336-344: The text splits genus-level nodes into anaerobic (13.51%) and aerobic (33.78%), but that only accounts for about half the network (as seen on Fig. 3c's legend shows a third "unknown" category)), which based on the numbers makes up roughly 53% of the 74 genera shown, and it's not discussed at all in the text. I suggest adding a line acknowledging this "unknown" group, since as written a reader could assume aerobic/anaerobic is the dominant split when actually it's closer to half.

We added followed sentence (Lines 362-364) to state that 39 of the 74 genera (52.70%) could not be confidently assigned as aerobic or anaerobic:

The remaining 52.70% of the genus-level nodes could not be confidently assigned as aerobic or anaerobic and were therefore classified as having unknown oxygen requirements.

And the revised caption of figure 3 c) (Lines 384-387) as follows:

(c) The co-occurrence network depicts correlations between bacterial groups at the genus level and sb/br/ob-GDGTs ($|r| > 0.6$, $p < 0.05$). Node colors indicate bacterial oxygen requirements (aerobic, anaerobic, or unknown), with “unknown” referring to genera for which oxygen requirements could not be confidently assigned; red and blue edges represent positive and negative correlations between microbial communities and sb/br/ob-GDGTs, respectively.

Discussion:

Lines 408-411: I'd elaborate a bit here on how the Halamka et al. (2021) evidence is being used, since the logic connecting the two culture based observations isn't fully explained. Authors first say Acidobacteria grown aerobically are brGDGT sources referencing Chen et al., and Halamka et al, then say oxygen limitation may stimulate brGDGT production "in certain strains". Are these the same strains showing both behaviors (I think Halamka et al does explain this fully in their paper, but it's best to

not assume reader knows that and fully give the context). The next sentence then jumps from oxygen limitation in certain strains to “facilitate the anaerobic production of brGDGTs”, which goes further than oxygen limited toward fully anaerobic, and it's not clear the cited evidence supports that jump. Since this paragraph is doing a lot of the work bridging the aerobic culture evidence to your anaerobic hypothesis, worth tightening up exactly what Halamka et al. (2021) showed.

Thank you for the suggestion. We rephrased this paragraph and added more details in Lines 437-450:

The currently culturable biological sources of brGDGTs are constrained in aerobic *Acidobacteria* species, such as *Ca. Solibacter usitatus* and *Edaphobacter aggregans* (Sinninghe Damsté et al., 2011; Chen et al., 2022; Halamka et al., 2023). These two strains can also grow under low-oxygen conditions (e.g., 1% O₂), suggesting that some aerobic producers may still synthesize brGDGTs under suboxic or reducing conditions (Halamka et al., 2021; Chen et al., 2022; Halamka et al., 2023). In addition, *E. aggregans* produced no detectable brGDGTs at 21% and 5% O₂ but more brGDGTs (up to $2.9 \pm 0.7\%$ in total lipids) at 1% O₂, demonstrating a trigger effect of oxygen limitation on brGDGT production in this strain (Halamka et al., 2021). This experimental evidence implies that, at least for some aerobic producers like *E. aggregans*, low oxygen availability may facilitate the production of brGDGTs, and they could contribute to the brGDGT pool under microaerophilic conditions or oxic-anoxic boundaries in peats, soils, and lakes, consistent with the increased abundance of brGDGTs observed in such oxygen-depleted environments.

Fig. 4: a couple of issues here, firstly the panels aren't labeled, are they combined dataset for both sites? or is each panel representing a different site? Secondly regarding the Lü et al. (2019) reference data, in the overlap range (SWC 0–50%), the grey points don't really track the same trend as your own data from what I observe, so it's worth a line addressing that, and clarifying whether Lü et al. was included in the R² calculation at all.

The panels showing (a) $MI_{ob/br}$ and (b) $MI_{ob/br/sb}$ have been added to the revised manuscript. Both panels include the combined NVI and LR permafrost-soil datasets.

We agree that the data reported by Lü et al. (2019) do not show a consistent increase in proxy with increasing water content (WC); instead, the proxy values tend to decrease at $WC > 5\%$. We also note, however, that the proxy values reported by Lü et al. (2019) remain relatively low across the entire dataset, including samples from the Xiamen mangrove wetland, where WC ranges from 39.8% to 56.1%. The mangrove sediments are characterized by highly dynamic hydrological conditions, in which the long-term redox conditions remain unknown and may decouple bulk WC from the instantaneous redox state. In addition, given the relatively slow turnover of sedimentary brGDGTs, $MI_{ob/br}$ and $MI_{ob/br/sb}$ may integrate redox conditions over longer timescales rather than respond directly to short-term redox fluctuations associated with tidal cycles. We therefore present the data from Lü et al. (2019) for comparison but do not include them in the regression analysis or in the calculation of R^2 . We have clarified this distinction and its rationale in the revised manuscript (Lines 473-477).

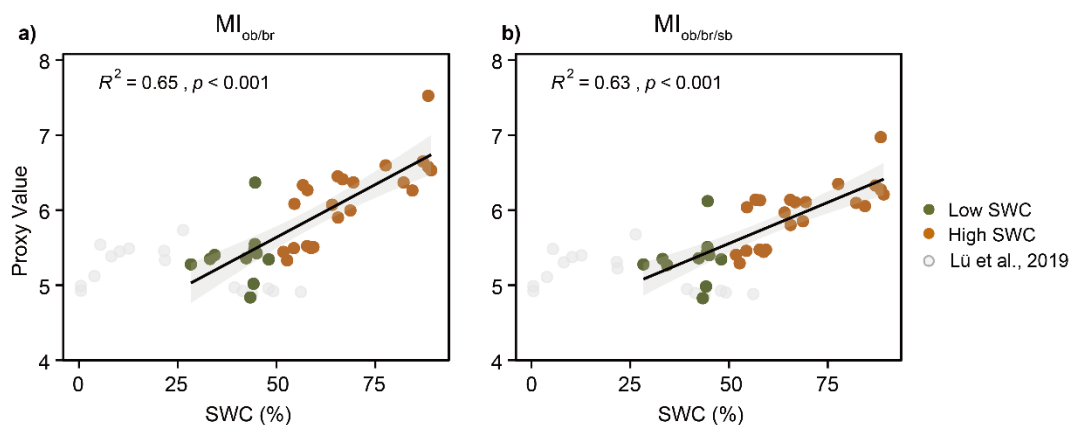


Fig. 4. Linear regressions between SWC (%) and (a) $MI_{ob/br}$ and (b) $MI_{ob/br/sb}$ proxies for the combined NVI and LR permafrost-soil samples. Samples are categorized into low SWC (<50%, green) and high SWC (>50%, orange). Shaded areas denote 95% confidence intervals. Both proxies show significant correlations with SWC ($R^2 \geq 0.6, p < 0.001$). Grey circles represent reference data from Lü et al. (2019), which are shown for comparison only and were not included in the regression calculations.

Lines 461-472: authors say the Gmm homolog's role in bacteria "has not yet been experimentally verified," which is fair and cautious. But two sentences later, that same unverified homology is used to say marine bacteria "may possess a greater capacity for producing highly methylated brGDGTs... probably gmm gene homologs" so you're building a fairly specific story on a mechanism you just said isn't confirmed to even work in bacteria. The wording used ("we infer," "may," "probably") is cautious, I agree it's not really overclaiming, but I would be more careful in taking a mechanism from a different domain (archaea) and applying it provisionally to bacteria without testing it directly.

We understand the reviewer's concern about this unverified mechanism, but we would like to propose a plausible biological explanation: the differences in patterns between marine and terrestrial environments could be related to the genetic capacity of source microorganisms to add methyl groups. Indeed, the gene responsible for brGDGT methylation has not been identified, but it's not our target to discuss this here. Considering the parallel structures and biosynthetic pathways between archaeal isoGDGTs and bacterial brGDGTs, we would like to extend recent findings on related mechanisms from archaeal research to bacterial brGDGTs. For example, a survey on archaeal GDGT cyclization gene (*grs*) homologs in hot springs indicates that organisms encoding more copies of *grs* have higher cyclization capacity and are more widespread at low pH (Blum et al., 2023). Therefore, we rephrased this paragraph with more caution in Lines 498-515:

Alternatively, such divergence could be attributed to differences in biosynthetic capacity for methylation among source microorganisms across diverse environments, which may be primarily controlled by the gene responsible for brGDGT methylation. Recently, the genes that encode GDGT cyclization in archaea have been identified (*grsA* and *grsB*) (Zeng et al., 2019). In hot springs, *grs* gene abundance and copy number increase towards lower pH, consistent with selection for archaeal groups with greater cyclization capacity under acid stress (Blum et al., 2023). Analogously, based on the distinct patterns of branched GDGTs, we infer that marine-sourced bacteria may

possess a greater capacity for producing highly methylated brGDGTs compared to terrestrial sources due to the diversification of the gene involved in the formation of methylation. The gene encoding glycerol monoalkyl glycerol tetraether (GMGT) methylase (*Gmm*) in archaea has recently been identified (Garcia et al., 2024). *Gmm* homologs are widely distributed across archaeal and bacterial lineages, with high diversification and substrate preferences, resulting in structural diversity among methylated archaeal GDGTs (Garcia et al., 2025). Prompted by these findings in archaea, we infer that the gene responsible for brGDGT methylation could also exhibit a high degree of diversification among source microorganisms, thereby shaping sb/br/ob-GDGT patterns alongside environmental stresses.

Figure 5: I think in the wetland sediments panel (orange datapoints, "ns" for not significant) is the same dataset from Lü et al. (2019) that shows up as the grey points in Fig. 4? Right? where the trend also didn't really hold in the 0-50% SWC overlap zone. So the claim that $MI_{ob/br}$ tracks SWC "particularly when SWC exceeded 50%" doesn't actually hold for the dataset sitting right next to permafrost soil in the same panel in my opinion, and this isn't mentioned anywhere. I agree that wetland sediments are the closest analog you have to permafrost out of the four datasets, so I think this needs addressing directly, is the SWC-MI relationship something specific to permafrost, or is something else going on with the Lu dataset? Also, same panel is mixing two different kinds of comparison. Mariana trench and water column are split by actual measured oxic/anoxic conditions, but wetland sediments and permafrost soil are split by low and high SWC as a proxy for redox state. Then line 451 reads " $MI_{ob/br}$ index is significantly higher in anoxic environments than in oxic environments" as a blanket statement for the whole figure, but for two of the four datasets "anoxic" is really just inferred from SWC, not measured. I would clarify this so the significance stars don't all read as the same kind of comparison.

Yes, the wetland sediment data shown in Fig. 5 are the same Lü et al. (2019) dataset shown as the grey points in Fig. 4. As the reviewer noted, the increasing $MI_{ob/br}$ pattern observed in our permafrost profiles is not apparent in the Lü et al. (2019) data within

the overlapping lower-water-content range. Consistently, the difference between the two water-content groups in Fig. 5c is not significant. However, we would like to clarify that our statement “particularly when SWC exceeded 50%” refers specifically to the permafrost soil profiles investigated in this study. The Lü et al. (2019) dataset contains very few samples with water content above 50%, and therefore provides limited coverage of the higher-SWC range, where the relationship is most apparent in our permafrost samples. We added a sentence (Lines 586-589) in the revised manuscript to explicitly acknowledge the different pattern observed in the Lü et al. (2019) dataset, while retaining the >50% SWC description as an observation specific to our permafrost profiles:

In contrast, the Lü et al. (2019) wetland dataset did not show the same increasing pattern within the overlapping lower-water-content range, and only a very few samples in that dataset exceeded 50% water content, implying SWC may decouple from the redox state of the samples.

We also agree with the reviewer that Fig. 5c combines comparisons based on different environmental classifications, which could make the significance brackets appear to represent the same type of oxic–anoxic comparison. We would like to clarify, however, that all statistical tests in Fig. 5c are within-dataset comparisons rather than comparisons among datasets. Therefore, the different grouping criteria do not affect the validity of the individual statistical tests, including the non-significant result for the Lü et al. (2019) wetland dataset. The issue, instead, is how these source-specific comparisons may be interpreted when presented together. We therefore revised the Fig. 5 caption (Lines 537-543) to explicitly state the grouping basis for each dataset and to clarify that all significance brackets represent comparisons within individual datasets, as follows:

Fig. 5c) Within-dataset comparisons of $MI_{ob/br}$ using the environmental classification available for each dataset. Mariana Trench sediments were grouped by sediment intervals associated with contrasting redox conditions (Zeng et al., 2023); water-column

samples were grouped according to dissolved O₂ and H₂S (Liu et al., 2014); wetland sediments were grouped by water content (WC <5% vs. WC ≥5%; Lü et al., 2019); and permafrost soils were grouped by SWC (SWC <50% vs. SWC >50%) in this study. The water-content and SWC groupings do not represent direct oxygen measurements. Significance brackets indicate comparisons within individual datasets.

Accordingly, we also revised the content in Section 4.2 (Lines 487-492):

Notably, MI_{ob/br} tended to be higher under conditions associated with lower oxygen availability or higher soil water content, except no significant difference was observed in the wetland sediments from Lü et al. (2019) (Fig. 5c).

References:

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