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REPORT OPEN ACCESS

Redox Gradient Shapes the Chemical Composition of Peatland Microbial Communities

Vincent P. Milesi 

ISTO, UMR 7327, Univ Orléans, CNRS, BRGM, OSUC, Orléans, France

Correspondence: Vincent P. Milesi (vincent.milesi@univ-orleans.fr)**Received:** 28 June 2024 | **Revised:** 28 September 2024 | **Accepted:** 8 October 2024**Funding:** This work was supported by Agence Nationale de la Recherche.**Keywords:** Marcell experimental forest | metagenomics | microorganisms | oxidoreduction potential | peatland | thermodynamic modeling

ABSTRACT

The response of soil carbon to climate change and anthropogenic forcing depends on the relationship between the physicochemical variables of the environment and microbial communities. In anoxic soils that store large amounts of organic carbon, it can be hypothesized that the low amount of catabolic energy available leads microbial organisms to minimize the energy costs of biosynthesis, which may shape the composition of microbial communities. To test this hypothesis, thermodynamic modeling was used to assess the link between redox gradients in the ombrotrophic peatland of the Marcell Experimental Forest (Minnesota, USA) and the chemical and taxonomic composition of microbial communities. The average amino acid composition of community-level proteins, called hereafter model proteins, was calculated from shotgun metagenomic sequencing. The carbon oxidation state of model proteins decreases linearly from -0.14 at 10 cm depth to -0.17 at 150 cm depth. Calculating equilibrium activities of model proteins for a wide range of chemical conditions allows identification of the redox potential of maximum chemical activity. Consistent with redox measurements across peat soils, this model Eh decreases logarithmically from an average value of 300 mV at 10 cm depth, close to the stability domain of goethite relative to Fe^{2+} , to an average value of -200 mV at 150 cm, within the stability domain of CH_4 relative to CO_2 . The correlation identified between the taxonomic abundance and the carbon oxidation state of model proteins enables predicting the evolution of taxonomic abundance as a function of model Eh. The model taxonomic abundance is consistent with the measured gene and taxonomic abundance, which evolves from aerobic bacteria at the surface including Acidobacteria, Proteobacteria, and Verrucomicrobia, to anaerobes at depth dominated by Crenarchaeota. These results indicate that the thermodynamic forcing imposed by redox gradient across peat soils shapes both the chemical and taxonomic composition of microbial communities. By providing a mechanistic understanding of the relationship between microbial community and environmental conditions, this work sheds new light on the mechanisms that govern soil microbial life and opens up prospects for predicting geochemical and microbial evolution in changing environments.

1 | Introduction

Microbial life relies on the catalysis of redox reactions to obtain energy, the amount of which depends on the physicochemical conditions of the environment. At the surface, aerobic respiration of organic carbon drives the vast bulk of carbon transfer from terrestrial soils to the atmosphere, the oceans, and

the subsurface (Mackenzie, Lerman, and Andersson 2004). At depth, the decreasing availability of oxidants limits the amount of energy available, resulting in lower rates of microbial activity and preservation of organic matter (LaRowe and Amend 2019). In peatlands where waterlogged conditions limit O_2 penetration, the scarcity of inorganic oxidants induces a sharp redox gradient from the surface to a few meters depth

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where anaerobic methanogenesis dominates (Galand et al. 2005; Godin et al. 2012; Bräuer et al. 2020). As a result, peatlands store 15%–30% of the world's soil carbon although they only cover 3% of the Earth's land surface (Batjes 1996; Lappalainen 1996; Limpens et al. 2008; Ciaia et al. 2013; Xu et al. 2018). However, climate change, through warming and CO₂ enrichment, alters the carbon balance of these ecosystems (Moore 2002; Page et al. 2002; Swindles et al. 2019), increasing microbial decomposition of organic matter and the resulting flux of CO₂ and CH₄ to the atmosphere (Freeman, Ostle, and Kang 2001; Waddington, Warner, and Kennedy 2002; Belyea and Malmer 2004; Moore and Basiliko 2006; Dise 2009; Fenner and Freeman 2011; Knox et al. 2015; Turetsky et al. 2015). Understanding the mechanistic relationship between physicochemical variables of the environment and microbial activity is essential for predicting the response of soil carbon to climate change and anthropogenic forcing (Bardgett, Freeman, and Ostle 2008; Allison, Wallenstein, and Bradford 2010; Manzoni et al. 2012; Wallenstein and Hall 2012).

Energy-based modeling provides a framework for quantifying microbial processes (LaRowe and Amend 2019). The occurrence of microbial life and its metabolic strategy depends on the energetics of catabolic and anabolic processes (McCullom and Shock 1997; McCullom and Amend 2005; Amend and McCullom 2009; Amend et al. 2011, 2013; Osburn et al. 2014; Reveillaud et al. 2016; Milesi et al. 2021). Except in reducing geologic fluids (Amend and Shock 1998; Shock and Canovas 2010; Dick and Shock 2021), anabolism is an endergonic process that stores Gibbs free energy through the production of structured organic molecules. Pioneering studies of Yellowstone National Park hot springs showed that in anoxic environments with low catabolic energy available, microbial organisms minimize the energy costs of biosynthesis (Dick and Shock 2011, 2013). The average carbon oxidation state of organic compounds proved to be a key parameter to characterize thermodynamic controls on biosynthesis (Dick and Shock 2011) and microbial degradation of organic compounds (LaRowe and Van Cappellen 2011). Recently, correlations between the average carbon oxidation state of biomacromolecules and redox potentials in low-energy environments have been accumulating, consistent with the minimization of biosynthesis energy costs (Boyer et al. 2020; Lecoeuvre et al. 2021; Dick 2022; Dick and Meng 2023; Dick and Tan 2023). These results open up prospects for the use of geochemical calculations involving biomacromolecules to quantify and better understand the co-evolution of the geosphere and biosphere (Dick et al. 2023). Whether this redox shaping applies to microbial communities controlling carbon cycling in terrestrial soils remains unknown.

To address this knowledge gap, thermodynamic modeling was performed to assess the link between peat soil redox gradients and the chemical composition of community-level proteins, inferred from shotgun metagenomic sequencing. Because proteins represent the largest mass fraction of prokaryotic cells (Milo and Phillips 2015), they provide an opportunity to investigate the relationship between the chemical composition of microbial communities and the physicochemical variables of the environment. The model is based on the extensive dataset of the SPRUCE experiment, a climate change manipulation

conducted in the Marcell experimental ombrotrophic bog forest in northern Minnesota (USA) which consists of 16 experimental plots undergoing peat soil heating and elevated CO₂ treatments (Wilson et al. 2016). This study highlights the thermodynamic relationship between redox gradient and the chemical and taxonomic composition of microbial communities, shedding new light on the mechanisms governing soil microbial life.

2 | Chemical Activity of Model Proteins

Metagenomic data from the SPRUCE experiment are available at four depths (10, 40, 100, and 150 cm) for 10 experimental plots that experienced either Deep Peat Heating (DPH) or Whole Ecosystem Warming at five warming levels (up to +9°C) during 1 year (see Appendix A and Table S1) (Wilson et al. 2016). For each metagenome, the amino acid composition of the community-level protein, called hereafter the model protein, was calculated as the sum of all protein sequences inferred from shotgun metagenomic sequencing weighted by the relative abundance of the protein-coding gene (Dick and Shock 2011) (see Table S2). The average carbon oxidation state of nominally uncharged model proteins was determined by the covalent bonding structure of carbon as follows:

$$Z_c = \frac{2(n_O + n_S) + 3n_N - n_H}{n_C} \quad (1)$$

where n is the number of atoms of C, H, N, O, and S. Therefore, the lower the Z_c , the more reduced the carbon.

The Z_c values of model proteins range from -0.14 to -0.17 , comparable to previous observations in other environments (Dick and Shock 2011; Dick and Meng 2023; Dick and Tan 2023). The Z_c values decrease with depth from an average value of -0.142 at 10 cm depth to -0.156 at 150 cm depth (Figure 1), consistent with the thermodynamic prediction that more reduced molecules are more stable in more reducing environments. No correlation is observed between the Z_c values and the warming levels nor the CO₂ partial pressure of experimental plots (see Figure B1), which indicates no impact of experimental treatments on the fraction of genetic information encoding proteins.

An independent method was used to calculate the Z_c values based on 16S rRNA gene sequencing of samples from the ombrotrophic bog before the soil heating experiment (Lin, Tfaily, Steinweg, et al. 2014). The 16S-based Z_c values were calculated as the summed product of the relative taxonomic abundance of major archaeal and bacterial phyla by the Z_c value of their reference proteome (Dick and Tan 2023). Although they exhibit a slightly higher rate of decrease with depth, the 16S-based Z_c values are consistent with those derived from shotgun metagenomic sequencing (Figure 1). Differences in sampling date, location, and soil temperature between metagenomic and 16S data may contribute to the discrepancy observed between the two Z_c estimates.

To determine the equilibrium activity of model proteins as a function of physicochemical variables, the *standard* molal

thermodynamic properties of model proteins were calculated from the sequence of amino acids using a group additivity method (Dick, LaRowe, and Helgeson 2006; Dick 2008; see Table S3). The *standard* molal Gibbs energy of the formation reaction of model proteins was then calculated at a pressure of 1 bar and the annual average temperature of 3°C (Kolka et al. 2011), considering the aqueous basis species CO_2 , H_2O , H_2S , NH_3 , H^+ , and e^- such as:

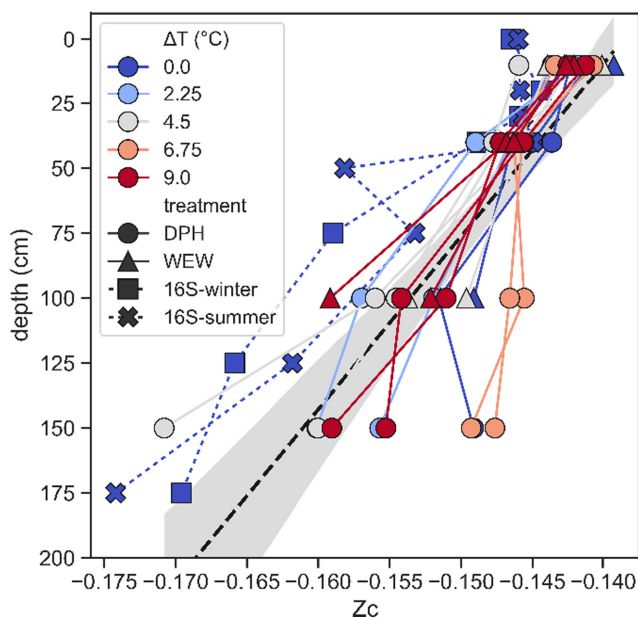
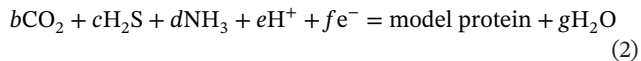


FIGURE 1 | Average carbon oxidation state (Z_c) of model proteins as a function of depth. The color code indicates the warming level of the Deep Peat Heating (DPH) and Whole Ecosystem Warming (WEW) manipulation. The black dashed line is the linear regression for the DPH and WEW manipulation. The 16S-based Z_c values are shown with dashed blue lines for the winter and summer seasons.

where b , c , d , e , f , and g are the reaction coefficient of CO_2 , H_2O , H_2S , NH_3 , H^+ , and e^- , respectively. In general, long proteins demand more energy than smaller ones to be synthesized just because they contain more atoms of reduced carbon, regardless of their average carbon oxidation state. To account for protein length, the *standard* molal Gibbs energy of formation reactions was normalized by the number of amino acid residues (Dick and Shock 2011). Deviations of the environmental composition from the standard composition were accounted for by considering the *actual* molal Gibbs energy change of the formation reaction of protein residues such as:

$$\Delta G_r = RT \ln \frac{\prod_{i=1}^n a_i^{\gamma_i}}{K_r} \quad (3)$$

where R is the gas constant, T is the absolute temperature in Kelvin, K_r is the equilibrium constant of the reaction, and a and γ are, respectively, the chemical activity and reaction coefficient of the reactants and products. Considering an equal-affinity state in which $\Delta G_r = 0$, the activity of protein residues can be calculated from Equation (3) as a function of the chemical composition of the environment such as:

$$a_{\text{protein residu}} = \frac{K_r a_{\text{CO}_2}^b a_{\text{H}_2\text{S}}^c a_{\text{NH}_3}^d a_{\text{H}^+}^e a_{\text{e}^-}^f}{a_{\text{H}_2\text{O}}^g} \quad (4)$$

The relative equilibrium activity of model proteins was obtained by dividing the equilibrium activity of its residue by the protein length, then normalizing by the sum of the equilibrium activities of all model proteins (Dick 2022) (see Appendix A).

Relative equilibrium activity of model proteins in experimental plot 6 after DPH treatment was calculated for a range of redox conditions constrained by the stability domain of water and logarithmic values of $a\text{H}^+$, $a\text{CO}_2$, $a\text{H}_2\text{S}$, $a\text{NH}_3$, and $a\text{H}_2\text{O}$ of -4 , -3 , -6 , -9 , and 0 , respectively, consistent with the speciation calculation of measured porewater compositions (Griffiths et al. 2016; Griffiths, Sebestyen, and Oleheiser 2019). As the

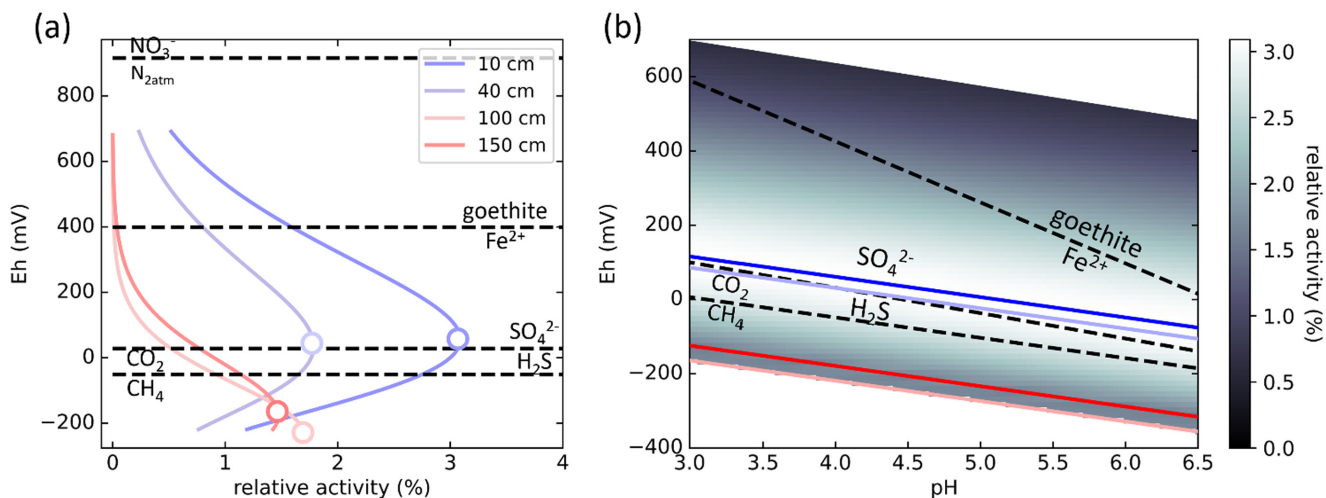


FIGURE 2 | Relative equilibrium activity as a function of redox potential (a) and pH (b) of model proteins at 10, 40, 100, and 150 cm depth in experimental plot 6 after DPH treatment. The dashed lines represent redox potentials at equilibrium with different redox couples (see Appendix A for details on calculations). The highest relative activity of model proteins, represented by open circles in diagram (a), is displayed as a function of pH in diagram (b) with colored lines. The color bar represents the surface of the highest relative activities.

depth increases, the model proteins reach their highest chemical activity at increasing reducing conditions (Figure 2a). The model proteins at 10 and 40cm depth are most stable for Eh values of ca. 0mV, within the stability field of Fe^{2+} relative to goethite and the predominance domain of SO_4^{2-} relative to H_2S . At 100 and 150 cm depth, that is, below the water table (Hanson et al. 2020), the model proteins reach their highest relative activity for more reducing conditions at Eh values of ca. -200mV, within the predominance domain of CH_4 relative to CO_2 and H_2S relative to SO_4^{2-} (Figure 2a). Although the Eh values of the highest activities decrease with increasing pH, the pH does not impact the relative stability between model proteins (Figure 2b). Compared to Eh and pH, the activity of CO_2 , H_2S , NH_3 , and H_2O have a negligible impact on the relative equilibrium activity of model proteins (see Figure B2).

The Eh value of the highest chemical activity of model proteins (as identified with open circles in Figure 2a), called hereafter the model Eh, was calculated as a function of depth for each experimental plot. Calculations were done considering the average value ($\pm\sigma$) of pH measured in each experimental plot which decreases from 3.6 at the surface to 4.7 at 150cm depth (Griffiths et al. 2016; Griffiths, Sebestyen, and Oleheiser 2019) (see Figure B3). The model Eh decreases with depth and with the Z_c value following a logarithmic trend (Figure 3a). At 10cm depth within the water table fluctuation range (Figure 3b) (Hanson et al. 2020), the model Eh has a mean value of 265 mV ($\sigma \pm 235$ mV) with the highest Eh values within the stability domain of goethite relative

to Fe^{2+} . At 40cm depth which corresponds to the deep limit of the water table fluctuation range, the model Eh values are scattered around 0mV, near the conditions of SO_4^{2-} - H_2S and CO_2 - CH_4 isoactivity. All model proteins at 100 and 150cm within the permanently saturated zone indicate model Eh values of highest chemical activities well within the predominance domains of H_2S relative to SO_4^{2-} and CH_4 relative to CO_2 .

The model Eh profile is compared to redox potentials measured during a 2-year redox monitoring experiment conducted in the Lakkasuo ombrotrophic peatland in southern Finland which exhibits a similar water table fluctuation range than the ombrotrophic bog of the Marcell Experimental Forest (Figure 3b,c) (Koskinen et al. 2024). The range of model Eh values in the SPRUCE experiment is comparable with the measured redox potentials at the Lakkasuo peatland. The slightly lower Eh values measured at 45cm depth in the Lakkasuo peatland may stem from the pH values, up to one pH unit higher than in the SPRUCE experiment (see Figure B3).

The model Eh represents a prediction of the optimal activity of electrons necessary to maximize the chemical activity of a model protein at a given depth. Its decrease in depth indicates that microbial communities reach a metastable state of thermodynamic equilibrium with the physicochemical conditions of their environment. Therefore, the model Eh depicts the redox potential that these microbial communities have experienced and have adapted to at these various depths. Measurements of redox

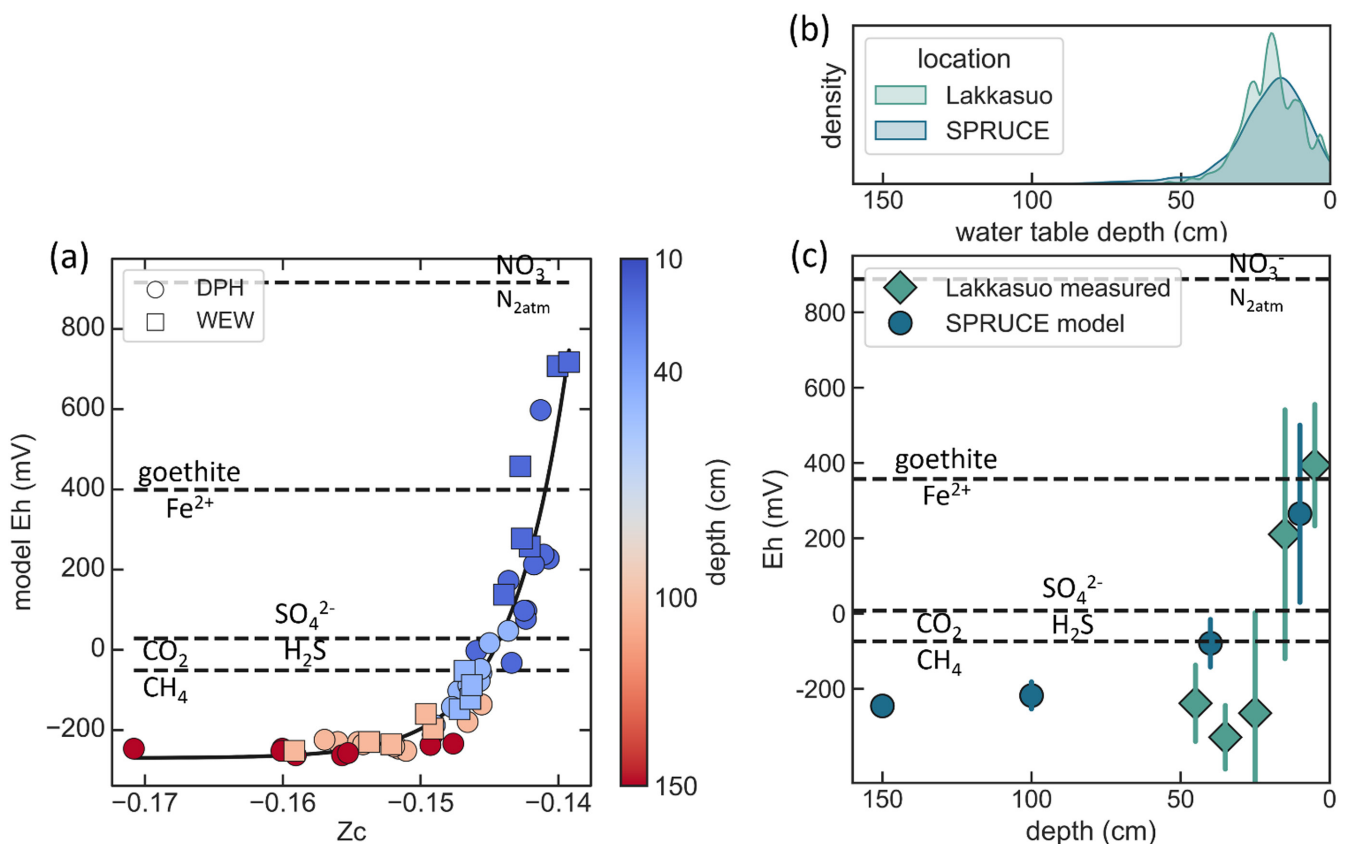


FIGURE 3 | Model Eh as a function of Z_c values (a), probability density functions of the water table level in the SPRUCE and Lakkasuo ombrotrophic peatlands (b), and model Eh as a function of depth compared to long-term redox monitoring in the Lakkasuo peatland (c). Diagram (c) shows the average values ($\pm\sigma$) of the model and measured Eh values.

potentials in natural systems are often difficult to interpret, as they are integrative of various redox couples that are generally not in mutual equilibrium (Bricker 1982). Metagenome-based estimates of redox potential may represent new geochemical information for characterizing redox conditions, integrative of environmental conditions on time and space scales relevant to microbial ecosystems.

These results demonstrate how soil microbial communities are chemical systems whose composition responds to thermodynamic forcing imposed by the physicochemical conditions of the environment. Several studies have investigated the energy needs for the synthesis of biomass monomers in various environments (McCollom and Amend 2005; Amend and McCollom 2009; Amend et al. 2011, 2013; LaRowe and Amend 2016). At the scale of biomass monomers, only the prevailing physicochemical conditions of the environment control the energy cost of biosynthesis as the chemical composition of monomers is fixed. At the scale of biomacromolecules, the polymeric nature of molecules such as proteins allows chemical variability while maintaining the function of the molecule. The results presented here show that this chemical flexibility results in proteins at the level of microbial communities whose chemical composition is shaped by redox conditions. This suggests an evolutionary process in which minimizing the biosynthesis energy costs through chemical adaptation of proteins benefits the microbial community in low-energy environments.

3 | Redox Conditions of Microbial Habitats

Because the chemical variability of model proteins results from differences in metagenomes, it can be hypothesized that this variability directly encodes for differences in taxonomic abundance (Dick and Tan 2023). This is supported by the consistency between 16S-based and metagenome-based estimates of Z_c values (Figure 1). To further test this hypothesis, the correlation between the Z_c values of model proteins and the taxonomic composition measured in samples from the SPRUCE ombrotrophic bog before the soil heating experiment was evaluated (Lin, Tfaily, Steinweg, et al. 2014). The Z_c value at the depth of taxonomic measurements was calculated using the linear correlation identified in Figure 1. The decrease of the Z_c values with depth is strongly correlated with the increase of Crenarchaeota, Chloroflexi, and Spirochaetes, and the decrease of Proteobacteria and Verrumicrobia (see Figure B4). Only Acidobacteria, Firmicutes, and Bacteroidetes fail the statistical test with a p -value > 5%. Consistent with previous observations (Dick and Tan 2023), these correlations suggest that the chemical shaping of microbial communities by the redox potential of the environment translates into variations of taxonomic abundance.

Using the correlations of Z_c values with both taxonomic abundances (Figure B4) and model Eh (Figure 3a), the relative taxonomic abundance was computed as a function of model Eh. This model taxonomic abundance is compared to the measured taxonomic abundance and the relative abundance of genes related to anaerobic processes and CH_4 cycle (Lin, Tfaily, Green, et al. 2014; Lin, Tfaily, Steinweg, et al. 2014) (Figure 4). For taxonomic groups with no meaningful correlation with Z_c , their average abundance was considered. The model abundances reproduce

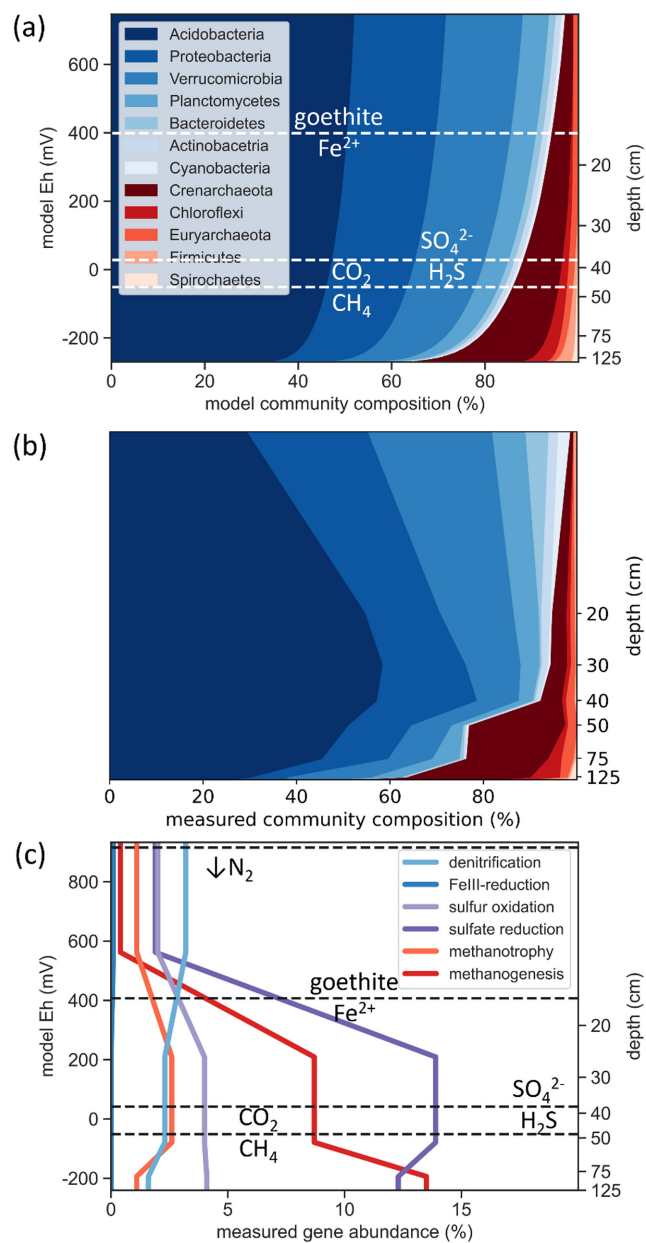


FIGURE 4 | Model taxonomic abundances (a), measured taxonomic abundances (b), and measured abundances of genes related to anaerobic respiration and CH_4 cycle (c) as a function of model Eh values and depth. The gene abundance corresponds to the sequence count for genes or pathways relative to the total count of the housekeeping gene *rpoB* (see Lin, Tfaily, Steinweg, et al. 2014 for details).

accurately the decrease in Acidobacteria, Proteobacteria, and Verrumicrobia with depth, and the concurrent increase in Crenarchaeota, Chloroflexi, and Spirochaetes (Figure 4a,b). For model Eh above 400 mV in the stability domain of goethite relative to Fe^{2+} , the microbial community is dominated by aerobic bacteria, including Acidobacteria, Proteobacteria, and Verrumicrobia, the combined abundance of which represents ca. 80% of the microbial community. Consistently, genes associated with anaerobic respiration are scarce (Figure 4c). As model Eh approaches 0 mV and the limits of CO_2 - CH_4 and SO_4^{2-} - H_2S isoactivity, the abundance of known anaerobes increases, among which Crenarchaeota, Chloroflexi, Firmicutes, and

Spirochaetes to a lesser extent. In parallel, genes associated with sulfate reduction, sulfide oxidation, methanogenesis, and methanotrophy increase whereas those assigned to denitrification and FeIII reduction decrease. Below model Eh of 0 mV within the stability domain of CH₄ relative to CO₂, the abundances of Crenarchaeota, Chloroflexi, Firmicutes, and Spirochaetes, and that of genes associated with methanogenesis keep increasing. The abundance of genes associated with methanotrophy decreases, consistent with the increasing reducing conditions that limit the availability of electron acceptors.

The consistency of model Eh with measured taxonomic and gene abundance indicates that the minimization of biosynthesis energy costs not only shapes the chemical composition of microbial communities but also controls the taxonomic abundance. This result can be explained by a phylogenetic or ecological evolutionary process or a combination of both (Dick and Tan 2023). Organisms with reduced proteomes might dominate in reducing environments, but the competition to save on the energy costs of biosynthesis may select for even more reduced proteomes. This feedback loop would lead to the stratification of organisms across a redox plane depending on metabolic strategy, as observed here.

Physicochemical parameters other than the redox potential influence the taxonomic abundance in peatlands, including pH, temperature, organic content, and nutrients (Kang et al. 2018; Putkinen et al. 2018; Xu et al. 2020). In the SPRUCE experimental site, the correlation between the nitrogen and phosphorus content of porewaters, and the abundance of N- and P-fixing genes as a function of depth provides support for P and N limitations explaining variations in taxonomic abundance (Lin, Tfaily, Steinweg, et al. 2014). The results presented here show that, together with nutrients and pH among other parameters, redox potential imposes thermodynamic constraints on biosynthesis reactions that contribute to shaping the chemical and taxonomic composition of the soil microbial community.

Multivariate analyses of genomic data and physicochemical parameters are commonly used to relate microbial communities with their environments (Ramette 2007; He et al. 2016). The metabolic function of genes especially provides qualitative information on the environmental conditions (Grossart et al. 2020). However, these approaches lack mechanistic and quantitative understanding. The thermodynamic modeling presented here allows us to quantitatively relate the redox conditions with the taxonomic abundance. Applied to peatlands, it brings insights into the habitats of microbial species playing a key role in carbon cycling. The Crenarchaeota phylum in the study of Lin, Tfaily, Steinweg, et al. (2014) includes the Bathyarchaeota phylum which was later determined as a distinct phylum (Meng et al. 2014). Crenarchaeota and Bathyarchaeota are among the most abundant archaea on Earth (Kubo et al. 2012; He et al. 2016; Lazar et al. 2016), but their role in soil and sediment carbon cycling is still unclear. In peatlands, they were proposed to mediate the coupling of carbon oxidation with the anaerobic respiration of unidentified organic electron acceptors (Lin, Tfaily, Steinweg, et al. 2014), possibly humic substances that may act as terminal electron acceptors and outcompete methanogenesis (Klüpfel et al. 2014; Tan et al. 2018; Walpen et al. 2018; Joshi, Schroth, and Sander 2021). Hence, determining the environmental conditions that allow Crenarchaeota and Bathyarchaeota to thrive is critical to predicting methane

emissions from wetlands. The thermodynamic model presented here establishes a quantitative link between the redox conditions and the abundance of Crenarchaeota and Bathyarchaeota.

4 | Conclusion

The metagenome-based thermodynamic model presented in this study highlights the metastable state of equilibrium between the chemical composition of community-level proteins and the sharp redox gradient that characterizes peat soils. The optimal redox potential necessary to maximize the relative activity of community-level proteins is consistent with expected redox conditions in peat soils. Hence, microbial communities tend to minimize the energy costs of biosynthesis by having a repertoire of producible proteins whose carbon oxidation state depends on environmental redox conditions. The correlation between the taxonomic abundances and the carbon oxidation state of community-level proteins indicates that this energy minimization not only shapes the chemical composition of microbial communities but also controls the taxonomic abundance.

These results open new prospects for characterizing microbial habitats and their evolution with environmental changes. How microbial communities will react to permafrost melting or deep-sea mining of marine sediments, that is, two environments characterized by sharp redox gradients, is unknown (Jansson and Taş 2014; Orcutt et al. 2020). The thermodynamic analysis of genomic data presented in this study provides new indicators to characterize physicochemical conditions and microbial evolution in changing environments.

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Conflicts of Interest

The author declares no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the [Supporting Information](#) of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.