Enhanced rock weathering boosts ecosystem multifunctionality via improving microbial networks complexity in a tropical forest plantation

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Abstract

1. Afforestation is expected to contribute to mitigate global change by promoting carbon stocks and multiple ecosystem services. However, the success of plantations may be limited by the availability of soil nutrients. This is especially critical for plantations in tropical ecosystems which are known to be nutrient poor ecosystems. Enhanced rock weathering (ERW) represents a promising strategy for improving soil health and carbon sequestration in such ecosystems.

2.We added wollastonite skarn, a calcium silicate rock, to soils in a rubber plantation in Yunnan, China, as part of an ERW strategy aimed at promoting soil functioning and biodiversity. Statistical significance was determined using a linear mixed-effects model, with p-values indicating the level of significance.

3. The addition of wollastonite skarn significantly enhanced key ecosystem functions related to carbon, nitrogen, phosphorous, silicon, biodiversity, and pathogen control. However, it did not significantly affect soil enzyme activity. Some of these responses to the addition of wollastonite skarn may be associated with an increase in soil pH.

4. Microbial network complexity played a critical role in explaining the changes in ecosystem multifunctionality in response to ERW, through both direct and indirect pathways.

5.**Synthesis and applications**: Our findings suggest that ERW is a viable strategy for improving soil health and ecosystem resilience in tropical plantations, which are limited in nutrients. Thus, ERW has implications for carbon management and climate change mitigation.

Keywords: Enhanced rock weathering; Co-occurrence networks; Ecosystem multifunctionality; Soil nutrient limitations; Microbial diversity; Forest plantation

1. Introduction

Afforestation has significant potential to mitigate global climate change by enhancing carbon sequestration and promoting a range of ecosystem services (Doelman et al., 2020; Wang and Yu, 2023). However, the effectiveness of these plantations is often hindered by soil nutrient limitations, which constrain plant growth and ecosystem productivity (Pérez-Silos et al., 2021). This challenge is particularly pronounced in tropical ecosystems, where soils are notoriously nutrient poor (Bond, 2010). One promising approach to addressing these limitations is enhanced rock weathering (ERW), through the addition of silicate rock like wollastonite skarn to soils. Wollastonite skarn is an important source of calcium and silicium and contains small amounts of iron, magnesium, and manganese substituting for calcium. The lack of these elements can limit ecosystem processes in tropical forests. Moreover, ERW can increase the pH of soils reducing acidification, which is typically found in tropical forests. Acidification is known to limit soil biodiversity and function (Cui et al., 2022). Application of ERW as a natural-based solution aims to improve soil fertility, boost soil biodiversity, and enhance overall ecosystem functioning (Beerling et al., 2018). However, studies investigating the benefits of ERW are still limited.

Current research has mainly focused on the agricultural applications of ERW (Dupla et al., 2023). However, its use in forestry and the restoration of natural ecosystems is less explored (Rzeznik and Nebe, 1968), despite its theoretical potential to enhance biological carbon sequestration (Goll et al., 2021). Further ecological impacts of ERW, particularly on ecosystem multifunctionality (EMF) and soil microbial communities, remain largely unexplored (Swoboda et al., 2022). EMF reflects the integrated capacity of an ecosystem to offer a spectrum of services, including nutrient cycling, carbon storage, and the preservation of the soil structure and biodiversity (Yuan et al., 2021). Soil microbial communities, with their diversity and complex interaction networks, play a pivotal role in maintaining ecosystem stability and functionality (Oliver et al., 2015; Yuan et al., 2020). One of the critical soil properties influenced by ERW is soil pH. The addition of wollastonite skarn has the potential to increase soil pH, thereby reducing acidification—a common limitation in tropical forest soils. Changes in pH can significantly affect nutrient availability and microbial processes, making it a key factor in understanding the broader impacts of ERW (Edwards et al., 2017; Zhong et al., 2023). Therefore, we treated soil pH as an important explanatory variable in our analyses to explore its role in mediating the effects of wollastonite skarn on soil functionality and ecosystem services...

Here, we conducted an experiment in a 28-year-old plantation wherein we added different amounts of wollastonite skarn aiming to investigate the effects of ERW on the diversity and network complexity of soil microbial communities, and its implications for ecosystem multifunctionality in a tropical ecosystem from Southern China. Specifically, we aim to answer the following research questions: (1) How does the ERW impact key ecosystem functions, specifically related to soil carbon, nitrogen, phosphorus, silicon, and pathogen control?? (2) How do soil microbial diversity, network complexity, and soil chemistry respond to ERW? and (3) What are the relative contributions of soil microbial diversity, network complexity, and soil chemistry to ecosystem multifunctionality including both above- and below-ground functions? We hypothesize ERW, by fostering microbial network complexity via improving soil conditions, will not only enhance above- and below-ground multifunctionality but also bolster the overall ecosystem multifunctionality. Our goal is to contribute to a better understanding of the ecological implications of ERW for further assessing its potential for ecosystem restoration and carbon management.

2. Materials and methods

2.1 Study sites and experimental design

The study was conducted in April 2021 in a 28-year-old rubber plantation at the Xishuangbanna Tropical Botanical Garden (XTBG), Yunnan Province, China (21°33′N, 101°28′E). The region had a tropical climate with distinct wet and dry seasons, an annual average temperature of 18-22°C, and yearly rainfall between 1100-1600 mm, predominantly during the rainy season (Cao et al., 2006). The soil was predominantly acidic Oxisol with a pH of approximately 4.9. The rubber plantation primarily consisted of *Hevea brasiliensis*, which were approximately 10 years old at the time of the experiment (Kou et al., 2018).The experiment used a Latin-square design with 20 × 20 m plots, separated by 20-m gaps. We tested three treatments: i) control with no wollastonite skarn, ii) 2.5 tons per hectare (0.25 kg m^{-2}) of wollastonite skarn, and iii) 5 tons per hectare (0.5 kg m^{-2}) of wollastonite skarn, applied uniformly as powder across the forest floor. The choice of two levels also considered their theoretical potential for CO_2 sequestration and the associated costs of quarrying, processing, and distributing the material. The application rates were derived from economic analyses that balanced effective carbon capture with financial viability, ensuring that the selected treatment levels were both feasible and effective for the scope of this study. The wollastonite skarn powder utilized in this research was obtained from Diaobing Mountain, a commercial mining site located in Liaoning, China. The chemical composition of the wollastonite skarn is as follows: $CaSiO_3$ (69.40%), SiO_2 (14.80%), $Ca_6Si_6O_{17}(OH)_2$ (13.10%), and $CaCO_3$ (2.6%). These components indicate that the rock is primarily composed of calcium silicate minerals, which are essential for enhancing soil properties. The particle size distribution was assessed using wet laser diffraction with a (Mastersizer 2000, Malvern), revealing that 90% of the particles were smaller than 58 μm, within a size range of 10 to 100 μm. Specifically, 10% of the particles fell between 10 and 22.41 μm, while 50% were within the 10 to 33.11 μm range. The specific surface area (SSA) was measured using multipoint Brunauer, Emmett, and Teller (BET) analysis (Micromeritics ASAP2460, USA), yielding an average SSA of 0.3327 $m^2\ g^{-1}$. The mineral composition was analyzed through X-ray diffraction (XRD) with a Malvern Panalytical Empyrean Series 3 diffractometer. The findings indicated significant levels of calcium (244.53 g kg^{-1}), silicon (178.54 g kg^{-1}), and magnesium (6.39 g kg^{-1}), accounting for the majority of the rock's composition. Further details on the experimental design and wollastonite skarn materials can be found in studies conducted at the same location (Bi et al., 2024; Xu et al., 2024b),and in the Appendix

S2.

2.2 Plant data collection

The above-ground properties encompassed tree productivity, herb diversity (Shannon index), and leaf litter production. Before any experimental treatment, all woody plants with a diameter at breast height (DBH) ≥ 1 cm were tagged and measured for their DBH and growth status at the starting point of the experiment, following protocols set by the Smithsonian Tropical Research Institute. Growth bands were installed to monitor changes in DBH. We assessed tree productivity by measuring the DBH increment over three years, specifically in October of each year.

In April 2023, to further explore the understorey diversity, three 1 × 1 m plots were randomly established within each plot for herbaceous plant surveys. In each plot, we placed one litter trap, which consisted of a 1 mm nylon mesh set within PVC frames covering a horizontal collection area of 0.75 m by 0.75 m. We collected the litter in these traps in November 31st of 2023. Although initially thought to lack shrub presence, subsequent observations during sampling indicated that shrubs were indeed present but had not significantly developed.

2.3 Soil collection

Soil collection for microbial and physicochemical analysis involved three soil cores (diameter of 2.5 cm) were extracted to a depth of 10 cm from each plot in April 2023, approximately two years after the initial treatment (April 2021). The region has distinct wet (May–October) and dry (November–April) seasons, which could impact soil properties, particularly during the nitrogen cycling processes. Each soil core from each plot was treated as an individual sample for microbial diversity analysis, totaling 27 samples (3 treatments × 3 plots × 3 soil cores). The physicochemical properties measured included soil pH, carbon content, nitrogen content, phosphorus content, sand, silt, and clay particle sizes. A summary of these diversity properties and soil microbial details is provided in Appendix S2. To assess the variability between replicates, we calculated the variances for both treatments and groups across all measured soil properties. Our results indicated that the variability between treatments was greater than the variability between groups. This finding suggests that the treatment effects are more pronounced and robust than the natural variability observed within the groups, lending support to the reliability of our conclusions (Appendix S1: Table S6).

2.4 Quantification of ecosystem multifunctionality

We quantified ecosystem multifunctionality using functions broadly relevant and potentially influenced by ERW. The functions were categorized into above-ground ecosystem functionality (EMF_{above}) and below-ground ecosystem functionality (EMF_{below}). EMF_{above} included tree production, herbaceous plant Shannon diversity, and litter production. EMF_{below} encompassed: i) Soil carbon-related ecosystem function (EMF_{c}), which was assessed using dissolved organic carbon (DOC), soil organic carbon (SOC), particulate organic carbon (POC), mineral-associated organic carbon (MAOC), soil carbon isotope content (SCC_{13}), and microbial biomass carbon (MBC); ii) Soil nitrogen-related ecosystem function (EMF_n), evaluated through dissolved organic nitrogen (DON), nitrate (NO_3^-), ammonium (NH_4^+), soil nitrogen isotope content (SNC_{15}), and microbial biomass nitrogen (MBN); iii) Soil phosphorus-related ecosystem function (EMF_p), assessed using inorganic phosphorus (Resin–P, $NaHCO_3$–P_i, NaOH–P_i, and C. HCl–P_i), organic phosphorus ($NaHCO_3$–P_o, NaOH–P_o, C. HCl–P_o, and Residual–P), and microbial biomass phosphorus (MBP); iv) Soil silicon-related ecosystem function (EMF_{Si}), evaluated using available silicon (ASi) and soil phytolith content (SPhC); v) Soil enzyme activity-related ecosystem function ($EMF_{Enzymes}$), assessed using β-1,4-glucosidase (BG), β-cellobiosidase (CHB), β-1,4-N-acetylglucosaminidase (NAG), leucine aminopeptidase (LAP), acid phosphatase (Aci-P), polyphenol oxidase (POX), and peroxidase; vi) The reduced relative abundance of fungal plant pathogens in soils ($EMF_{Pathogen}$), estimated by analyzing soil phylotypes obtained from high-throughput amplicon sequencing using the FUNGuild database (Nguyen et al., 2015). For the analysis, inverse values were used, meaning that higher values indicate a lower abundance of fungal plant pathogens, thus representing a more favorable function. Further details on the measurement methods are provided in the Appendix S2.

2.5 DNA extraction from soil and amplicon sequencing

We extracted total soil DNA from 0.25 g of fresh soil using the PowerSoil DNA Isolation Kit (MO BIO Laboratories, Carlsbad, CA, USA) following the manufacturer's instructions. For metabarcoding analysis, the bacterial 16S rRNA V4 region was amplified using the primer sets 515F and 806R, and the fungal ITS1 region was amplified using the primer sets ITS1F and ITS2-2043R. Shannon–Wiener diversity indices for soil fungi and bacteria were calculated separately, after rarefying to 30000 sequences for bacteria and 22000 sequences for fungi per soil sample. Further details on the methods are available in the supplementary materials (Appendix S2).

2.6 Statistical analyses

We created microbial association networks at plot levels for the three ERW treatment using the bacterial and fungal OTUs. Prior to the network construction, we removed rare and low-abundant OTUs (Operational Taxonomic Units, a term used to categorize bacteria based on DNA sequence similarity)which are OTUs that are present in six or fewer samples of each treatment and comprising less than 0.01% of the total number of reads. We used the "igraph" package for obtaining the network properties, with sub-networks for topological characteristics of each sample implemented in the subgraph function as previously described (Ma et al., 2016). We used linkage density, which represents the average number of connections per OTU, to denote network complexity (Wagg et al., 2019). Visualization of co-occurrence network was performed by using Gephi (Bastian et al., 2009).

We employed a linear mixed-effects model using the *lmer* function from the "lme4" package in R to explore how ERW impacts soil properties, microbial diversity, microbial network complexity, EMF_{above}, EMF_{below}, and EMF_{all}. This model utilized the

Latin-square blocking's rows and columns as random effects while treating the ERW application levels as fixed effects. The various amounts of ERW application were classified into categorical groups ("high", "low", and "control"). We assessed the statistical significance of the variations across the "ERW application groups" with the "emmeans" package (Lenth and Lenth, 2018). Then, we performed ordinary least squares linear regressions to evaluate the relationships of the soil microbial diversity and network complexity with multifunctionality approaches.

Finally, we conducted PLS-PM analysis to elucidate the direct and indirect impacts of ERW on ecosystem multifunctionality (EMF). Our priori model hypothesized that ERW could influence EMF through several pathways: a) direct impact of ERW on EMF; b) indirect impact on EMF through pH: ERW might alter soil pH, which can impact EMF directly or indirectly via its effects on microbial diversity and network complexity; c) indirect impact on EMF through microbial diversity: changes in soil pH due to ERW could affect microbial diversity, which might influence microbial network complexity (Kerfahi et al., 2024); d) indirect impact on EMF through network complexity: both ERW and microbial diversity are anticipated to affect microbial network complexity, which is hypothesized to be a significant predictor of EMF. In this model, microbial diversity impacts network complexity, which is crucial for maintaining ecosystem functionality (Wang et al., 2023) The pathway model thus incorporates both direct and indirect pathways through which ERW can affect EMF. PLS-PM was executed utilizing the "plspm" package (Sanchez et al., 2013). All statistical analyses were performed in R 4.6.1.

3. Results

3.1 Impact of ERW on soil properties, ecosystem functions and multifunctionality

The application of ERW strongly impact the biodiversity and function of soils in tropical plantations. Soil pH showed an average increase compared to the control ($p < 0.001$), from 4.98 in the control to 5.48 in the high ERW treatment. The low ERW treatment (5.08) did not result in a statistically significant change compared to the control. The high treatment increased clay content by approximately 11.0% compared to control ($p < 0.05$). The high treatment significantly decreased sand content by 49.59% compared to control ($p < 0.05$). Both high and low treatments resulted in non-significant changes in silt content (Appendix S1: Table S1).

The application of ERW significantly increased various soil functions. EMF_C increased by 63% with high ERW treatment and 31% with low ERW treatment (Fig. 1 a), driven by substantial increases in SOC (85%), MAOC (77%), and DOC (32%), though POC did not significantly change (Appendix S1: Table S1). EMF_N rose by 36% with high ERW treatment and 25% with low ERW treatment (Fig. 1 b), primarily due to significant increases in NO_3^- (97%) and NH_4^+ (102%). EMF_P increased by 67% with high ERW treatment and 32% with low ERW treatment (Fig. 1 c), particularly in Resin-P (116%), C. HCl–P_o (193%), and $NaHCO_3$-P_i (360%), although NaOH–P_i, C. HCl–P_i, $NaHCO_3$–P_o, and NaOH–P_o did not change significantly. EMF_{Si} increased by 106% with high ERW treatment and 18% with low ERW treatment (Fig. 1 d), with ASi (210%) and SPhC (82%) showing significant gains. $EMF_{Enzymes}$ varied, with significant increases in NAG (57%), BG (30%), and CHB (18%), while other enzymes showed no significant change (Fig. 1 e). The abundance of fungal pathogens decreased, improving $EMF_{Pathogen}$ by 152% with high ERW treatment and 31% with low ERW treatment (Fig. 1 f). EMF_{above} functions were not significantly affected (Fig. 2 a). Overall, EMF_{below} increased by 54% with high ERW treatment and by 25% with low ERW treatment (Fig. 2 b). EMF_{all} increased by 36% with high ERW treatment and by 17% with low ERW treatment (Fig. 2 c).

3.2 Responses of microbial properties to ERW

The inferred bacterial and fungal co-occurrence networks were predominantly characterized by positive associations, with the proportion of positive correlations ranging from 74% to 84% for bacterial networks and from 56% to 67% for fungal networks across the treatment with ERW. The increase in positive correlations with ERW application suggested that ERW fosters cooperative interactions among microbial taxa. Linkage density refers to the average number of connections that each node (microbial taxon) has within the network. Linkage density among taxa, for both bacteria and fungi, consistently increased with ERW application (Fig. 3 and Table S2) indicating an increase in network complexity. The Shannon index for microbial diversity showed non-significant differences among treatments for both bacteria (Appendix S1: Fig. S3 a & c) and fungi (Appendix S1: Fig. S3 b & d).

The major bacterial phyla identified were Chloroflexi, Planctomycetota, Proteobacteria, Acidobacteriota, and Actinobacteriota, comprising about 80% of all phyla (Appendix S1: Fig. S4). The ERW treatment significantly increased the relative abundance of Proteobacteria ($P<0.05$). For bacterial classes, Planctomycetes, Ktedonobacteria, Acidobacteriae, Alphaproteobacteria, Gammaproteobacteria, and Actinobacteria made up 65% of the total, with Ktedonobacteria significantly decreasing under 'high' ERW treatment ($P<0.05$) (Appendix S1: Fig. S5).

In fungal communities, Basidiomycota, Ascomycota, and Mortierellomycota dominated, accounting for 93.2% of the total (Appendix S1: Fig. S6). 'High' ERW treatment increased Basidiomycota and decreased Ascomycota relative abundance significantly ($P<0.05$) (Appendix S1: Fig. S6). The major fungal classes, Tremellomycetes, Sordariomycetes, and Agaricomycetes, represented 52% of the total, with Agaricomycetes significantly increasing under 'high' ERW treatment ($P<0.05$) (Appendix S1: Fig. S7).

3.3 Contribution of soil microbial diversity and network complexity to ecosystem multifunctionality

Our linear regression modeling showed that bacterial network complexity significantly influenced EMF_{above}, EMF_{below}, and EMF_{all}, whereas network complexity and the diversity of both bacteria and fungi had minor or no significant effect on EMF_{above}. Bacterial network complexity, on average, explained 57.9% (ranging from 18.0% to 80.5%) of EMF_{above}, EMF_{below}, and EMF_{all}, while fungal network complexity explained, on average, 59.8% (ranging from 57.4% to 62.1%) of EMF_{below} and EMF. Bacterial diversity explained, on average, 19.5% (ranging from 16.6% to 23.3%) of EMF_{below} and EMF_{all}, while fungal diversity explained 17.5% (ranging from 17.0% to

18.0%). The model slopes indicated that the influence of network complexity was greater than that of diversity.

PLS-PM analysis for EMF showed that ERW primarily increased multifunctionality indirectly (Fig. 5). PLS-PM analysis for EMF_{above} revealed relatively weak impacts of ERW. The total effect of ERW on EMF_{below} was 0.3479, with direct contributions from ERW (0.0696), and indirect contributions from pH (0.2336), network complexity (0.1601), and microbial diversity (-0.1241). The total effect of ERW on EMF_{all} was 0.7857, with direct contributions from ERW (0.1933), and indirect contributions from pH (0.2824), network complexity (0.3282), and a minimal effect from microbial diversity (-0.0182). For EMF_{below}, the analysis indicated substantial indirect effects of ERW (0.5802) compared to direct effects (0.2493). The total effect of ERW on EMF_{below} was 0.8295, with direct contributions from ERW (0.2493), and indirect contributions from pH (0.2667), network complexity (0.2868), and a minimal effect from microbial diversity (0.0137). Overall, the PLS-PM analysis highlighted the significant role of pH and network complexity in mediating the effects of ERW on ecosystem multifunctionality, particularly EMF_{below}, through indirect pathways involving soil pH and microbial interactions.

4 Discussion

Our results showed that ERW significantly increase EMF_{all} and EMF_{below}, but had a limited effect on EMF_{above}, highlighting the potential of ERW to indirectly enhance soil health in nutrient poor ecosystems such as those of tropical plantations. Changes in EMF_{all} in response to ERW were especially important for carbon, phosphorus, and silicon, as well as for plant pathogen control. Some of these results may be the consequence of nutrient addition from ERW and further associated reductions in soil acidity, which are both known to be critical limiting factors of soil processes and biodiversity. This knowledge is important to better understand how to promote ecosystem function in afforested ecosystems in nutrient poor ecosystems such as those of tropical forests.

4.1 The impacts of ERW on soil properties and ecosystem multifunctionality

The observed reduction in sand content following the ERW treatment can be attributed to the particle size distribution of the added mineral. The wollastonite skarn particles primarily ranged from 10 to 57.534 μm, which is closer to silt or fine sand (Bittelli et al., 1999). Additionally, the application timing coincided with the onset of the rainy season, which enhances weathering processes. The significant rainfall promotes the weathering of wollastonite skarn, leading to an increase in smaller clay particles (Jariwala et al., 2022).

We found that ERW significantly increases EMF_c (Fig. 1a) mainly due to increased SOC (represents the total organic carbon in the soil) and MAOC (fraction of stable SOC that is bound to soil minerals. ERW treatment at the site was found to have significantly increased soil Ca, Si, Fe, and Mg concentrations (Xu et al., 2024a), in line with theoretical understanding of their impact on adsorption, co-precipitation, and complexation of organic matter, reducing the bioavailability of organic carbon and increasing its storage (Wang et al., 2024; Xu et al., 2021; Zhao et al., 2024). Moreover, we observed that SCC_{13} increased with the treatments, suggesting enhanced carbon stabilization. This may be due to increased mineral interactions that protect organic carbon from microbial decomposition (Rowley et al., 2018).

Regarding nitrogen, the treatment with ERW significantly increased EMF_N (Fig. 1b). There was a substantial rise in nitrate (NO_3^-) and ammonium (NH_4^+), indicating that ERW enhances nitrogen availability in the soil. While higher pH levels generally create a more favorable environment for microbial activity (Yan et al., 2023), enhancing processes such as nitrification and ammonification (Cheng et al., 2019), the response of soil bacterial diversity might be muted if the soils are already approaching an optimal pH range for these communities, as suggested by Lauber et al.(2009). The study found that bacterial phylogenetic diversity peaks at subneutral pH, which might explain the relatively modest effects of pH increases on bacterial diversity in our study. ERW treatment led to a significant increase in EMF_P (Fig. 1c), with notable changes in both inorganic and organic phosphorus availability. These findings highlight the enhanced mobilization and mineralization of phosphorus due to ERW. Bi's research supports these results by explaining that ERW enhances soil microbial functional groups involved in phosphorus cycling, including increased solubilization of inorganic phosphorus and mineralization of organic phosphorus by microbial phosphatases and root exudates (Bi et al., 2024). Additionally, ERW shifts plant phosphorus acquisition strategies from reliance on fine roots to mycorrhizal collaboration, improving phosphorus uptake efficiency (Bi et al., 2024). In our study, the increase in phosphorus stocks can be attributed to the phosphorus released from the added ERW. Thus, while Bi's study emphasized changes in microbial activity and root exudates as mechanisms for increased phosphorus availability, our findings suggest that the direct contribution of phosphorus from ERW also plays a crucial role. Recent findings by Wood et al. (2023) suggest that phosphorus dynamics in ERW are influenced by soil adsorption processes, limiting phosphorus's role in enhancing wollastonite weathering. This highlights the need to consider soil interactions when assessing phosphorus's impact on CO_2 sequestration. Together, these findings suggest that both direct contributions from ERW and soil adsorption dynamics play crucial roles in phosphorus mobilization and availability.

A key finding in our study was the significant reduction in the relative abundance of potentially pathogenic fungi in the soil following ERW treatment (Fig. 1d). This reduction can be linked to increased silicon cycling in the soil, which has been shown to influence the structure and function of the soil microbial community (de Tombeur et al., 2020). Enhanced silicon may improve plant health indirectly by fostering a more balanced microbial community, potentially reducing the presence of pathogens (Debona et al., 2017; Fauteux et al., 2005). Additionally, silicon has been reported to enhance plant resilience to environmental stresses, such as drought and salt stress, by improving plant stress tolerance (Guntzer et al., 2012).

While ERW treatment increased EMF_{below} and EMF, the impact on EMF_{above} was not statistically significant (Fig. 2a). One possible explanation is that ERW primarily affected ecosystem functions by improving soil conditions and fostering the complexity of soil microbial networks, which more directly influence soil-related processes and functions (Deng et al., 2023). The effects of ERW on EMF_{above} are indirect and likely take longer than the experiment duration of two years to manifest as it is often found in P addition experiments (Lin et al., 2019). The observed changes in root traits and root exudates could be a first indication for an overall plant response to ERW (Bi et al., 2024). We acknowledge that the observed increase in pH remained within the optimal range for *Hevea brasiliensis* (4.0 to 6.5)(Yeang et al., 1986), which likely reduced aluminum toxicity in the soil. However, repeated or higher ERW treatments could potentially raise pH beyond the tolerance range of *Hevea*, negatively affecting plant growth. In future studies, careful monitoring of pH levels will be essential to prevent this. Dharmakeerthi et al. (2012) have suggested the use of sulfate of ammonia to arrest pH increases, which could serve as a potential management strategy should pH rise excessively with continued ERW applications.

While our current study observed mostly linear increases in multifunctionality with increased ERW treatment, we acknowledge the importance of considering potential nonlinear or plateauing effects at higher application levels. These effects could emerge as ecosystem responses reach a saturation point, beyond which additional wollastonite skarn may not yield proportional benefits or could even have negative impacts. Future studies employing a broader range of wollastonite skarn levels would be invaluable in elucidating such potential dynamics more comprehensively.

4.2 Network complexity drives ecosystem multifunctionality

Our analysis demonstrates that microbial network complexity is a more significant and factor influencing soil multifunctionality than microbial diversity (Fig. 4). This supports our hypothesis of a positive relationship between complexity of microbial networks and ecosystem multifunctionality. The ecological functions from microbes result from numerous interactions among and within different microbial communities, affecting resource use efficiency and metabolic regulation (Ghosh et al., 2016; Li et al., 2022).

The improvement of microbial network complexity through ERW can be attributed to several factors. ERW increases the availability of essential nutrients such as silicon, calcium, and other minerals, which are critical for microbial growth and function (Beerling et al., 2018; Debona et al., 2017). Bi et al 2024 showed that ERW at the site indeed improved soil phosphorus fertility which was shown to increase soil nitrogen stocks and soil carbon stabilization in a range of ecosystems (Wang et al., 2022). ERW affects soil physicochemical properties, particularly soil pH. In the case of acidic soils, an increase in pH levels creates a more favorable environment for microbial communities, enhancing their growth and metabolic activities (Pietri and Brookes, 2008; Rousk et al., 2009). The presence of calcium carbonate in the wollastonite skarn may also contribute to pH buffering effects in the soil, enhancing nutrient availability (Jariwala et al., 2022).The increase in soil pH, along with the addition of silicon, provides better conditions for the formation of stable microbial networks. This observation resonates with recent studies suggesting that structural properties of networks, such as complexity and connectivity, may play a decisive role in maintaining ecosystem functions under environmental changes (Delgado-Baquerizo et al., 2020;

Morriën et al., 2017).
Our analysis demonstrates that network complexity is a more significant and stable factor influencing soil multifunctionality than microbial diversity (Fig. 4). This supports our hypothesis that complex microbial networks enhance multifunctionality to a greater extent. The ecological processes driven by microbes result from numerous interactions among microbial communities, leading to higher resource use efficiency and metabolic regulation through integrated metabolic pathway (Ghosh et al., 2016; Li et al., 2022).

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4.3 The direct and indirect effects of ERW on EMF_{all} and EMF_{below}

ERW significantly increased EMF and EMF_{below} primarily through indirect pathways, such changes in soil pH and an increased complexity of soil microbial networks, highlighting the complex interplay between soil chemistry and microbial ecology in enhancing ecosystem functions (Philippot et al., 2024).

The significant role of microbial network complexity in mediating the effects of ERW on EMF_{all} and EMF_{below} underscores the importance of microbial interactions in soil health, which are crucial for efficient nutrient cycling and organic matter decomposition (Soong et al., 2020). The greater indirect effects from microbial network complexity on EMF and EMF_{below} compared to pH suggest that the structural changes in microbial communities have a profound impact on ecosystem functions.

Soil pH directly influences nutrient availability and microbial activity, creating favorable conditions for plant growth and microbial processes (Taylor et al., 2021). However, the larger influence of microbial network complexity indicates that the synergistic interactions within the microbial community are more critical for driving the multifunctionality of the ecosystem. In the case of EMF_{above}, the indirect effects of ERW mediated by soil pH are more than those mediated by microbial network complexity. This difference can be attributed to the direct influence of soil pH on plant nutrient uptake and growth (Guo et al., 2023). Above-ground functions, such as plant growth and productivity, are more directly affected by soil pH, which alters nutrient availability in a way that is immediately accessible to plants (Guntzer et al., 2012; Marschner, 2011) and thus, pH plays a more dominant role in enhancing EMF_{above}.

Interestingly, the impact of microbial diversity on EMF and EMF_{below} is minimal, and it even has a negative effect on EMF_{above}. This finding suggests that while microbial diversity is generally considered beneficial for ecosystem resilience and function (Gentry et al., 2015),, it may not always correlate directly with enhanced ecosystem multifunctionality The negative effect on EMF_{above} could be due to competitive interactions among diverse microbial taxa, which might lead to less efficient nutrient use and lower plant productivity (Chen et al., 2024; Jariwala et al., 2022). Additionally, the functional redundancy within microbial communities means that increases in diversity do not necessarily translate to increased functionality if key functions are already performed by existing taxa (Yan et al., 2023). In addition, following ERW treatment, soil calcium concentrations significantly increased (Xu et al., 2024a), which may have influenced fungal community composition. Tedersoo et al. (2014) emphasized that calcium is an important predictor of fungal, particularly

Basidiomycetes, species richness. Although this study primarily focused on the role of pH in driving microbial processes, it can be inferred that increased calcium concentrations also played a role in influencing fungal richness and community structure. The potential effects of calcium on fungi (especially Basidiomycetes) and its interactions with changes in other soil nutrients may help explain the observed fungal community responses. In addition, future studies should explore how ERW-induced calcium ion availability might influence microbial life-history strategies that are not captured by microbial diversity and network analyses. For instance, calcium may induce shifts in bacterial community composition from r-strategists to K-strategists, which are characterized by higher carbon and nitrogen use efficiencies, thus potentially affecting ecosystem multifunctionality in ways not fully reflected by network complexity alone (Hu et al., 2023; Shabtai et al., 2023).

Repeated ERW applications, as recommended for sustained carbon dioxide removal (Beerling et al., 2020), may alter soil chemistry by further increasing pH and calcium levels. While higher pH can enhance nutrient availability, exceeding the optimal range for *Hevea brasiliensis* could negatively impact plant health. It is essential to monitor these changes to maintain soil ecosystem function without adverse effects.

Additionally, ongoing and future studies at our site will further explore the interactions of ERW with other soil amendments and their effects on soil water retention capacity, as well as examine CO_2 removal rates associated with these practices. Complementary studies are being conducted to quantify CO_2 removal rates in relation to ERW, including the sampling of pore waters to measure chemical changes over time (Jerden et al., 2024). Such studies will provide a more holistic understanding of the impacts of ERW on ecosystem functionality, carbon sequestration, and soil chemistry. Although we did not measure base cation levels outside the plantation, we acknowledge this as a limitation in assessing potential calcium depletion due to harvesting (Turner and Lambert, 2011). Future studies will aim to compare these levels to better understand the impacts of harvesting.

5. Conclusions

Our research highlights the potential of ERW to increase key ecosystem functions related to biogeochemical cycles, resistance to plant pathogens, thereby enhancing soil carbon storage, nutrient status and overall ecosystem health. Our findings underscore the pivotal role of changes in soil pH and microbial interactions in mediating the changes in ecosystem multifunctionality. ERW fosters a richer and more interconnected microbial network, which drives changes in soil multifunctionality, surpassing the influence of microbial diversity alone. Direct effects of ERW on EMF were less pronounced. The changes in ecosystem functioning, mediated by interconnected responses of plants, microbes and the physico-chemical soil environment highlights the need for a holistic assessment of ecosystem responses to ERW to avoid unwanted side-effects and maximize wanted ones.

Data Availability Statement

Raw sequencing data have been uploaded to the NCBI sequencing Read Archive under the BioProject identifiers PRJNA1072228 (https://www.ncbi.nlm.nih.gov/sra/).

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Fig. legends

Fig. 1 The comparisons of ecosystem functions across the different ERW application rates by a linear mixed-effects model. (a) EMF_C: ecosystem function related to carbon; (b) EMF_N: ecosystem function related to nitrogen; (c) EMF_P: ecosystem function related to phosphorus; (d) $EMF_{Pathogen}$: ecosystem function related to the resistance to plant pathogens ; (e) $EMF_{Enzymes}$: ecosystem function related to the activities of soil enzymes; (f) EMF_{Si}: ecosystem function related to silicon. Values and 95% confidence intervals in the figure are derived from a contrast analysis of the model. Asterisks represent significant differences among wollastonite application treatments. Significant path coefficients are marked with asterisks: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. “Control” referred to no wollastonite skarn addition(n=3); “Low” referred to an addition of 0.25 kg m^{-2}, n=3; “High” referred to an addition of 0.50 kg m^{-2}, n=3.

Fig. 2 The comparisons of above-ground multifunctionality (EMF_{above}) (a), below-ground multifunctionality (EMF_{below}) (b) and ecosystem multifunctionality (EMF_{all}) (c) across the different ERW application rates by a linear mixed-effects model. Data has been transformed using the z-score method. Values and 95% confidence intervals in the figure are derived from a contrast analysis of the model. Significant path coefficients are marked with asterisks: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.. “Control” refers to no wollastonite skarn addition (n=3); “Low” refers to an addition of 0.25 kg m^{-2}, n=3; “High” refers to an addition of 0.50 kg m^{-2}, n=3).

Fig. 3 Network visualization of bacterial (a) and fungal (b) co-occurrence patterns in the treatment with ERW at different amounts: "low" and "high". The size of each node represents the relative abundance of Operational Taxonomic Units (OTUs), and the colors of the nodes correspond to different network modules identified using the greedy modularity optimization method. The lines connecting nodes, referred to as "edges," illustrate interactions between OTUs. Green edges indicate positive interactions, while red edges indicate negative interactions, demonstrating the complex interplay within microbial communities. “Control” referred to no wollastonite skarn addition(n=3); “Low” referred to an addition of 0.25 kg m^{-2}, n=3; “High” referred to an addition of 0.50 kg m^{-2}, n=3.

Fig. 4 Linear regression of microbial diversity (in red) and network complexity (in blue) on EMF_{above} (a, b), EMF_{below} (c, d), and EMF_{all} (e, f) for bacteria (a, c, e) and fungi (b, d, f). Data has been transformed using the z-score method. Only significant models ($P<0.05$) are presented with their R-squared and slope values. “Control” refers to the addition of no wollastonite (n=3); “Low” refers to an addition of 0.25 kg m^{-2} of wollastonite (n=3); High refers to an addition of 0.50 kg m^{-2} of wollastonite (n=3). HB, Shannon diversity index for bacteria; HF, Shannon diversity index for fungi; NCB, network complexity of bacteria; NCF, network complexity of fungi.

Fig. 5 Partial least squares pathway modeling (PLS-PM) was performed to determine the indirect and/or direct effects on EMF_{above} (a), EMF_{below} (b), and EMF_{all} (c) among wollastonite, pH, microbial diversity and network complexity. "Model GOF" stands for "Goodness of Fit," which evaluates how well the model fits the observed data. Significant path coefficients are marked with asterisks: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

769 **Fig. 1**

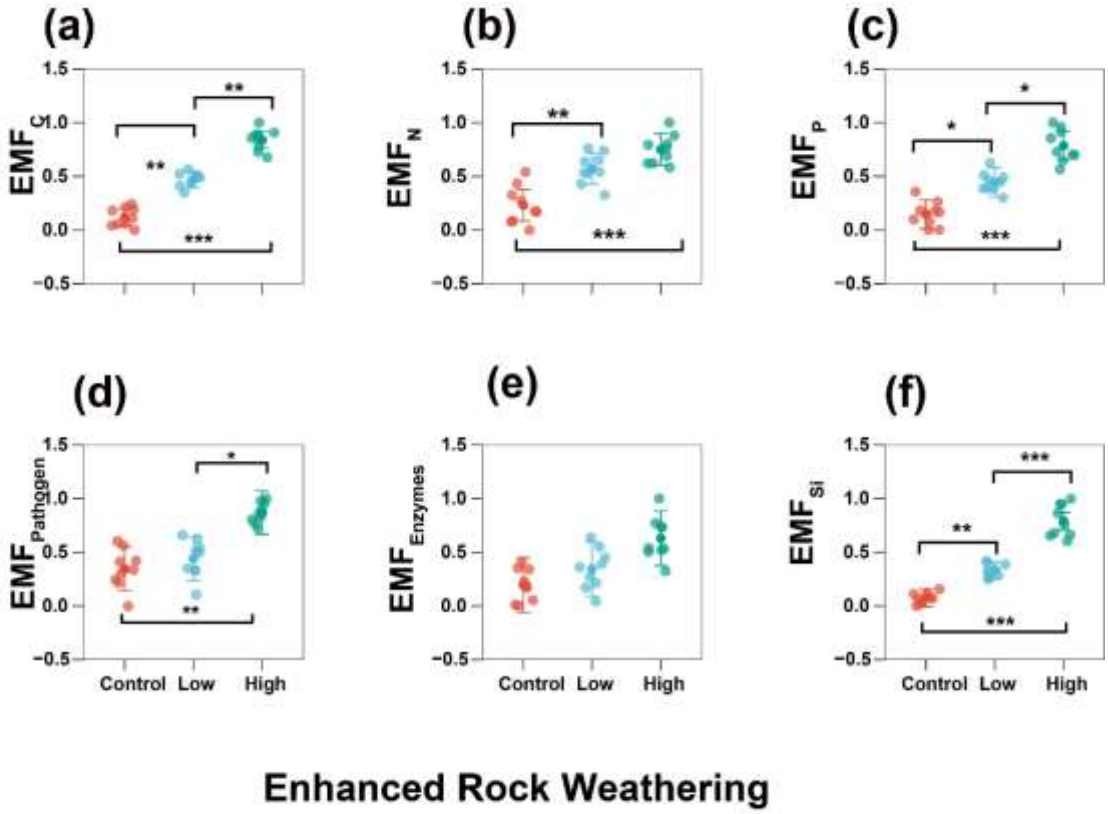

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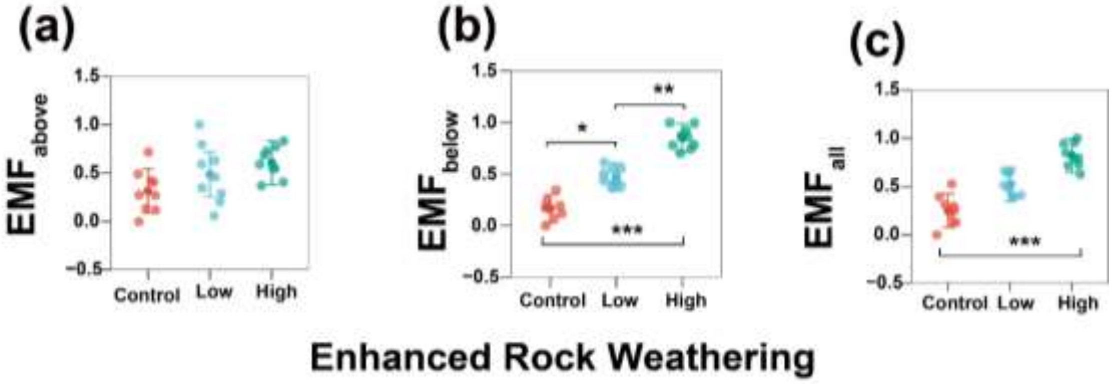
Fig. 2



(a)
EMF_above
1.5
1.0
0.5
0.0
−0.5
Control
Low
High
(b)
EMF_below
*
**
***
(c)
EMF_all
***
Enhanced Rock Weathering

778 **Fig. 3**

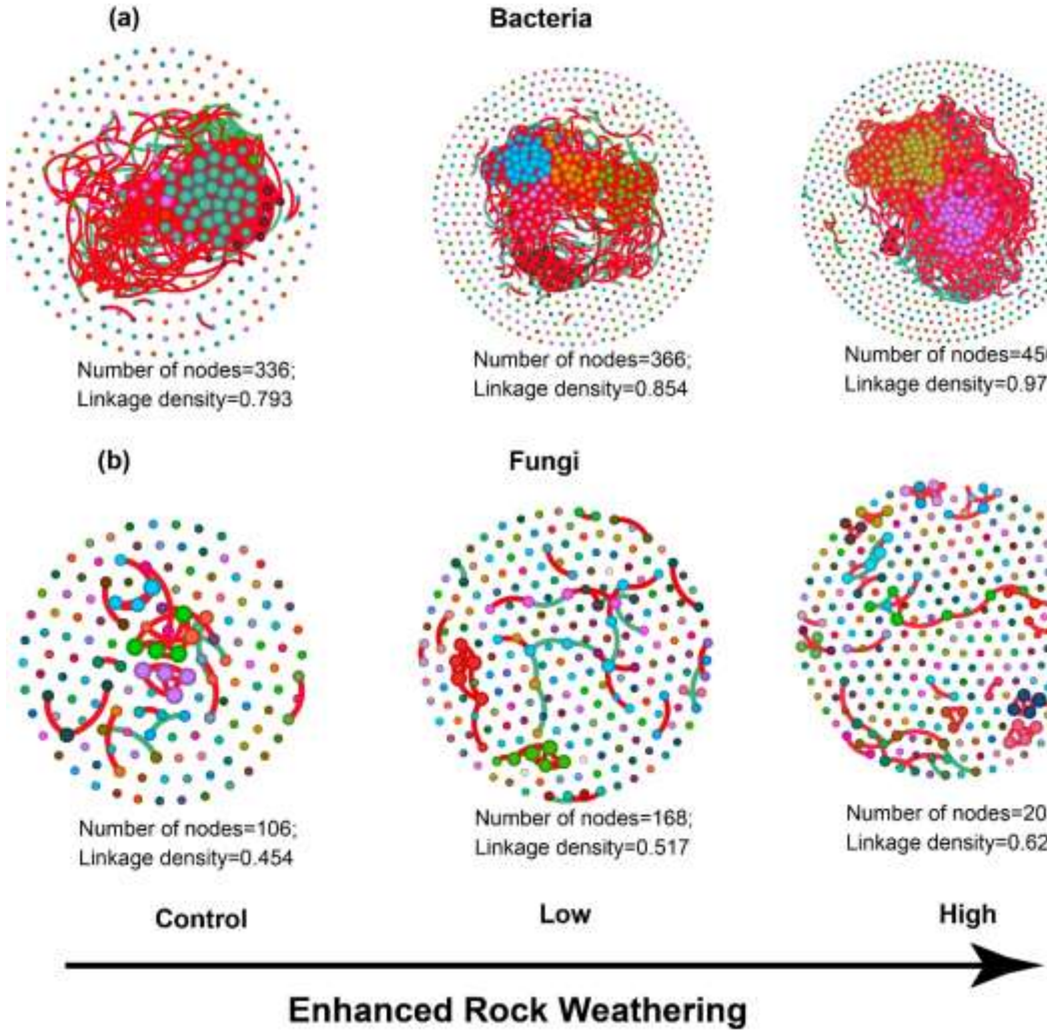


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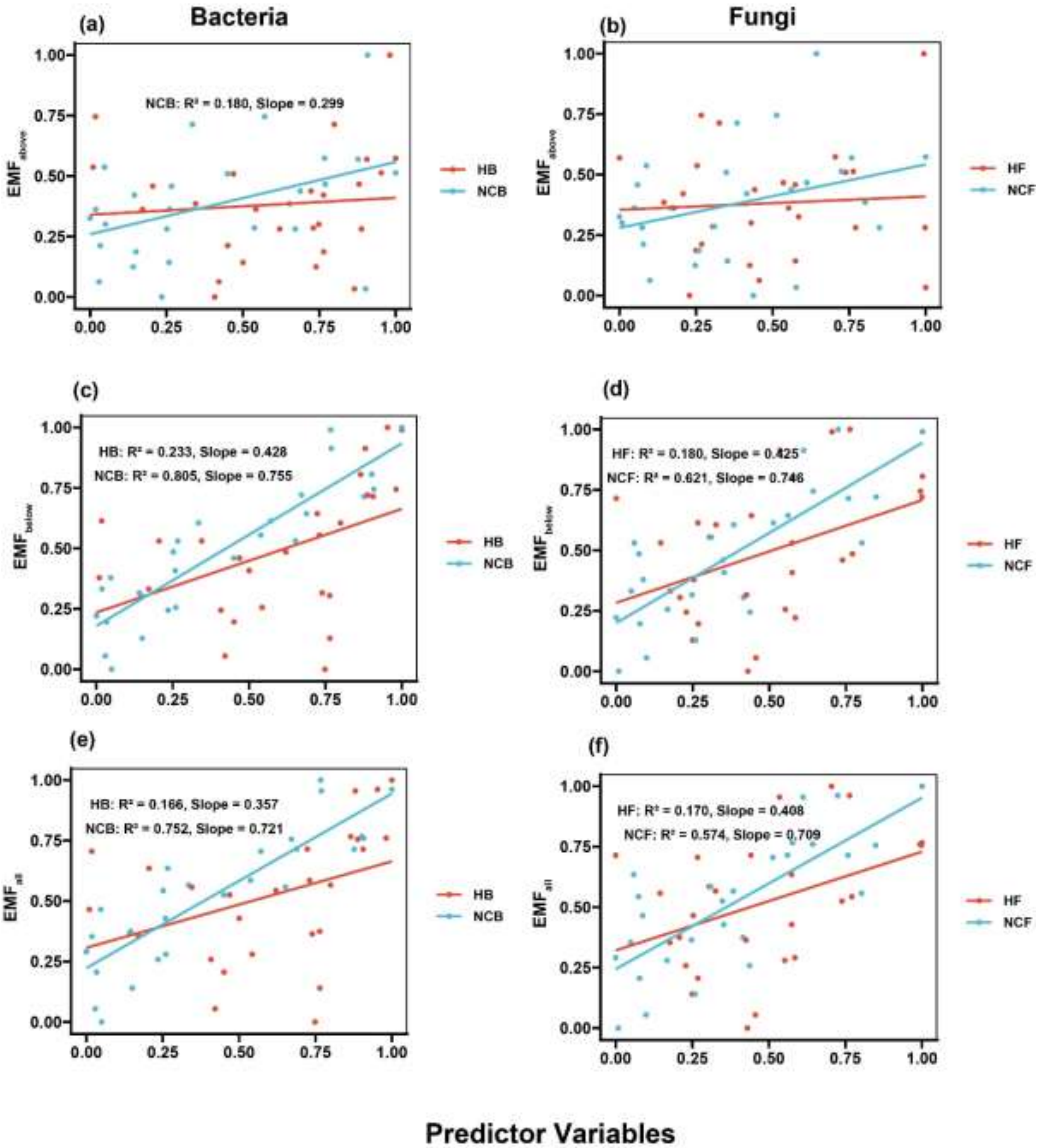
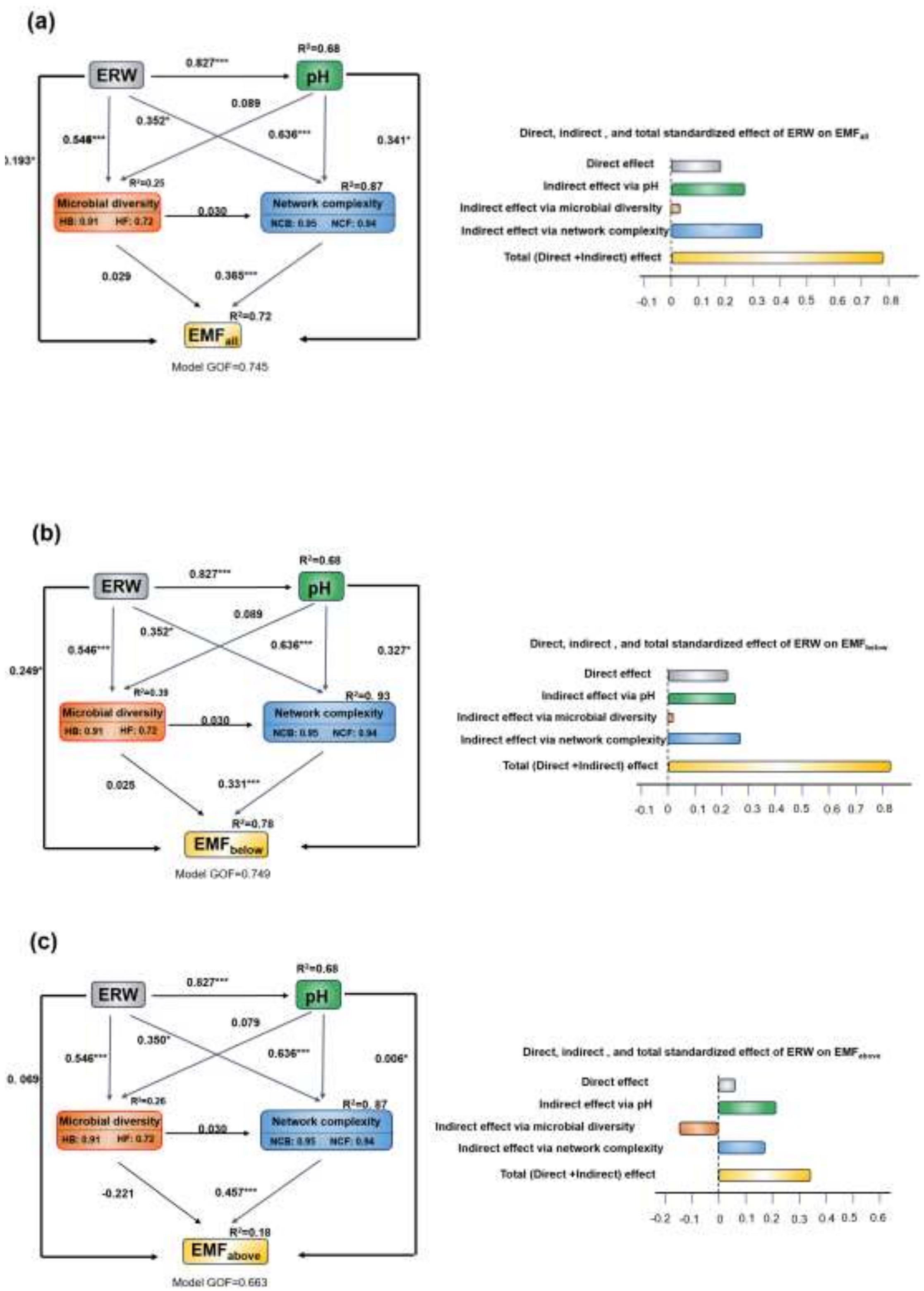
Fig. 4



(a)
Bacteria
NCB: R² = 0.180, Slope = 0.299
EMF_above
HB
NCB
(b)
Fungi
EMF_above
HF
NCF
(c)
HB: R² = 0.233, Slope = 0.428
NCB: R² = 0.805, Slope = 0.755
EMF_below
HB
NCB
(d)
HF: R² = 0.180, Slope = 0.425
NCF: R² = 0.621, Slope = 0.746
EMF_below
HF
NCF
(e)
HB: R² = 0.166, Slope = 0.357
NCB: R² = 0.752, Slope = 0.721
EMF_all
HB
NCB
(f)
HF: R² = 0.170, Slope = 0.408
NCF: R² = 0.574, Slope = 0.709
EMF_all
HF
NCF
Predictor Variables

Fig. 5



(a)
ERW
pH
R²=0.68
0.827***
0.089
0.352*
0.546***
0.636***
0.341*
0.193*
R²=0.25
R²=0.87
Microbial diversity
HB: 0.91 HF: 0.72
Network complexity
NCB: 0.95 NCF: 0.94
0.030
0.029
0.365***
R²=0.72
EMFall
Model GOF=0.745
Direct, indirect , and total standardized effect of ERW on EMFall
Direct effect
Indirect effect via pH
Indirect effect via microbial diversity
Indirect effect via network complexity
Total (Direct +Indirect) effect
-0.1 0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8
(b)
ERW
pH
R²=0.68
0.827***
0.089
0.352*
0.546***
0.636***
0.327*
0.249*
R²=0.39
R²=0. 93
Microbial diversity
HB: 0.91 HF: 0.72
Network complexity
NCB: 0.95 NCF: 0.94
0.030
0.025
0.331***
R²=0.78
EMFbelow
Model GOF=0.749
Direct, indirect , and total standardized effect of ERW on EMFbelow
Direct effect
Indirect effect via pH
Indirect effect via microbial diversity
Indirect effect via network complexity
Total (Direct +Indirect) effect
-0.1 0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8
(c)
ERW
pH
R²=0.68
0.827***
0.079
0.350*
0.546***
0.636***
0.006*
0. 069
R²=0.26
R²=0. 87
Microbial diversity
HB: 0.91 HF: 0.72
Network complexity
NCB: 0.95 NCF: 0.94
0.030
-0.221
0.457***
R²=0.18
EMFabove
Model GOF=0.663
Direct, indirect , and total standardized effect of ERW on EMFabove
Direct effect
Indirect effect via pH
Indirect effect via microbial diversity
Indirect effect via network complexity
Total (Direct +Indirect) effect
-0.2 -0.1 0 0.1 0.2 0.3 0.4 0.5 0.6