

The trade-offs among fungal guilds are associated with soil organic carbon dynamics in alpine ecosystems

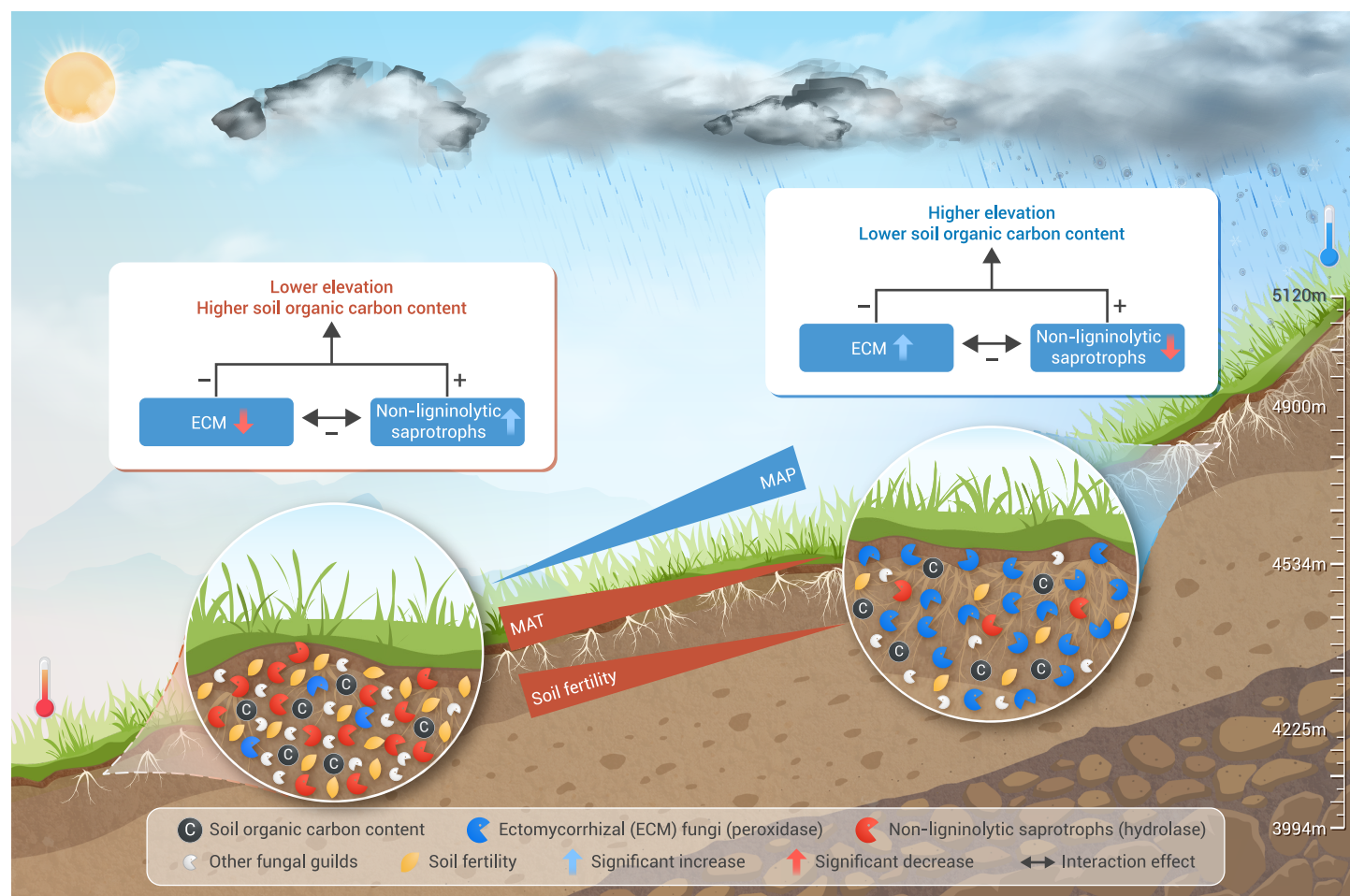
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GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- Soil organic carbon (SOC) decreases by 28% along the 3,994–5,120 m alpine gradient.
- This decline is linked to trade-offs between ectomycorrhizal fungi and non-ligninolytic saprotrophs.
- At higher elevations, ectomycorrhizal fungi dominate, linked to peroxidase activity and SOC turnover.
- SOC fate is linked to trade-offs between fungal guilds along elevation gradients in alpine ecosystems.

The trade-offs among fungal guilds are associated with soil organic carbon dynamics in alpine ecosystems

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Alpine ecosystems have vast amount of soil organic carbon (SOC) and are highly sensitive to climate change. Soil fungi play a crucial role in SOC cycling as decomposers but their contribution to alpine SOC dynamics across high elevation gradients remain poorly understood. Here, we explored fungal communities and their relationships with SOC content across an elevational gradient from 3,994 to 5,120 m on the Tibetan Plateau. We found that SOC content decreased by 28.3% from low to high elevation caused by the trade-offs between ectomycorrhizal fungi and non-ligninolytic saprotrophs. Higher elevation soils, with colder, wetter conditions and lower fertility, were dominated by ectomycorrhizal fungi at the expense of non-ligninolytic saprotrophic fungal species through environmental filtering and nutrient competition. Furthermore, ectomycorrhizal fungi are positively correlated with peroxidative enzyme activities, suggesting enhanced SOC turnover. Our work provides new evidence of, and insights into, the potential role of specific fungal guild trade-offs in shaping SOC fate in fragile alpine ecosystems.

INTRODUCTION

As the largest and highest alpine ecosystem, the Tibetan Plateau holds a large yet unstable soil organic carbon (SOC) pool shaped by its sensitivity to climate change.^{1–3} Even a minor change in SOC content in this region could significantly elevate atmospheric CO₂ levels, thereby triggering positive climate feedback.⁴ The build-up of SOC content depends on the balance between plant C inputs and microbial-mediated soil C losses, with soil fungi as key regulators of SOC turnover.⁵ The Tibetan Plateau's elevation gradients span distinct climate regimes, offering a space-for-time framework to investigate how climate warming alters fungal-mediated SOC decomposition. However, how fungal communities regulate SOC turnover across distinct alpine gradients remains unclear, constraining our ability to predict C-climate feedbacks in warming.

Current uncertainties regarding the link between fungal communities and SOC fate in alpine ecosystems arise from two main gaps. First, empirical data on SOC dynamics above 4,000 m, or even 5,000 m, remain scarce. Such data can enhance our understanding of the global C balance and alpine ecosystem stability.⁶ Second, although fungal communities have been identified as key drivers of SOC turnover in temperate and boreal ecosystems,^{7–11} their functional roles under high elevation alpine ecosystems remain poorly documented. For example, the "Gadgil effect" proposes competitive interactions between Ectomycorrhizal (ECM) fungi and saprotrophs that regulate SOC processes in boreal ecosystems,¹² but its applicability in alpine environments remains uncertain. High elevation environment, including nutrient scarcity and climatic stress, likely reshape fungal communities through environmental filtering and competitive exclusion, with significant implications on SOC decomposition and stabilization.¹³ Furthermore, recent evidence also ques-

tions the capacity of ECM fungi to retain peroxidase gene expression, indicating that ECM fungi may either impede or enhance SOC accumulation through trade-offs with saprotrophic fungi.^{11,14,15} Thus, a thorough understanding of fungal contributions to SOC dynamics across alpine environmental gradients is necessitated for predicting alpine SOC fate and securing the stability of terrestrial ecosystems under climate change.

We investigated how fungal communities are associated with SOC content along an elevational gradient from 3,994 to 5,120 m in the Tibetan Plateau. We hypothesize that (1) elevational SOC patterns may be linked to trade-offs between ECM fungi and saprotrophs; (2) soils at higher elevations, constrained by nutrient limitation and climatic stress, tend to be increasingly dominated by ECM fungi at the expense of non-ligninolytic saprotrophic fungi; (3) ECM fungi potentially influence SOC turnover through their capacity to secrete peroxidases. Our work aims to fill knowledge gaps in understanding alpine SOC fate, providing insights into microbial-driven alpine SOC processes as well as associated C-climate feedback.

MATERIALS AND METHODS

Study sites and data collection

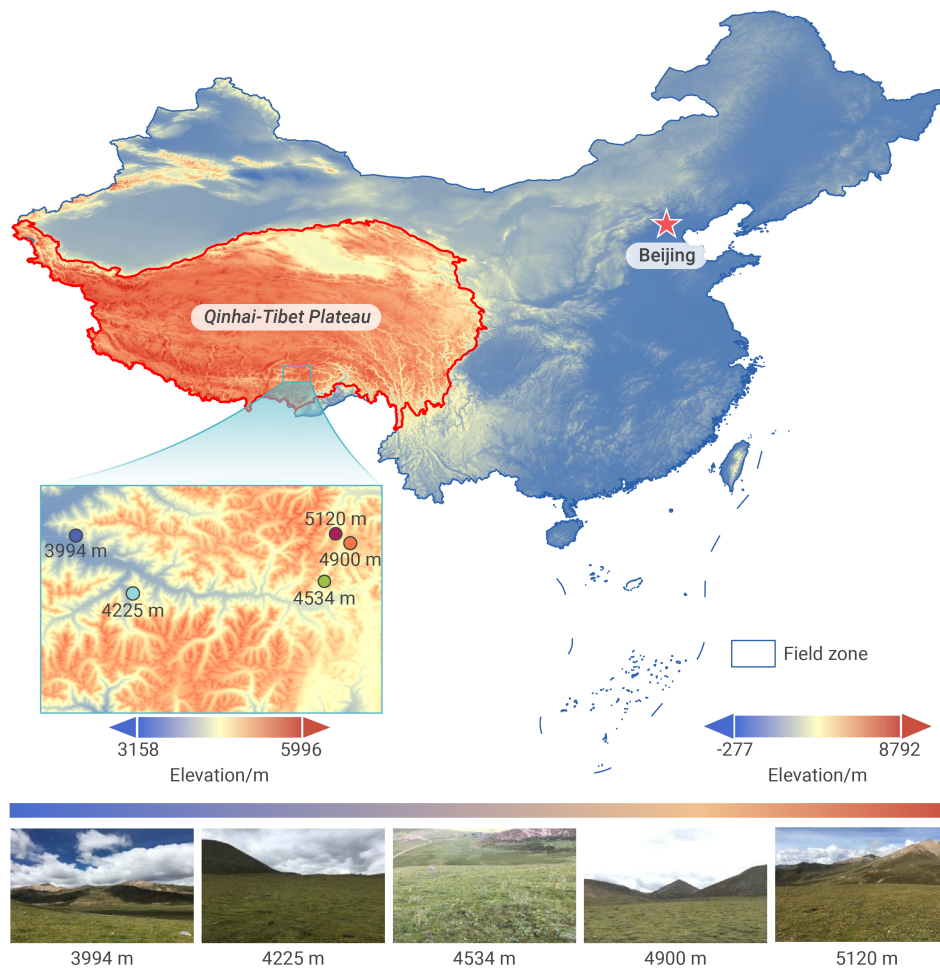
The study was conducted in the Mount Mila region (29°42'26" to 29°49'42" N, 91°48'55" to 92°21'31" E) in Lasa, China, covering an elevational gradient at 3,994, 4,225, 4,534, 4,900, 5,120 m above sea level (m a.s.l.) (Figure 1). The sampling sites were selected to represent typical vegetation types (alpine meadow) and soil types (frigid calcic soils) of the southeastern Tibetan Plateau.¹⁶ All selected sites were devoid of topographic variations (< 5%, as measured by the App VELUX), visible effects of grazing, and anthropogenic activities. To avoid climatic bias, mean annual temperature (MAT) and mean annual precipitation (MAP) of the study sites were extracted from the WorldClim database (<https://www.worldclim.org/>) using the geographical coordinates.

Sampling occurred in early August 2019, coinciding with peak vegetation growth and maximum microbial activity. At each elevation, 10 plots (1×1 m each, spaced approximately 50 m apart) were established to assess plant biomass, including both aboveground and belowground (i.e., root) biomass, as well as the biomass of the dominant species (i.e., *Kobresia*). Within each plot, 6–7 surface soil cores (5 cm in diameter, 15 cm in depth) were collected and combined into a single composite sample per plot. In total, 50 soil samples were collected. After sieving through a 2 mm mesh to remove visible stones, samples were divided into two portions: one was stored at -20°C for physicochemical parameter analysis, while the other was frozen at -80°C for DNA extraction.

Soil physicochemical properties and enzyme activities

Soil texture was determined by dispersing 15 g of air-dried soil in a 3% aqueous hexametaphosphate solution (hexametaphosphate: Soil ratio = 3:1)

Figure 1. Information about the sampling sites Schematic representation of the Qinghai-Tibet Plateau in China, detailing the spatial distribution of each sampling site along with photographic depictions of each location.



and stirring at 120 rpm. The percentages of sand and silt were calculated based on the mass of the original sample after drying at 105°C to constant weight. The clay fraction was then computed as the remainder, obtained by subtracting the combined percentages of sand and silt from 100%. Soil pH was measured using a pH meter (UV-1800; Shimadzu) in a 1:5 soil-to-deionized water suspension, with equilibration for 30 minutes.

SOC content was measured using an auto-analyzer (Shimadzu, Kyoto, Japan) after the removal of inorganic C with 1 mol/L HCl. Soil ammonium nitrogen ($\text{NH}_4^+\text{-N}$) was extracted with 2 mol/L KCl and analyzed using a Flow-Solution analyzer (Flowsys, Ecotech, Essen, Germany). Soil available phosphorus (SAP) was quantified from NaHCO_3 extracts using the molybdenum blue method on a UV-1800 spectrophotometer (Shimadzu, Kyoto, Japan). Total nitrogen (TN) was determined by the Kjeldahl wet digestion method using a 2300 Kjeltec Analyzer Unit (Foss, Hillerod, Sweden).

To investigate how different fungal guilds regulate SOC dynamics in alpine ecosystems, this study measured the activity of a range of enzymes, including both hydrolytic and oxidative enzymes. Hydrolytic enzymes decompose readily degradable organic substances, while oxidative enzymes break down more resistant compounds like lignin. Both activities reflect the microbial mechanisms driving SOC turnover. Specifically, enzyme activities were measured using standardized fluorimetric and colorimetric protocols on 96-well microplates. Hydrolytic enzymes were analyzed, including α -glucosidase (AG), β -xylosidase (BX), β -glucosidase (BG), cellobiohydrolase (CBH), leucine aminopeptidase (LAP), N-acetylglucosaminidase (NAG), and acid phosphatase (AP). Oxidases were also analyzed, including Mn-peroxidase, lignin peroxidase (Li-peroxidase), and laccase. A moist soil sample was homogenized in maleate buffer and mixed with a fluorometric substrate. After 4 hours of incubation in the microplate, enzyme activity was measured using 7-amino-4-methylcoumarin and 4-methylumbelliferone as standards for ten enzymes, respectively. Fluorescent signals were measured using BioTek Synergy H1

(Winooski, VT, USA), with substrate controls and homogenate blanks included. Enzyme activity was expressed in units of nmol activity/h/g dry soil ($\text{nmol h}^{-1} \text{g}^{-1}$).

DNA isolation, amplification, and sequencing procedures

Total soil DNA was extracted from 0.25 g of moist soil using the PowerSoil DNA Isolation Kit (MO BIO laboratories, Carlsbad, CA, USA) following a standardized protocol. Soil DNA of each sample was extracted in triplicate and then pooled to decrease extraction bias. DNA extracts were assessed on 1% agarose gels, and both the quality and quantity of DNA were determined using a NanoDrop UV-Vis spectrophotometer (ND-2000c, NanoDrop Technologies, Wilmington, DE, USA).

To assess the richness and composition of fungal communities, the ITS1 region was amplified using the ITS1F (5'-CTTGGTCATT-TAGAGGAAGTAA-3')/ITS2-2043R (5'-GCTGCG TTCTTCATCGATGC-3') primer set, which was combined with adapter sequences and barcode sequences. Subsequently, the primer sets were subjected to PCR reactions and the resulting purified amplicons were pooled in equimolar and paired-end sequences (2×300) on an Illumina MiSeq platform, following standard protocols from Majorbio Bio-Pharm Tech-

nology Co., Ltd. The raw ITS sequence data were then subjected to demultiplexing and quality-filtering before sorting into valid reads, using the Quantitative Insights into Microbial Ecology (QIIME) pipeline version 1.9.1.

The ribosomal database project (RDP) classifier was used to assign ITS gene sequences to taxonomic groups based on the SILVA database (version 132) and the UNITE fungal ITS database (version 7.2), respectively, at an identity threshold of 75%. To estimate the abundance of communities, quantitative PCRs (qPCRs) were utilized as proxies. The use of qPCRs has been shown to provide results similar to direct cell counting via microscopy.¹⁷

Fungal guilds

Fungal guild classification was performed using FUNGuild¹⁸ and corroborated with relevant literature.^{7,14,15,18-24} ECM fungi were identified primarily based on their potential to secrete peroxidases, with a focus on species from the *Agaricomycetes*, which are known for their specialized capacity for peroxidase production.^{8,9,11} Further classification was refined through literature reviews that confirmed the presence of peroxidase genes ('AA2' CAZymes^{11,14,15,19,21,23,24}). Saprotrophic fungi were subdivided into two categories: saprotrophic basidiomycetes, recognized for their ability to degrade complex organic compounds such as lignin,^{8,11} and non-ligninolytic saprotrophs that lack such capabilities. Pathogens, other symbionts, and uncertain ecological groups were also classified using FUNGuild with relevant literature.²²⁻²⁴ Although the genus-level classification based on enzyme presence has inherent limitations, such as variability in gene copy numbers, it offers a reasonable first approximation of fungal functional capacity. This framework could be further refined as additional genomic data become available, deepening our understanding of fungal functional roles in these ecosystems.

Statistical analyses

To investigate the relationship between fungal community composition

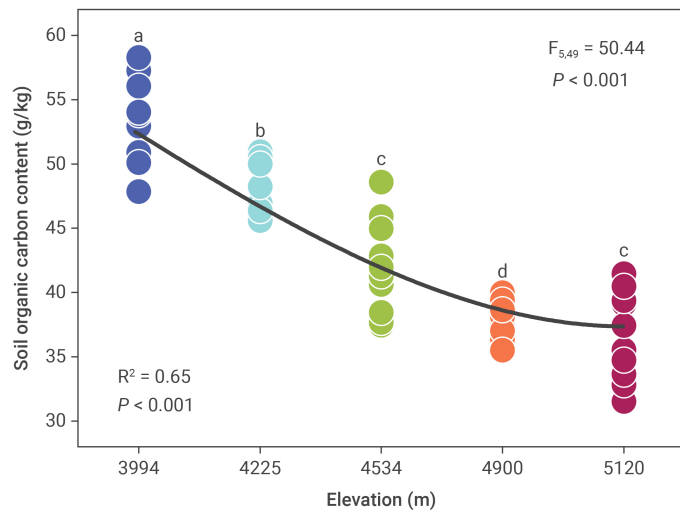


Figure 2. The changes in soil organic carbon (SOC) content along an elevational gradient The solid black lines indicate statistical significance for the relationship of SOC content and elevation. Significant differences among elevation were tested by ANOVA and Duncan's test, with different lowercase letters indicating significant differences at the $P < 0.05$ level between elevations.

and SOC content along an elevational gradient, we first analyzed SOC changes using one-way analysis of variance (ANOVA) followed by Tukey's test, implemented with the *aov* and *TukeyHSD* functions in the *stats* package in R. Then, we assessed the coupling between fungal community distribution patterns and SOC changes along the elevational gradient using detrended correspondence analysis (DCA), based on genus-level fungal composition derived from PacBio sequencing of ITS markers.

To further identify specific fungal guilds and predict SOC changes across all fungal taxa, we applied machine learning with random forest modeling using the *randomForest* package in R, with variable importance evaluated by the increase in mean square error (MSE).²⁵ Pearson correlations were used to evaluate the interactions among specific fungal guilds and their positive or negative associations with SOC content using the *cor.test* function in R. To cross-validate the role of specific fungal guilds in SOC changes, we examined the relationship between each fungal genus and SOC across all fungal guilds using TITAN analysis via the *TITAN2* package in R.²⁶ Finally, we used DCA and Pearson correlation analysis to explore the relationships between specific fungal guilds and the activities of hydrolytic and peroxidative enzymes, and to further clarify their contributions to SOC turnover. Hydrolytic enzymes were characterized by the first principal component (PC1), which integrated all SOC-related hydrolytic enzymes, including LP, AP, BG, BX, and CBH (Figure S1).

Given the environmental factors may mediate the effects of fungal community shifts on SOC dynamics, we applied DCA and Mantel analyses to quantify the relationships between fungal community changes, soil fertility, vegetation productivity, and climate (e.g., MAT and MAP). Mantel analyses were conducted with the *vegan* package in R. Soil fertility was characterized by the first principal component (PC1) that explained 71.5% of the total variance, including soil pH, $\text{NH}_4^+\text{-N}$, SAP, carbon-to-nitrogen ratio (C/N), clay content, and TN. The loadings of the six variables on PC1 were: pH = 0.973, $\text{NH}_4^+\text{-N}$ = 0.943, SAP = 0.904, Clay = 0.327, C/N = 0.242, and TN = 0.114. Vegetation productivity was represented by the PC1 derived from total plant biomass and the biomass of dominant species such as *Kobresia*. Additionally, we applied TITAN analysis to validate the relationships between soil fertility and the relative abundance of fungal guilds at the genus level, which reveals the potential effects of soil nutrient limitations on fungal community shifts. Finally, we used the *mantel* function of the *vegan* package in R to validate the response patterns of the fungal community to all environmental variables at the Operational Taxonomic Unit (OTU) level.²⁷

Before the statistical analysis, all data were assessed for normality (Shapiro-Wilk test) and homogeneity of variance (Brown-Forsythe test) to

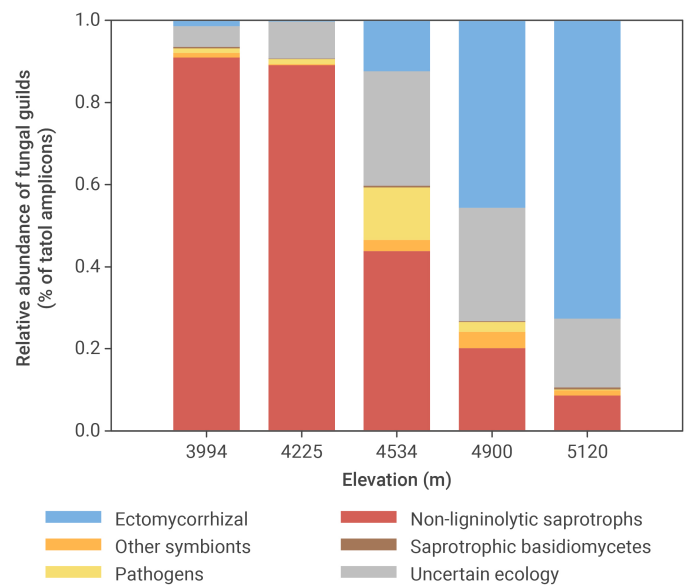


Figure 3. The changes in the relative abundance of fungal guilds along an elevational gradient.

confirm they met both criteria. All microbial data were square root transformed to meet normality assumptions. Fungal genera were selected if they were found in at least one sampling site and displayed a sequence percentage no less than 0.1%. Ordination analyses were executed using CANOCO 5 software (Microcomputer Power, Ithaca, NY, USA), and other statistical analyses were performed in R (v.4.0.0).

RESULTS AND DISCUSSION

Alpine SOC changes are closely linked to shifts in specific fungal guilds across elevational gradients

We first synthesized the fungal community composition along the elevational gradient (3,994–5,120 m) and identified its associations with SOC dynamics at the guild level. We observed a significant 28% decrease in SOC content with increasing elevation (Figure 2), accompanied by a shift in fungal community composition (Figures 3 & 4A). Specifically, the relative abundance of ECM fungi increased from 10% at lower elevations to 70% at higher elevations, where SOC content was lower. In contrast, non-ligninolytic saprotrophs, which were more abundant at lower elevations with higher SOC content (71% vs. 24%), showed a corresponding decline (Figures 3 & 4A). Other fungal guilds did not exhibit consistent relationships with SOC changes along the gradient (Figures 3 & 4A), suggesting weak or no associations with SOC decline at higher elevations.

Random Forest analysis also identified ECM fungi and non-ligninolytic saprotrophs as the most significant predictors of SOC changes when considering all fungal guilds (Figure 4B). Pearson correlation analysis further confirmed a significantly negative correlation between ECM fungi and non-ligninolytic saprotrophs (Figure 4C). Thus, a significant negative correlation was observed between ECM fungi and SOC content, in contrast to the positive association observed for non-ligninolytic saprotrophs (Figure 5). These results were consistent with genus-level analyses, which showed that SOC decline was associated with increased abundance of all ECM genera and declines in 10 of 12 non-ligninolytic saprotrophic genera (Figure 6A). Together, these results are partly consistent with recent studies in temperate or boreal ecosystems showing that specific fungal guilds are linked to SOC dynamics.^{7,9-11,14,15} More importantly, we present the first evidence that ECM fungi, which predominate over non-ligninolytic saprotrophs at higher elevations, are strongly associated with the marked decline in SOC content in alpine ecosystems. Thus, our finding supports the hypothesis that alpine SOC fate is coupled with the trade-offs between ECM fungi and non-ligninolytic saprotrophs.

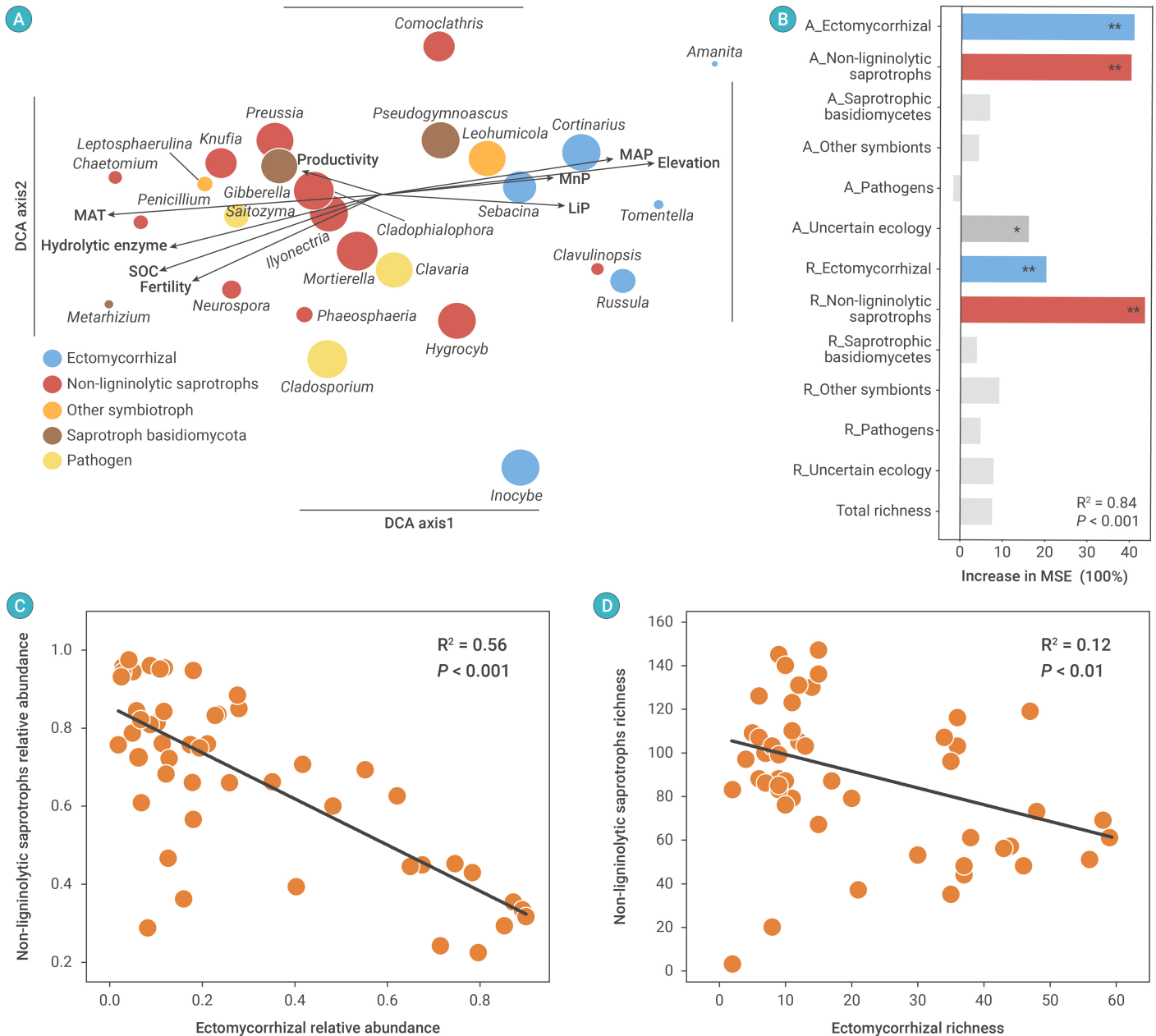


Figure 4. Fungal community composition and its relationship with SOC content across an elevational gradient in alpine ecosystems (A), Distribution of fungal genera across an elevational gradient (3,994–5,120 m) in alpine ecosystems, visualized through a species plot of a detrended correspondence analysis (DCA) based on PacBio sequencing of ITS markers. Circles are color-coded according to fungal guilds, with the area indicating relative abundance. Vectors represent environmental variables plotted in ordination space. Axes 1 and 2 explain 26.3% and 4.9%, respectively, of the total inertia of 1.6. SOC: Soil Organic Carbon; MnP: Mn-Peroxidase; LiP: Lignin Peroxidase; MAT: Mean annual temperature; MAP: Mean Annual Precipitation. (B), The random forest mean predictor importance (% increase of mean square error (MSE)) of fungal guilds on SOC content. Significance levels of each microbial predictor are as follows: *, $P < 0.05$; **, $P < 0.01$. "R_" indicates richness, and "A_" indicates abundance for each fungal guild. (C-D), Regression analyses show relationships between ectomycorrhizal fungi and non-ligninolytic saprotrophs in relative abundances and richness. R^2 indicates the coefficient of determination. The relative abundances of fungal guilds were square root-transformed prior to regression analysis.

Trade-offs between ECM fungi and non-ligninolytic saprotrophs in mediating SOC are attributed to enzyme activities

The trade-offs between ECM fungi and non-ligninolytic saprotrophs in shaping alpine SOC dynamics are further supported by their distinct relationships with enzyme activities. ECM fungal abundance was significantly correlated with both Mn-peroxidase and Li-peroxidase activities, and these enzymes were more active at higher elevations with reduced SOC content (Figures 4A & S2-S3). These observations indicate that ECM fungi are more actively involved in the oxidative degradation of recalcitrant C at higher elevations. High elevation soils were characterized by considerable root biomass (~3,000 g/m²) in surface layers (Figure S4). This supports the notion that alpine ecosystem is characterized by extensive root systems of the predominant plants, representing abundant inputs of polymeric C such as lignin.^{28,29}

However, non-ligninolytic saprotrophs showed negative correlations with Mn-peroxidase and Li-peroxidase activities but positive correlations with hydrolytic enzyme activities (Figures 4A & S5). Although hydrolytic enzymes can convert most polymers (e.g., celluloses, chitins, proteins, and others) into more labile organic molecules, they are less effective at degrading more recalcitrant materials like lignin.^{7,8} As the readily metabolizable C depletes as elevation increases, co-metabolic oxidation gradually becomes dominant to maintain biological degradation.^{8,11} Oxidase, particularly Mn-peroxidase and lignin peroxidase, are recognized for their role in decomposition of complex phenolic macromolecules such as lignin.^{7,11,14,30}

Notably, ECM fungi were dominated by *Agaricomycetes* (Table S1), particularly genera *Cortinarius* and *Russula* (Figure 4A & Table S1), which are well known for their ability to metabolize complex organic substrates^{7,11} and are

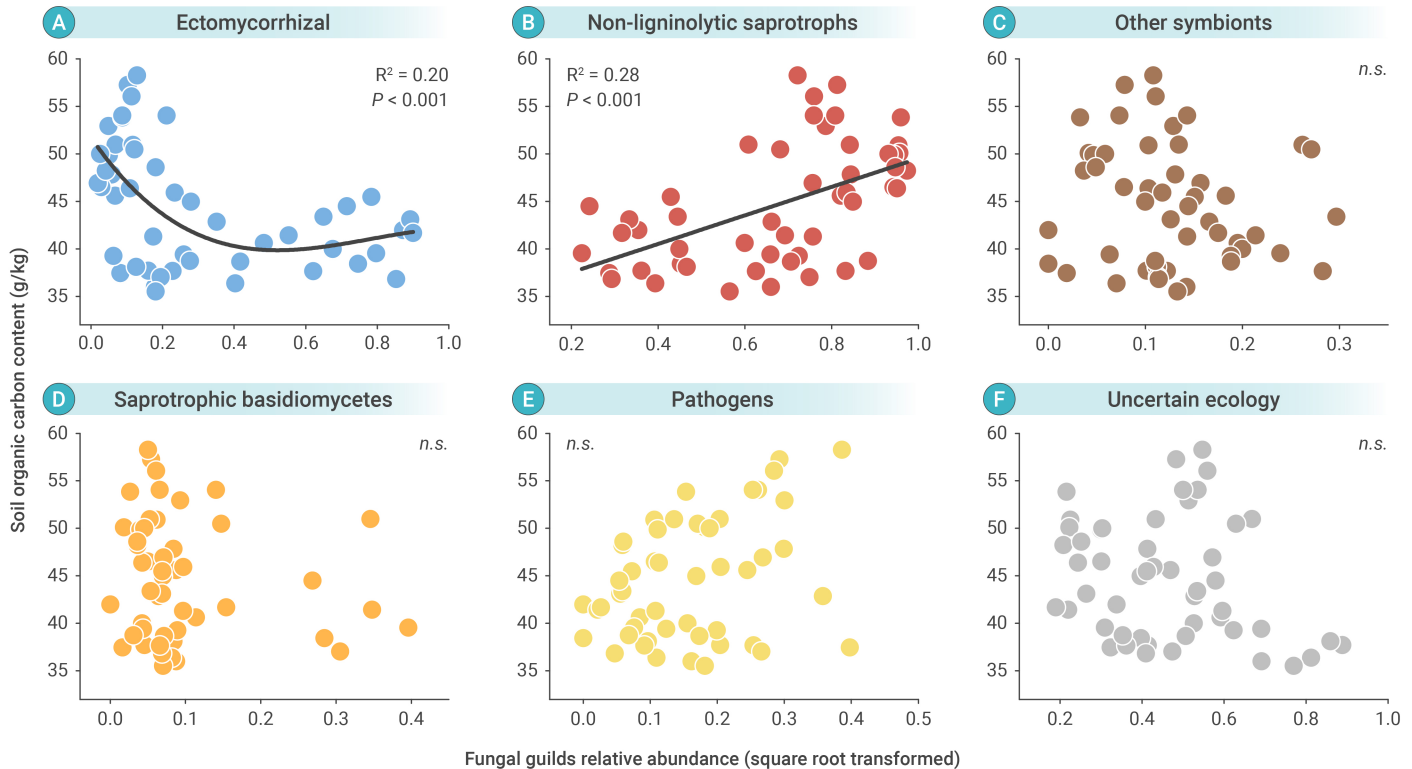


Figure 5. Main fungal predictors of SOC content Correlations of SOC content with the relative abundance of (A) ectomycorrhizal fungi, (B) non-ligninolytic saprotrophs, (C) other symbionts, (D) saprotrophic basidiomycetes, (E) pathogens, and (F) uncertain ecology. R^2 indicates the coefficient of determination. The relative abundances of fungal guilds were square root-transformed prior to regression analysis.

associated with the expression of peroxidase genes.^{9,14,15} These findings further suggest that ECM fungi, through peroxidase activity, may have a stronger association with SOC decomposition than non-ligninolytic saprotrophs. While some saprotrophic basidiomycetes may also have oxidative decomposition capability,^{8,11} their negligible abundance and lack of significant associations with peroxidase activity or SOC content indicate a limited role in SOC turnover (Figures 5D & S2-S3). Additionally, *Agaricomycetes* can also express laccases that are involved in the degradation of lignin and aromatic compounds. Interestingly, we observed no significant correlations between laccase activity and SOC content (Figure S1). Two non-exclusive mechanisms may explain this phenomenon. First, laccases rely on molecular oxygen as the terminal electron acceptor, but the high-elevation alpine ecosystems are oxygen-limited.^{31,32} Second, laccases primarily act on small aromatic compounds or lignin-derived monomers. However, alpine soils are often dominated by complex macromolecular organic matter with limited substrate accessibility.³¹ These conditions may favor ECM fungi to express peroxidases and promote SOC turnover under environmentally stressful conditions. Taken together, these findings contrast with previous studies showing that ECM fungi promote C accumulation by outcompeting saprotrophs.^{11,12} By comparison, our results imply that ECM fungi may functionally complement, or even partially occupy ecological niches similar to saprotrophs by associating with nutrient mobilization from recalcitrant organic C in alpine ecosystems.

Soil fertility regulates the trade-off between ECM fungi and non-ligninolytic saprotrophs in alpine SOC turnover

The trade-off between ECM fungi and non-ligninolytic saprotrophs was modulated by soil fertility, highlighting its pivotal role in determining microbial control over SOC turnover. As soil fertility declined with increasing elevation, ECM fungi increased in relative abundance, while non-ligninolytic saprotrophs became less prevalent (Figures 4A & 6B). TITAN analysis further supported this pattern showing that ECM genera were more abundant with declining soil fertility, while 9 out of 12 non-ligninolytic saprotrophic genera exhibited the opposite trend (Figure 6B). ECM fungi tend to dominate in nutrient-limited soils due to symbiotic relationships with host plants that enable

them to acquire nutrients efficiently. Their extensive hyphal networks enhance nutrient foraging in soils with low nutrient availability.^{11,14,33-35} Supporting this, we observed well-developed root systems in the topsoil of higher elevation sites (Figure S4), likely expanding the spatial niches for ECM fungi relative to non-ligninolytic saprotrophs. The accumulation of ECM fungi under nutrient-limited conditions may stimulate SOC turnover by promoting the decomposition of recalcitrant organic matter. Moreover, ECM fungi, particularly those within the *Agaricomycetes* (Table S1), possess an ecological advantage conferred by their extensive mycelial networks. These networks enhance nutrient acquisition from recalcitrant organic matter through peroxidase activity.^{11,36-38} Spanning several square meters, the mycelial networks not only provide access to scarce resources but also stabilize their presence in the soil over decades. This can ensure sustained nutrient mobilization and SOC turnover.^{15,39} This characteristic gives ECM fungi a competitive edge, especially in high elevation and nutrient-poor soils.

Non-ligninolytic saprotrophs rely on the autonomous decomposition of organic matter.^{10,40} The slow nutrient cycling of high elevation soils may constrain their growth and energy acquisition. Comparably, ECM fungi have higher metabolic and reproductive activity supported by host plants. Higher soil fertility at lower elevations may reduce competition among fungal guilds and enable greater niche overlap, thereby supports the proliferation of non-ligninolytic saprotrophs,^{11,41} while potentially suppressing net mineralization mediated by ECM fungi. Previous studies also suggested that increased nutrient availability favors hydrolytic over oxidative microorganisms and potentially hinders SOC decomposition.^{30,42} Our work highlights that ECM fungi tend to dominate over non-ligninolytic saprotrophs in nutrient-limited conditions, contributing to SOC turnover at higher elevations. This underscores the role of soil fertility in structuring fungal communities and modulating microbial control of C cycling.

Although plant productivity is often positively related with soil C dynamics,⁴³ we observed no significant relationship between plant productivity and SOC content (Figures 4A & 7). Plant productivity often represents the main C input to soils in natural ecosystems.⁴³ However, it is noteworthy that we observed substantial root biomass across sites (Figure S4), indicating that roots have undoubtedly contributed to soil C inputs. Therefore, one possible

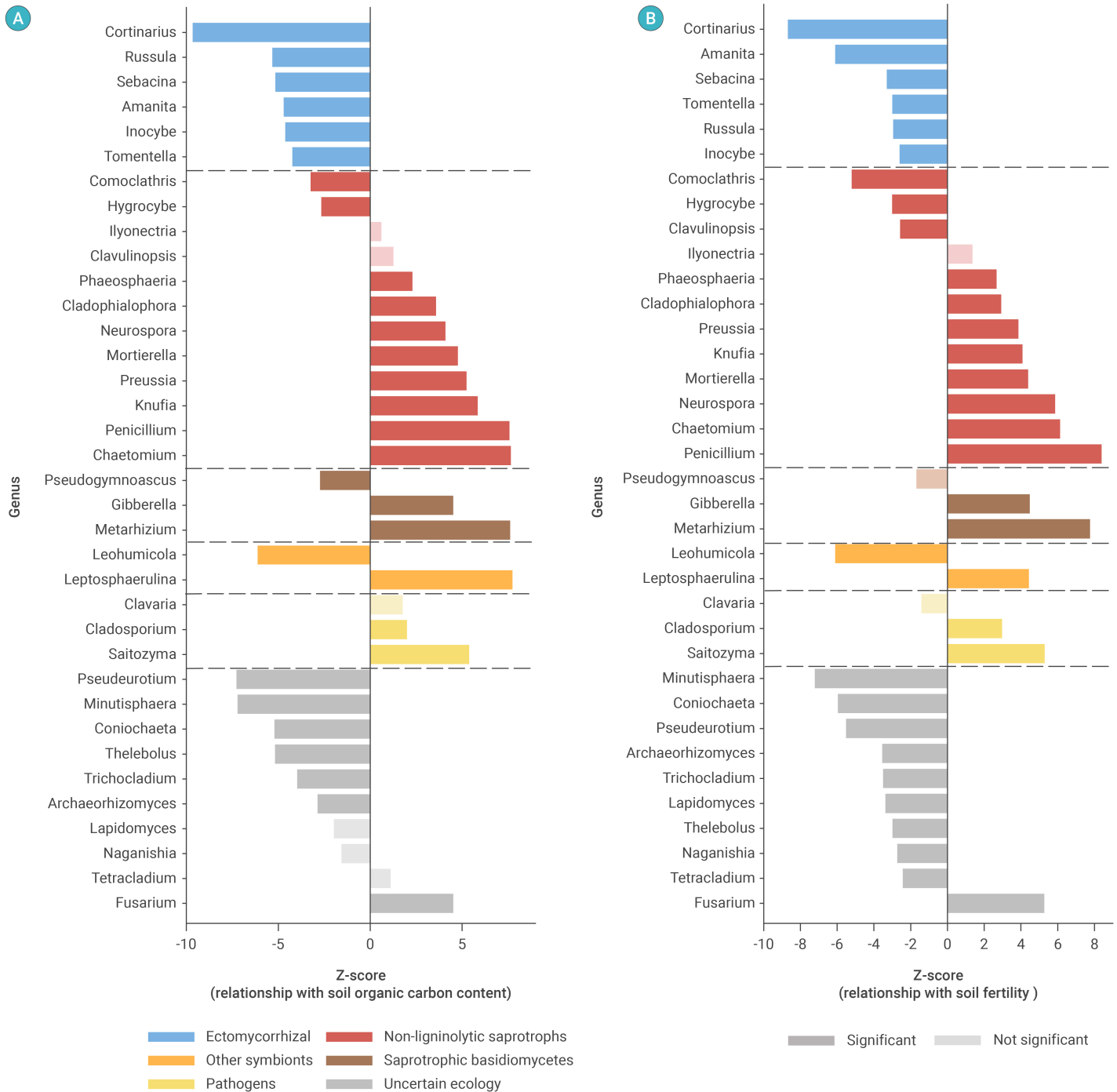
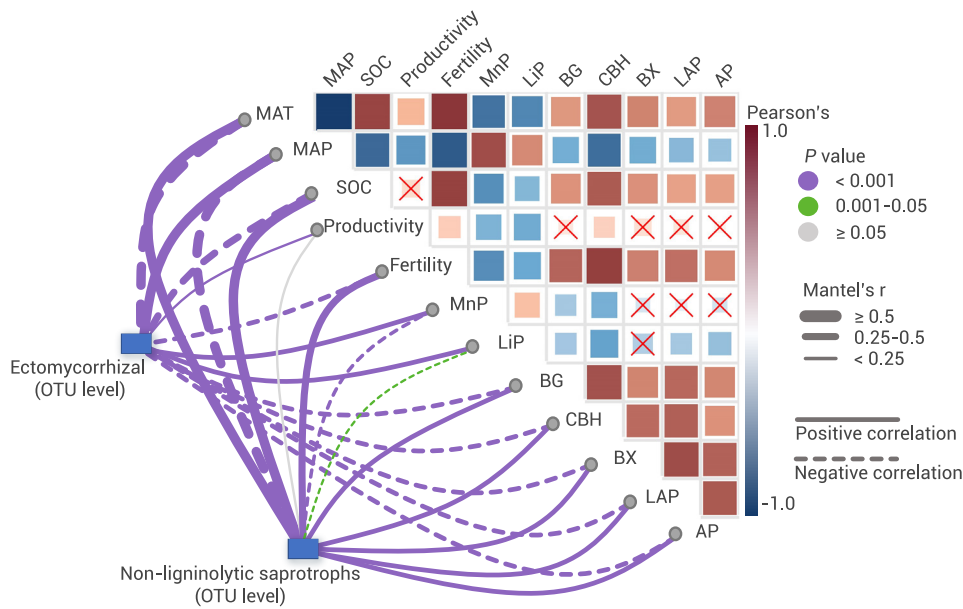


Figure 6. Relationships between fungal genera and SOC content (A) and soil fertility (B) The column chart presents the median Z-scores (computed through 1000 bootstrap iterations), representing the associations of SOC content and soil fertility with the relative abundance of fungal genera. Positive Z-scores indicate that higher relative abundance corresponds to higher SOC content and soil fertility, while negative Z-scores indicate the reverse. Associations with purity and reliability ≥ 0.95 were considered statistically significant (solid columns), while changes with purity or reliability < 0.95 were deemed non-significant (pale columns).

explanation for the lack of correlation between plant biomass and SOC stock is that static root biomass may not adequately reflect the belowground processes. These processes truly regulate SOC dynamics, such as root exudation, root turnover rates, and root chemical traits (e.g., lignin or phenolic compound content). These qualitative features of plant inputs may structurally influence fungal community composition and affect their functional contributions to SOC turnover. Accordingly, our observations at elevations above 4000 m suggest that shifts in fungal guilds are associated with changes in SOC content. These patterns also support the notion that plants may indirectly influence SOC turnover by modulating fungal communities, particularly through promoting ECM fungi proliferation.

Climate influence the trade-off between ECM fungi and non-ligninolytic saprotrophs in alpine SOC turnover

Climate conditions are significantly associated with the trade-off between ECM fungi and non-ligninolytic saprotrophs, potentially shaping SOC dynamics. Lower temperature and higher precipitation at high elevation are directly related to lower SOC content (Figures 4A & 7), which are consistent with earlier findings.^{44,45} This is because low temperatures reduce soil biogeochemical cycling, which in turn lowers SOC stability; however, excessive moisture can lead to soil oxygen deficiency, thereby inhibiting the effective SOC accumulation.^{44,45} Beyond these direct relationships, we observed that ECM fungi were negatively correlated with MAT and were positively correlated with MAP, whereas non-ligninolytic saprotrophs exhibited the opposite



trend (Figure 7). These results suggest that as environmental stress intensifies with elevation, ECM fungi become dominant over non-ligninolytic saprotrophs. This highlights the ecological adaptation and functional advantages of ECM fungi in colder and wetter conditions. ECM fungi exhibit cold tolerance by secreting antifreeze proteins, modulating membrane fluidity, and expanding hyphal networks.^{13,46-48} Additionally, their symbiotic nature reduces reliance on external resources, allowing sustained growth and reproduction under resource-limited conditions. These findings suggest that environmental filtering at high elevation may favor ECM fungi, thereby influencing SOC turnover.

Although our study provides significant insights into the role of fungal guilds in alpine SOC turnover, several limitations warrant further exploration. First, we did not specifically measure the plant litter quality, which could potentially affect soil fungal activity and being associated with soil C dynamics.^{49,50} Future studies should examine the interactions between plant litter quality and fungal guilds to better understand their collective impact on SOC cycling. Second, although our study reveals significant correlations, its observational nature precludes causal inference. Future manipulative experiments are needed to confirm the causal mechanisms driving the observed relationships between ECM fungi, non-ligninolytic saprotrophs, and SOC dynamics. Third, an inherent challenge in our study is disentangling the direct effects of fungi from covarying environmental factors, such as MAT and MAP, which also influence SOC dynamics. This limitation underscores the need for future studies to better isolate and assess the relative contributions of soil fungi and environmental factors in shaping SOC turnover. Fourth, although our study suggests a potential link between ECM fungi, oxidative enzyme activity, and SOC turnover, the inference is primarily based on fungal taxonomic composition, associated enzyme activity patterns, and prior functional studies. Therefore, this study lacks direct in situ evidence—such as peroxidase gene expression or lignin degradation rates—to validate this mechanism. Future work should incorporate metatranscriptomic analyses, targeted enzyme assays, and stable isotope tracing to directly validate ECM-mediated lignin decomposition and its role in SOC dynamics. Finally, our work also opens the door to future studies that will deepen our understanding of SOC dynamics and fungal-driven mechanisms in alpine ecosystems.

CONCLUSION

Our work shows that trade-offs between ECM fungi and non-ligninolytic saprotrophs are linked to SOC content in alpine ecosystems. ECM fungi predominate at higher elevations and are positively correlated with the activity of peroxidative enzymes that are associated with SOC turnover. Our work therefore revealed the role of specific fungal guilds in regulating the C dynamics of macroscopic ecosystems. These findings highlight the necessity of including specific fungal guilds in biodiversity conservation strategies

Figure 7. The relationships between environmental factors and fungal guild composition Pairwise comparisons of environmental factors were conducted by calculating Pearson's correlation coefficients. Relationships between taxonomic community structure at the OTU level and each environmental factor were assessed using Mantel tests. SOC: Soil Organic Carbon; MAT: Mean Annual Temperature; MAP: Mean Annual Precipitation; MnP: Manganese Peroxidase; LiP: Lignin Peroxidase; BG: β -glucosidase; CBH: Cellobiohydrolase; BX: β -xylosidase; LAP: Leucine aminopeptidase; AP: Acid Phosphatase.

and land management practices, particularly in fragile alpine environments. Integrating microbial traits into broader ecological and biogeochemical models may offer novel insights into ecosystem resilience and inform strategies for mitigating global climate change.

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AUTHOR CONTRIBUTIONS

Y.P.W., W.Q.C., and Z.X.M. conceived the research idea. Z.X.M. compiled the database and performed analysis of the data. Z.X.M., W.Q.C., H.W.L., and Y.X.C. contributed to the interpretation of the results. Z.X.M. wrote the manuscript. Y.P.W., W.Q.C., Z.X.M., Y.X.C., J.C., D.A., Y.L.H., and F.B.Z. reviewed and edited the manuscript. All authors contributed to the manuscript and approved the final version.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DATA AND CODE AVAILABILITY

Climate variables, namely mean annual temperature and mean annual precipitation were acquired from the WorldClim database (<https://www.worldclim.org/>). Data and code are available from the corresponding author upon reasonable request.

SUPPLEMENTAL INFORMATION

It can be found online at <https://doi.org/10.59717/j.xinn-geo.2026.100178>