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Level terraces improve the generation of fungal niches and modify fungal communities under post-megafire conditions: Soil management insights in the context of climate change

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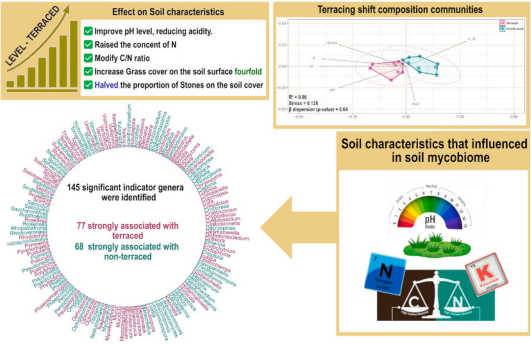
HIGHLIGHTS

- Post-fire, terraces support early stages of nutrient cycling and ecosystem recovery
- Level terraces improve soil pH, C/N ratio, N and K availability, and grass cover
- Grass cover generates microhabitats that act as nutrient islands for fungi
- Terraces modify fungal community composition but not trophic guild composition
- Fifty fungal indicator genera were exclusively detected in terraced plots

GRAPHICAL ABSTRACT



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ABSTRACT

Forest plowing to create level terraces was part of Spain's 1950s reforestation strategy, preparing sites for planting. Although this practice has been controversial due to its short-term negative impacts on soil properties, its long-term effects on ecosystems affected by megafires may have important implications for fungal community recovery. This study evaluates the impact of historical terraces on soil fungal communities under post-megafire conditions. The research was conducted in the Sierra de la Culebra (Zamora, Spain), the site of the largest recorded wildfire in the country's history. The objectives were: (a) to compare soil chemical properties and vegetation cover between terraced and non-terraced plots; (b) to assess the diversity and composition of fungal communities; (c) to analyze the composition of fungal trophic guilds; and (d) to examine fungal interactions under post-fire conditions. Terraces significantly modified pH, the C/N ratio, and grass cover, generating microhabitats that act as nutrient islands for fungi. Fungal richness and diversity remained stable, but community composition shifted. Fifty out of 145 fungal indicator genera were exclusive to terraced plots, including the arbuscular mycorrhizal genera *Acaulospora* and *Ambispora*, and the saprotrophic genera *Pyronema* and *Holtermanniella*. Saprotrophic fungi, the dominant trophic guild, were more abundant in terraced soils. Soil pH, nitrogen, potassium, C/N ratio, and grass cover were significantly correlated with fungal dynamics. These results

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suggest that historical soil management infrastructures offer a climate change adaptation strategy, meriting their integration into post-fire restoration plans in Mediterranean landscapes.

1. Introduction

Within the framework of the national reforestation planning of the 1950s, level terraces were a method used for site preparation in forest plantations (Vadell et al., 2022). However, this practice is highly controversial due to its short-term negative effects, such as the inversion of soil horizons and the rejuvenation of soil profiles (Deng et al., 2021; Vadell et al., 2022). These processes are particularly problematic in Mediterranean environments, where soil development is inherently slow and limited (Martins et al., 2023, 2024). For this reason, current reforestation guidelines tend to minimize or even prohibit the use of such invasive soil techniques. Nevertheless, in areas prone to frequent wildfires events, the use of terraces may offer long-term benefits (Fernández-Raga et al., 2021). In this context, terrain reshaping through terracing can promote post-fire restoration by reducing slope length, enhancing nutrient accumulation, and improving water retention (Fernández et al., 2019; Fernández-Raga et al., 2021; Holz and Augustin, 2021). These conditions may exert a positive influence on the composition of the soil fungal community and, thus, play a key role in the ecological regeneration of fire-affected ecosystems.

In the context of climate change and global warming, the frequency and intensity of megafires have increased across the planet (Carrillo-García et al., 2023; Espinosa et al., 2023; Linley et al., 2022). Megafires, defined by Linley et al. (2022) as wildfires devastating more than 10,000 ha, profoundly impact ecosystems by, for example, reducing biological niches and altering biogeochemical cycles (Dove et al., 2020; Linley et al., 2022). Wildfires not only affect vegetation but also modify the physicochemical properties of the soil, decreasing its fertility, moisture retention capacity, and the availability of essential nutrients such as nitrogen (N) and carbon (C) (Ondik et al., 2022; J. Zhang et al., 2023). These alterations restrict biological activity in the soil and pose a threat to biodiversity in forest ecosystems.

Soil fungi are keystone components in nutrient and energy flow within the trophic network of terrestrial ecosystems (Espinosa et al., 2025; O'Dea, 2007; H. Wang et al., 2025). Several studies have highlighted the crucial role of soil fungi in the recovery of ecosystems devastated by wildfires because they contribute to soil pH modification, enhance aggregation capacity, increase nutrient availability, and facilitate vegetation reestablishment (Duponnois et al., 2011; Espinosa et al., 2023; O'Dea, 2007), which are all essential for soil restoration and the recovery of forest ecosystems.

Saprotrophic fungi stand out as one of the most abundant fungal guilds detected in the soil after a wildfire (Bruns et al., 2020; Cuberos et al., 2024; Enright et al., 2022; Filialuna and Cripps, 2021; Fischer et al., 2021; Fox et al., 2022; Pulido-Chavez et al., 2021). Various species of saprotrophic fungi have adaptations that provide them with competitive advantages to survive and thrive after a fire (Fox et al., 2022), such as the resistance of their propagules to high temperatures (Bruns et al., 2020; Fischer et al., 2021; Glassman et al., 2016), the formation of spore banks that facilitate rapid dispersal (Bruns et al., 2020), germination induced by high temperatures (Glassman et al., 2016) and the metabolic capacity to assimilate carbon in pyrolyzed organic matter, which is often toxic to other fungi (Fischer et al., 2021; Fox et al., 2022).

In a post-fire context, fungi play a key role in ecosystem recovery because they are responsible for decomposing organic matter, and for reincorporating nutrients and increasing their availability at higher levels of the trophic chain (Espinosa et al., 2025; Fernández-González et al., 2024; Gołębiewski et al., 2019; Meng et al., 2024). Therefore, designing soil management techniques that favor fungal recolonization in fire-affected areas is a crucial step toward mitigating the devastating effects of wildfires (Cuberos et al., 2024; Espinosa et al., 2023, 2025). Another key factor in enhancing the survivability of soil fungi is the concomitant recovery of vegetation because it represents the regeneration of new microbial niches, which favours the recolonization of fungal species that are less tolerant to hostile post-fire conditions but that are also key to ecosystem recovery (Baynes et al., 2012; Duponnois et al., 2011; Hewitt et al., 2023; Overby et al., 2015).

Amid the growing risks associated with the effects of global climate change, protecting ecosystems (such as Mediterranean forests) and biodiversity is a key part of the United Nations Sustainable Development Goals (Chandra and Muchan, 2024; Dube, 2025). The Intergovernmental Panel on Climate Change report (IPCC, 2019) highlights the need for management techniques that aim to preserve forests to mitigate the effects of climate change and that strengthen the resilience of ecosystems. Although several studies have focused on the design and evaluation of soil management techniques for the restoration of forests affected by fires, few studies have addressed the management of forest ecosystems affected by megafires with a specific focus on soil fungal communities as key factors for ecosystem recovery (Cuberos et al., 2024; Enright et al., 2022; Espinosa et al., 2023, 2025; Pulido-Chavez et al., 2021).

In 2022, a severe megafire occurred in the Sierra de la Culebra region, which devastated more than 56,000 ha, making it the largest and most destructive fire in the history of Spain. During post-fire walks to assess the damage caused by the fire, an interesting phenomenon was identified: at sites where the soil had historically been plowed to form level terraces, there was a notable accumulation of ash, organic matter, soil, and moisture retention. By contrast, unplowed areas showed clear signs of erosion, with bare soil and significant runoff. Based on these observations, we **hypothesized that (1)** level terraces modify key soil properties associated with biological activity, such as pH and the C/N ratio, and promote the accumulation of nutrients and organic matter, and the establishment of pioneer vegetation cover; **(2)** the microenvironmental changes induced by level terraces enhance fungal richness and diversity while significantly modifying the composition of soil fungal communities; **(3)** the composition of functional trophic guilds within the fungal community substantially shift; and **(4)** the influence of terraces brings about important changes in soil microenvironmental conditions, triggering positive responses in the soil fungal communities, particularly among functionally relevant trophic guilds involved in post-megafire ecosystem recovery.

Previous studies concur that pronounced slopes significantly impact soil erosion, vegetation cover loss, and water dynamics, which have a negative effect on the recovery of fungal communities to their pre-fire conditions (Fernández-Raga et al., 2021; Lucas-Borja et al., 2018; Qi et al., 2020). A slope reduction has been shown to improve soil chemical properties and promote organic matter accumulation, thereby enhancing the biological activity of soils and supporting the recovery of ecological niches (Deng et al., 2021; Fernández-Raga et al., 2021; Qi et al., 2020).

Therefore, based on the previously mentioned, this study was aimed as follows: (1) compare soil chemical properties and vegetation cover in terraced and non-terraced plots; (2) assess the diversity and composition of fungal communities; (3) assess the composition of fungal trophic guilds; and (4) analyze soil fungal communities' interactions under post-megafire conditions. To the best of our knowledge, the effect of level terraces on fungal communities under post-fire conditions has not previously been reported. To explore the potential use of terraces as a management technique to improve fire-affected soil recovery, we examined the effect of level-terraces on the dynamics between soil characteristics and fungal communities by addressing the following research questions: (1) what is the short-term effect of level terraces on soil cover and soil chemical properties following a megafire? (2) What is the short-term effect of abandoned level terraces on soil fungal diversity and community composition after a megafire? (3) What is the short-term effect of abandoned level terraces on soil fungal trophic guild composition after a megafire? (4) If level terraces influence soil chemical characteristics, ground cover, and fungal dynamics, what implications do these effects have for the recovery of ecosystems affected by megafires? We analyzed soil chemical properties and soil cover in plots with and without terraces. In addition, fungal community composition was compared using next-generation sequencing with the general objective of evaluating the effect of level terraces on the diversity and composition of soil fungal communities.

2. Material and methods

2.1. Study area

The study area is situated in the northwestern region of Spain, specifically within the province of Zamora. In 2022, a series of severe megafires occurred in the Sierra de la Culebra region (41.89953969496468, −6.334384873924196), with the largest fire, named "Losacio," burning an area of 31,473 ha (de Castilla y León, 2022). We established plots within the burned area.

The Sierra de la Culebra is characterized by a temperate climate, with mild dry summers classified as Csb. The annual temperature is between 10.0 °C and 12.5 °C, with monthly mean temperatures ranging from 2.5 °C in January to 22.0 °C in August. The mean annual precipitation is 1000 mm, with 100 mm occurring during the summer months and 300 mm on average during the summer season. The average reference potential evapotranspiration (ETo) is 1000 mm (Mapas Climáticos de España (1991–2020) y ETo (1996–2020)) (Chazarra Bernabé et al., 2024).

The Sierra de la Culebra is characterized by a hilly topography, with the highest point 1241 m above sea level (asl). Most hilltops are approximately 1000 m asl, whereas the valleys typically lie between 850 and 950 m asl.

The Sierra de la Culebra is home to a diverse array of ecosystems and plant communities. The slopes and valleys are predominantly forested, with species belonging to the genera *Quercus* and *Pinus* being the most common. Trees typically achieve a height of approximately 5 m and approximately 80 % canopy cover. The most prevalent families of shrubs observed below and between the tree cover are Ericaceae and Cistaceae. Herbaceous plants and grasses are also prevalent. Mountain peaks typically exhibit reduced soil coverage, with an increase in rocky outcrops. Shrubs and grasses are prevalent in these environments, whereas trees are comparatively less common (de Castilla y León, 2022).

2.2. Experimental design

Three distinct sites were selected within the area affected by the Losacio fire. Each plot was situated within a single forest stand, as delineated by the forest services. To enable a comparison of the long-term impact of terraces constructed in the 1950s on post-fire soil properties, each site comprised an area that was terraced in the 1950s and an adjacent area where no terracing had occurred prior to the establishment of the stand.

Although each site possesses distinctive site characteristics, the sites were selected based on their similarity with respect to their pre-fire vegetation and site conditions. Each site comprised plantation forests with mature trees providing between 75 % and 80 % tree cover. The dominant species was *Pinus pinaster*, which occupied between 60 % and 80 % of the tree-covered area, with *Pinus sylvestris* making up 10–20 % of the vegetation in each plot. *Pinus nigra* represented 10 % of the flora in one plot. The area not covered by trees was populated by herbaceous plants (15–20 %) and shrubs (0–5 %).

Six plots were established at each of the three sites (i.e., 18 plots in total). Three of the six plots were located in the terraced area and three in the non-terraced area. The three plots in each soil preparation type were situated at three different altitudes, distributed along the altitude gradient along the slopes.

2.3. Data collection

In each sampling plot, a 5-m transect was established perpendicular to the slope. Along this transect, five soil cores were collected from the top 10 cm of the soil profile. The five subsamples were homogenized to produce a single composite sample of approximately 500 mL. We used this composite sampling strategy to capture the spatial heterogeneity of the soil fungal community and to reduce the influence of localized disturbances or anomalies that could bias the results. Samples were immediately frozen to preserve microbial integrity and were subsequently transported to the laboratory, where they were air-dried and sieved before further analysis.

The 5-m transects that were used for soil sampling were also utilized to assess the surface cover. The percentage cover of each vegetation type and substrate (e.g., grasses, shrubs, bare soil, stones, and litter) was recorded along each transect. In addition, the number of juvenile *Pinus* seedlings growing within 1 m of either side of the transect line was documented.

2.4. Analysis of soil characteristics

Soil pH was measured using the potentiometric method with a 1:2.5 soil-to-water ratio. Organic carbon content (OC, %) was determined using the Walkley and Black (1934) method, which involves oxidation with a potassium dichromate solution. Total nitrogen (N, %) was analyzed using a modified Kjeldahl method (Bremner, 1960). Phosphorus content (P, mg kg^{-1}) was measured following Olsen's method (Olsen and Khasawneh, 2015). Potassium content (K, mg kg^{-1}) was determined via inductively coupled plasma-optical emission spectrometry (ICP-OES). Finally, dry matter content (%) was established by heating samples at 105 °C.

2.5. Genomic DNA isolation and identification

Genomic DNA was isolated from 250 mg of each collected soil sample following the manufacturer's instructions for the commercial DNeasy PowerSoil Kit (Qiagen, Germany). The isolated DNA was quantified using a Qubit 4 Fluorometer (Thermo Fisher Scientific, USA) and the initial concentration was adjusted to 5 ng μg^{-1}. The library was set up following the Fungal Metagenomic Sequencing Demonstrated protocol (Illumina, 2019) for amplification of the ITS1 region using a limited cycle PCR. The amplification of the fungal ITS1 region during the first amplicon PCR step was carried out using the primer pool shown in Table 1.

Amplified PCR products were purified using AMPure XP beads prior to the second indexing PCR step. This step incorporated Illumina sequencing adapters and dual-index barcodes into the amplicons using

Table 1
Primers used for ITS1 sequencing based on the Illumina (2019) protocol.

Forward primer set (ITS_fwd_1 to ITS_fwd_8)	Reverse primer set (ITS_rev_1 to ITS_rev_7)
5'–CTTGGTCATTTAGAGGAAGTAA–3'	5'–GCTGCGTTCTTCATCGATGC–3'
5′– CTCGGTCATTTAGAGGAAGTAA–3'	5'–GCTGCGTTCATCGATGG–3'
5'–CTTGGTCATTTAGAGGAACTAA–3'	5'–GCTACGTTCTTCATCGATGC–3'
5'–CCCGGTCATTTAGAGGAAGTAA–3'	5'–GCTGCGTTCTTCATCGATGT–3'
5'–CTAGGCTATTTAGAGGAAGTAA–3'	5'–ACTGTGTTCTTCATCGATGC–3'
5'–CTTAGTTATTTAGAGGAAGTAA–3'	5'–GCTGCGTTCTTCATCGTTGC–3'
5'–CTACGTCATTTAGAGGAAGTAA–3'	5'–GCGTTCTTCATCGATGC–3'
5'–CTTGGTATTTAGAGGTCGTAA–3'	

the Nextera XT Index Kit v2. The indexed PCR products were purified as described for the previous step, and the resulting fragment library was quantified, normalized, and pooled. Sequencing was performed using the Illumina iSeq100 System using a 2 × 150 bp paired-end run, following the manufacturer's instructions.

Bioinformatic analyses were conducted using the Illumina BaseSpace 16S Metagenomics App, which performs taxonomic classifications of amplicon sequencing reads based on the UNITE database, providing results across all taxonomic levels (Abarenkov et al., 2024). Sequences were taxonomically categorized and grouped via pairwise similarity searches against the curated UNITE Fungal ITS Database (version 7.2), which contains identified fungal sequences assigned to Species Hypothesis (SH) groups defined by variable sequence similarity thresholds (Kõljalg et al., 2020). Taxonomic assignments were further validated using the PlutoF web workbench (Abarenkov et al., 2010). Operational taxonomic units (OTUs) with more than 90 % similarity to SH groups with known ecological functions were assigned to functional categories based on the FungalTraits database published by Põlme et al. (2020).

2.6. Statistical analysis

All statistical analyses were set up in the R environment version 4.3.2 using sequence counts for each OTU at the genus level as a measure of abundance (Danzeisen et al., 2011) Treatment effects were evaluated using a linear mixed-effects model (LME) (Pinheiro et al., 2012), which was applied to edaphic variables, fungal alpha diversity indices (richness, Shannon, and Pielou), and the relative abundances of trophic guilds that met assumptions of normality and homoscedasticity (Shapiro–Wilk test). Variables that did not meet these assumptions were analyzed using the non-parametric Kruskal–Wallis test. In the LME analysis, plot was defined as a random factor and terracing as a fixed factor. Significant differences were grouped using Tukey's post-hoc test using the *HSD.test* function of the agricolae package (de Mendiburu, 2006).

Taxonomic hierarchy information and associated metadata were managed using the Metacoder package (Foster et al., 2017). Relative OTU abundances were visualized with the *taxa_heatmap* function, and taxonomic heat trees were created using *heat_tree*.

To assess the effect of terracing on total fungal community composition and trophic guilds, a permutational multivariate analysis of variance (PERMANOVA) was performed using the Bray–Curtis dissimilarity method using the *adonis2* function. OTUs with ≤ 2 reads were excluded, and matrices were transformed by Hellinger using the *decostand* function. A non-metric multidimensional scaling (NMDS) analysis was developed using *metaMDS* (k = 2; 999 permutations), and environmental variables were fitted using *envfit*. All functions were part of the Vegan package (Oksanen et al., 2001).

A similarity percentage (SIMPER) analysis was carried out using the *simper* function in the Vegan package to identify specialized genera that most contributed to differences between fungal communities in terraced and non-terraced soils post-megafire. A 90 % cumulative contribution threshold was used; moreover, indicator taxa significantly associated with each treatment ($p < 0.05$) were identified even if they were not within this threshold.

Correlations among edaphic variables were assessed using Pearson's method using the *corr* function. Correlations between edaphic variables and either specialized genera (within the 90 % SIMPER threshold) or trophic guilds were evaluated using Spearman's method, given the non-linearity assumption. In addition, Mantel tests were performed using the *mantel* function in the Vegan package to assess the significance of the relationship between soil characteristics and fungal communities or trophic guilds.

Finally, structural equation modeling (SEM) was used to construct a model to evaluate whether the soil management factor (i.e., level-terrace plowing) directly or indirectly influenced edaphic variables previously identified in the NMDS correlation, and whether these, in turn, directly or indirectly affected fungal diversity (richness, Shannon, and Pielou) and specific trophic guilds (litter, pollen, and soil saprotrophs). The SEM model was developed using the lavaan (Rosseel, 2012) and semPlot (Epskamp, 2013) packages.

3. Results

3.1. Soil cover and chemical characteristics (RQ1)

Chemical characterization of the soil revealed that the soil pH level was significantly higher in terraced plots than in non-terraced plots ($F = 31.55$, $p = 0.000$). By contrast, the C/N ratio was significantly lower in terraced than in non-terraced plots ($F = 13.11$, $p = 0.002$). Characterization of the soil cover revealed that level-terraced plots had approximately four times as much grass cover as non-terraced plots ($F = 6.394$, $p = 0.022$), demonstrating the positive effect of terraces on grass growth. Moreover, there were approximately half as many stones in terraced plots as there were in non-terraced plots ($F = 7.04$, $p = 0.017$) (Table 2).

3.2. Overview of fungal communities

Soil sample sequencing yielded 943,720 high-quality reads (498,895 reads for terraced and 444,825 reads for non-terraced plots), with an average of 52,429 reads per sample (ranging from 23,386 to 85,704 reads). A total of 2729 OTUs were classified across 17 phyla. In addition, 378 families (from 2640 OTUs) and 1094 genera (from 2480 OTUs) were identified. The fungal microbiome was predominantly composed of the phyla Ascomycota (81.79 %) and Basidiomycota (16.14 %) (Fig. 1A). The main families within the phylum Ascomycota were Aspergillaceae (39.75 %), Helotiaceae (11.5 %), and Pezizaceae (7.38 %). The predominant families in the phylum Basidiomycota were Strophariaceae (4.38 %) and Thelephoraceae (3.37 %). The most abundant genera were *Penicillium* (41.25 %), *Calyptrozyma* (12.43 %), *Pholiota* (4.78 %), *Oidiodendron* (3.54 %), *Terfezia* (3.42 %), *Microidium* (2.6 %), *Aspergillus* (2.35 %), *Talaromyces* (2.11 %), *Venturia* (1.98 %), *Alternaria* (1.37 %), and *Hebeloma* (1.3 %) (Fig. 1B).

3.3. Diversity and composition of fungal communities (RQ2)

The diversity indices of terraced plots showed a marginal positive trend (Fig. 2A); however, differences in richness, structure (Shannon index), and evenness (Pielou index) were not significant (PERMANOVA, $R^2 = 0.05$, $F = 0.88$, $p = 0.330$). The NMDS clustering analysis of the entire fungal community revealed that the composition of the fungal community in terraced and non-terraced plots differed significantly (PERMANOVA: $F = 2.68$, $R^2 = 0.14$, $p = 0.001$). This indicates that terracing had a significant effect on the composition of the fungal community in the soil (Fig. 2B). The following environmental variables were significantly associated with fungal community composition: pH ($p = 0.001$), K ($p = 0.004$), C/N ratio ($p = 0.049$), grass cover ($p = 0.022$), and, with marginal significance, N ($p = 0.051$) and soil cover ($p = 0.082$).

The SIMPER analysis estimated that 90 % of the fungal community was distributed across 52 OTUs at the genus level (Fig. 3A and B). The analysis identified 145 significant indicator genera whose contribution significantly differed between terraced and non-terraced plots (Fig. 3C). Eight indicator genera that were particularly abundant (within the 90 % accumulated contribution) and significant are listed in Table 3.

Of the 145 significant indicator genera estimated, 77 showed a greater association with terraced plots and 68 were associated with non-terraced plots. Moreover, 50 were exclusively found in terraced plots. The most ecologically relevant indicator genera were the pyrophilic fungus *Pyronema* ($p = 0.001$), and the arbuscular mycorrhizal fungi (AMF) *Ambispora* ($p = 0.001$) and *Acaulospora* ($p = 0.001$). In addition, the ectomycorrhizal fungi *Hebeloma*, *Terfezia*, and *Tuber* showed a greater accumulated contribution associated with terraced plots than

Table 2

Chemical characterization and soil cover associated with terraced and non-terraced plots (mean ± SD). Asterisks indicate variables that were significantly different between treatments: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Soil variables	Terraced	Non-terraced	ANOVA (Linear mixed-effects model)		Shapiro–Wilk test	
			F value	*p* value	W value	p value
pH	5.49 ± 0.23	4.99 ± 0.14	31.56	0.000 ***	0.991	0.999
N (%)	0.28 ± 0.07	0.22 ± 0.07	3.54	0.078	0.935	0.238
P (mg kg^{-1})	7.95 ± 4.04	7.47 ± 2.64	0.09	0.770	0.962	0.646
K (mg kg^{-1})	4.75 ± 0.47	4.44 ± 0.32	2.68	0.120	0.922	0.142
OM (%)	6.82 ± 1.55	8.08 ± 2.01	2.23	0.160	0.968	0.755
Total OM (%)	9.37 ± 2.42	9.61 ± 2.49	0.05	0.830	0.964	0.673
OC (%)	5.45 ± 1.41	5.59 ± 1.45	0.05	0.830	0.964	0.673
C/N ratio	19.9 ± 2.54	26.89 ± 5.2	13.17	0.002 **	0.930	0.197
Grass (%)	30.4 ± 25.99	7.71 ± 6.99	6.395	0.020 *	0.927	0.174
Shrubs (%)	26.34 ± 19.59	42.69 ± 17.58	3.47	0.080	0.950	0.423
Soil (%)	28.68 ± 15.25	21.33 ± 13.66	1.16	0.298	0.930	0.199
Stones (%)	10.24 ± 9.37	22.71 ± 10.53	7.04	0.017 *	0.956	0.525
Soil variables	Terraced	Non-terraced	Kruskal–Wallis			
			X^2 (W value)	p value		
Litter (%)	1.06 ± 3.17	1.22 ± 2.99	0.226	0.634		
Pinus (No.)	2.83 ± 4.53	4.33 ± 8.94	0.003	0.958		

Abbreviations: OC, organic carbon content; OM, easily oxidizable organic matter; total OM, total organic matter. K values were Ln transformed to fulfill ANOVA assumptions. *Pinus*, *Pinus* seedlings.

with non-terraced plots. Although these three genera were not statistically significant, they were among the most abundant taxa (within the 90 % accumulated contribution). Similarly, *Trichoderma*, which is a mycoparasitic fungus and plant growth promoter, was also more associated with terraced plots. Although *Trichoderma* was not a statistically significant genus, it was among the 52 most abundant genera.

3.4. Composition of fungal trophic guilds (RQ3)

Comparisons of the relative abundance of each fungal trophic guild detected in terraced plots with that in non-terraced plots revealed that only the following guilds showed a significant difference: animal endosymbiont ($p = 0.003$), animal parasite ($p = 0.019$), litter saprotroph ($p = 0.030$), mycoparasite ($p = 0.017$), and pollen saprotroph ($p = 0.033$) (Fig. 4A). The SIMPER analysis corroborated these findings, identifying the same guilds as significantly differing in their relative abundance in terraced and non-terraced plots; however, their contributions were not sufficient to generate a statistically significant differentiation. The litter saprotroph guild stood out as making the greatest contribution among the significant guilds (Table 4). However, despite collectively accounting for 93.6 % of the contribution, unspecified saprotroph, wood saprotroph, plant pathogen, ectomycorrhizal, and soil saprotroph guilds were not statistically significant.

The NMDS analysis, considering all trophic guilds, showed an overlap between treatments, and PERMANOVA demonstrated that terracing did not exert a significant overall effect on fungal trophic guilds ($F = 1.62$, $R^2 = 0.09$, $p = 0.146$) (Fig. 4B). The only soil variable that demonstrated a marginal correlation with fungal guild composition was K ($p = 0.082$).

3.5. Dynamics between soil characteristics and fungal community (RQ4)

Among the edaphic variables, N showed the greatest number of significant correlations with other variables, with highly positive correlations with P ($R^2 = 0.71$, $p = 0.001$), K ($R^2 = 0.62$, $p = 0.005$), easily oxidizable organic matter (OM) ($R^2 = 0.5$, $p = 0.040$), and total organic matter (total OM) ($R^2 = 0.75$, $p = 0.004$), and negative correlations with the C/N ratio ($R^2 = -0.62$, $p = 0.005$) and stones ($R^2 = -0.48$, $p = 0.040$) (Fig. 5A). P, K, OM, and total OM showed four significant positive correlations. Noteworthy correlations included: K with pH ($R^2 = 0.49$), OM ($R^2 = 0.5$), and total OM ($R^2 = 0.6$); and P with OM ($R^2 = 0.5$) and total OM ($R^2 = 0.63$). The C/N ratio was negatively correlated with pH ($R^2 = -0.54$) but positively correlated with stones ($R^2 = 0.67$). Grass showed significant negative correlations with shrubs ($R^2 = -0.65$) and stones ($R^2 = -0.5$).

The interaction between soil variables and significant indicator genera demonstrated that environmental conditions had a moderate but significant impact on the distribution of fungal indicator genera (Fig. 5B-1). A total of 92 significant correlations were observed. Grass stood out as the variable with the highest number of significant associations, with 15 in total. Grass showed the strongest positive correlations with the genera *Pholiota* ($R^2 = 0.71$, $p = 0.001$), *Rhodosporidiobolus* ($R^2 = 0.7$, $p = 0.001$), *Aspergillus* ($R^2 = 0.63$, $p = 0.005$), *Coniochaeta* ($R^2 = 0.55$, $p = 0.01$), and *Neurospora* ($R^2 = 0.55$, $p = 0.030$), and showed the strongest negative correlations with *Alternaria* ($R^2 = -0.68$, $p = 0.001$), *Rasamsonia* ($R^2 = -0.64$, $p = 0.003$), and *Mycosphaerella* ($R^2 = -0.62$, $p = 0.005$). OM, litter, and soil showed nine significant correlations with indicator genera; followed by P with seven; and N and K each showed six significant correlations.

The interaction between soil variables and fungal trophic guilds was not significant (Fig. 5B-2). However, the soil saprotroph guild showed a significant positive correlation with soil ($R^2 = 0.53$) and a significant negative correlation with total OM ($R^2 = -0.53$), litter ($R^2 = -0.53$), and *Pinus* seedlings ($R^2 = -0.62$). By contrast, litter saprotrophs showed a significant positive correlation with OM ($R^2 = 0.52$) and the C/N ratio ($R^2 = 0.48$).

SEM revealed that the presence or absence of terraces had significant direct effects on selected soil chemical characteristics (i.e., pH, C/N ratio, grass, and N) and indirect effects on fungal richness, diversity, and specific trophic guilds. The soil saprotroph guild stood out as the guild most influenced by soil characteristics (Fig. 5C). SEM estimated that level-terrace plowing had a direct positive influence on pH ($\beta = 0.81$, $p < 0.001$), N ($\beta = 0.42$, $p = 0.046$), and grass ($\beta = 0.53$, $p = 0.007$), and a negative influence on the C/N ratio ($\beta = -0.67$, $p < 0.001$). In addition, level-terrace plowing had a marginally significant positive influence on K. Furthermore, the model identified K and the C/N ratio as the most influential edaphic characteristics affecting diversity and fungal guilds. K significantly influenced the litter saprotroph ($\beta = 0.745$, $p < 0.001$) and soil saprotroph guilds ($\beta = -0.38$, $p < 0.001$), and marginally impacted pollen saprotrophs. Meanwhile, the C/N ratio had a significant effect on soil saprotrophs ($\beta = 0.67$, $p < 0.001$), richness ($\beta = 0.43$, $p = 0.002$), and the Shannon index ($\beta = 0.36$, $p = 0.040$). Among ground cover factors, grass showed the strongest causal relationships, affecting soil saprotrophs ($\beta = 0.56$, $p < 0.001$) and richness ($\beta = 0.37$, $p = 0.03$).

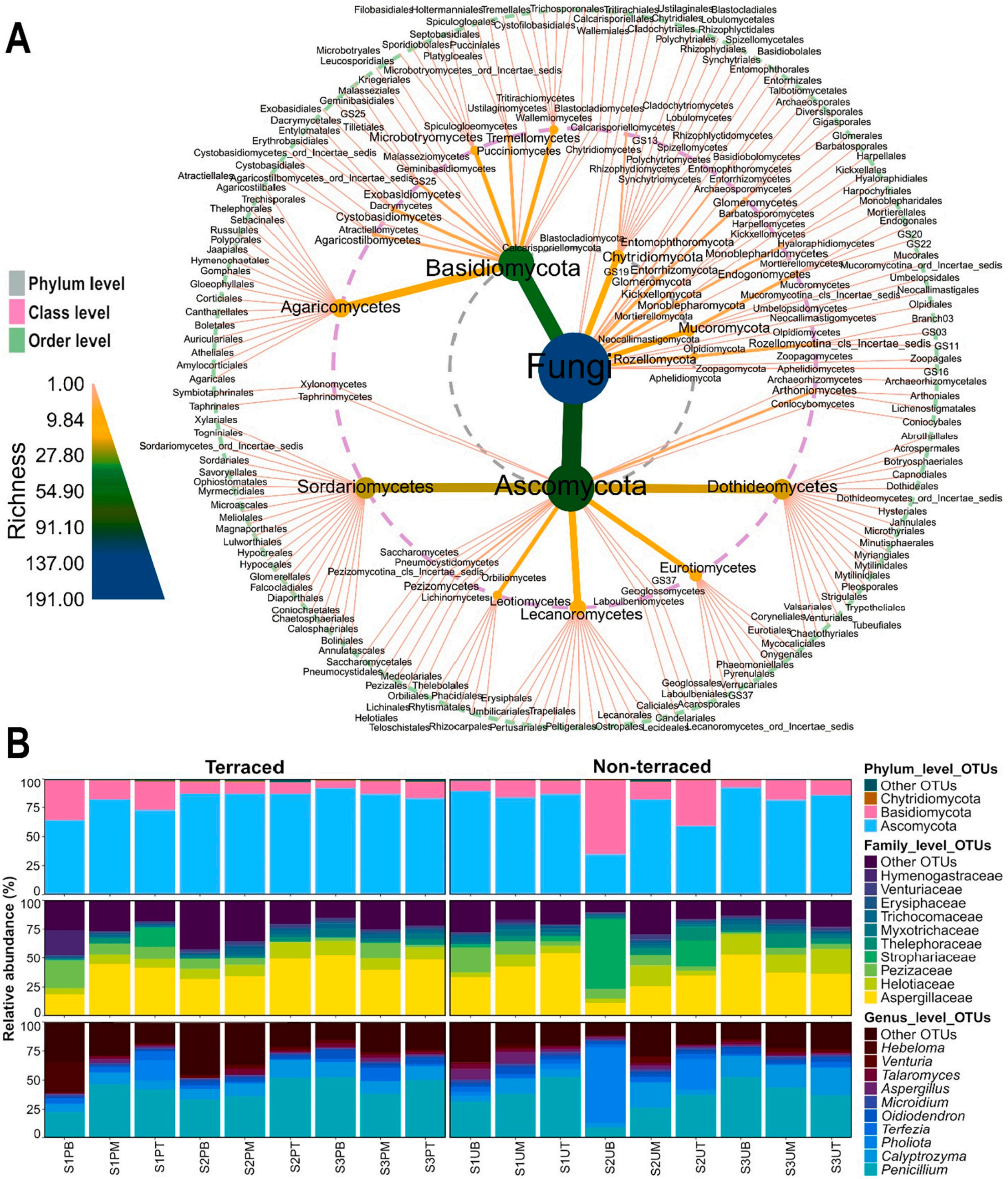

Fig. 1. Composition of fungal communities in terraced and non-terraced plots. (A) Heat tree depicting the taxonomic richness of the fungal microbiome. Dashed circles indicate taxonomic levels: phylum (gray), class (pink), and order (green). (B) Relative abundance of fungal communities at the phylum, family, and genus levels.

In addition, pH significantly influenced richness ($\beta = 0.38$, $p = 0.03$) and marginally affected soil saprotrophs ($\beta = 0.23$, $p = 0.060$). By contrast, N significantly impacted soil saprotrophs ($\beta = 0.34$, $p < 0.001$) but marginally influenced richness. Finally, soil cover had a significant negative effect on soil saprotrophs ($\beta = -0.29$, $p = 0.005$) and richness ($\beta = -0.33$, $p = 0.060$).

4. Discussion

4.1. Soil cover and chemical characteristics (RQ1)

Our analyses supported our first hypothesis that level-terrace plowing would induce significant changes in soil properties. Specifically, there was almost four times more grass cover in terraced plots than in non-terraced plots. By contrast, there were significantly more

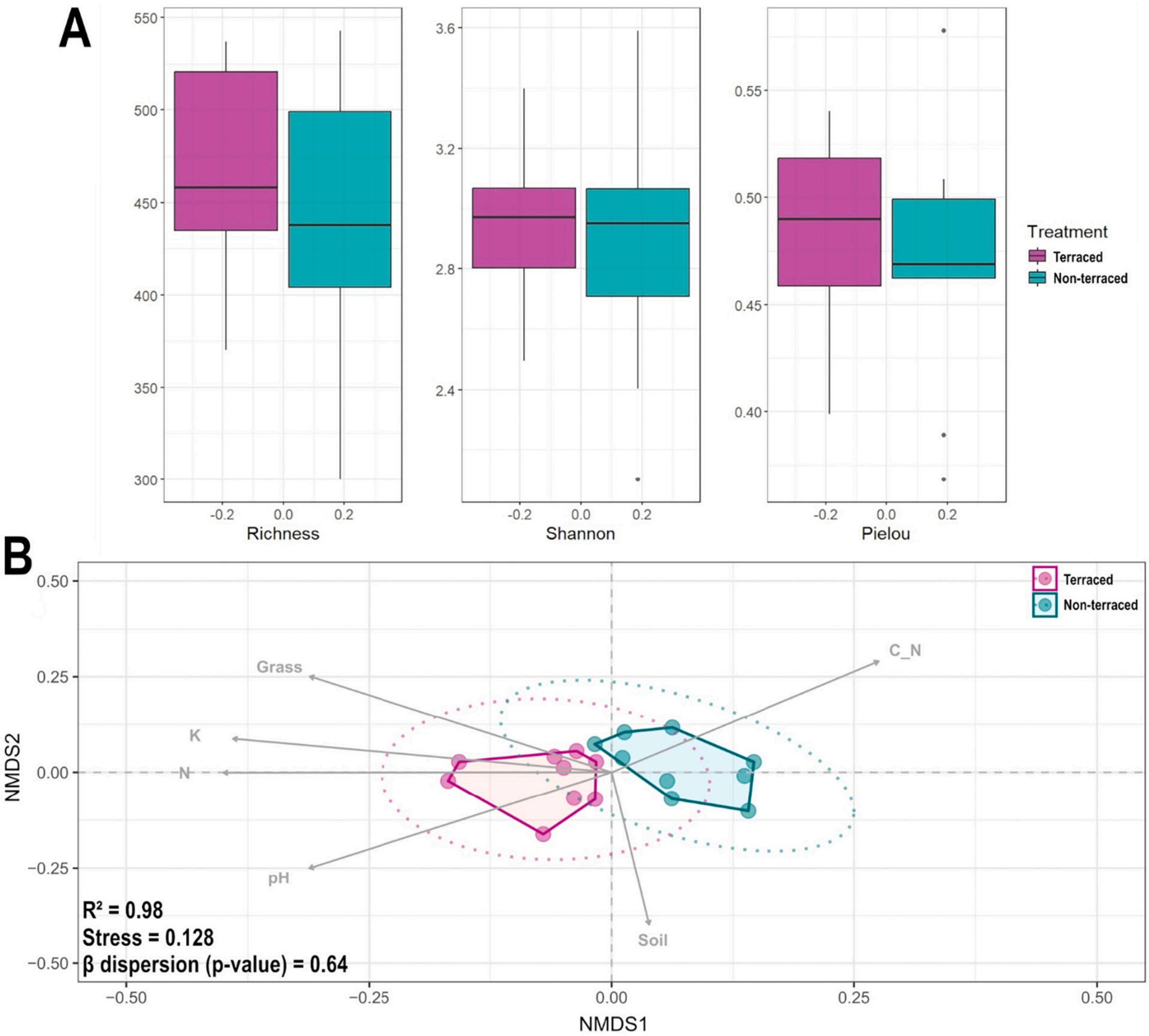

Fig. 2. Effect of treatments on fungal diversity and communities. (A) Total diversity indices of fungal operational taxonomic units detected in terraced and non-terraced plots. Bars represent the standard error. The absence of letters above the bars indicates no significant difference between treatments ($p > 0.05$). (B) Non-metric multidimensional scaling (NMDS) of fungal community composition in terraced and non-terraced plots, which is represented by solid-line polygons. Dashed-line ellipses indicate the 95 % confidence interval for observations within each group. Soil variables significantly correlated with the ordination are shown in gray.

stones in non-terraced plots than in terraced plots, which could be because burned soils with steep slopes and little ground cover are more susceptible to physical erosion (Cheng et al., 2025; Espinosa et al., 2023; O'Dea, 2007). Several studies concur that wildfires alter soil fertility because they modify its chemical properties, reduce ground cover, and decrease the nutrient content, which accelerates erosion and hinders ecosystem regeneration (Carrillo-García et al., 2023; Fernández et al., 2019). Furthermore, in the context of climate change, the frequency and severity of megafires continue to rise, leading to efforts focused on developing soil management techniques to mitigate degradation and preserve ecosystem stability (Carrillo-García et al., 2023; Fernández et al., 2019; Fox et al., 2022; O'Dea, 2007).

Soil management to reduce the inclination of slopes leads to a decrease in erosion and in the runoff-induced erosive force, facilitating the retention of sediments, nutrients, and organic matter, such as leaf litter, thus promoting soil fertility (Cheng et al., 2025; Deng et al., 2021; Qi et al., 2020). However, the impact of level-terrace plowing on soil cover, soil chemical properties, and fungal communities in areas that have been burnt by megafires is scarce; thus, to our knowledge, this is the first study to evaluate the effect of terraces on the dynamics of fungal communities in burned forest soils.

The reduction of the C/N ratio, despite no significant changes in OC (related to OM), suggests that terracing did not prevent organic matter loss, which was to be expected because wildfires reduce C sources through the incineration of OM (Fernández et al., 2019; Ondik et al., 2023). However, the marginal trend for slightly higher N concentrations in terraced plots suggest that terraces may play a key role in mitigating N loss. Our findings suggest that the use of terraces as a soil management technique has broader implications for C and N dynamics that affect their ratio rather than their absolute values. This highlights an opportunity for more in-depth investigations of post-fire C and N dynamics in future studies.

Malvar et al. (2013) and Fernández et al. (2019) concur with our findings, demonstrating that terraces do not prevent the incineration of organic matter (OC) during wildfires. However, Cheng et al. (2025) showed that terracing promotes the reestablishment of grass cover and the natural accumulation of organic C. These authors concluded that slope reduction was key for soil recovery; however, their study did not include wildfires as a factor.

The restoration of soil cover is crucial for the regeneration of forested

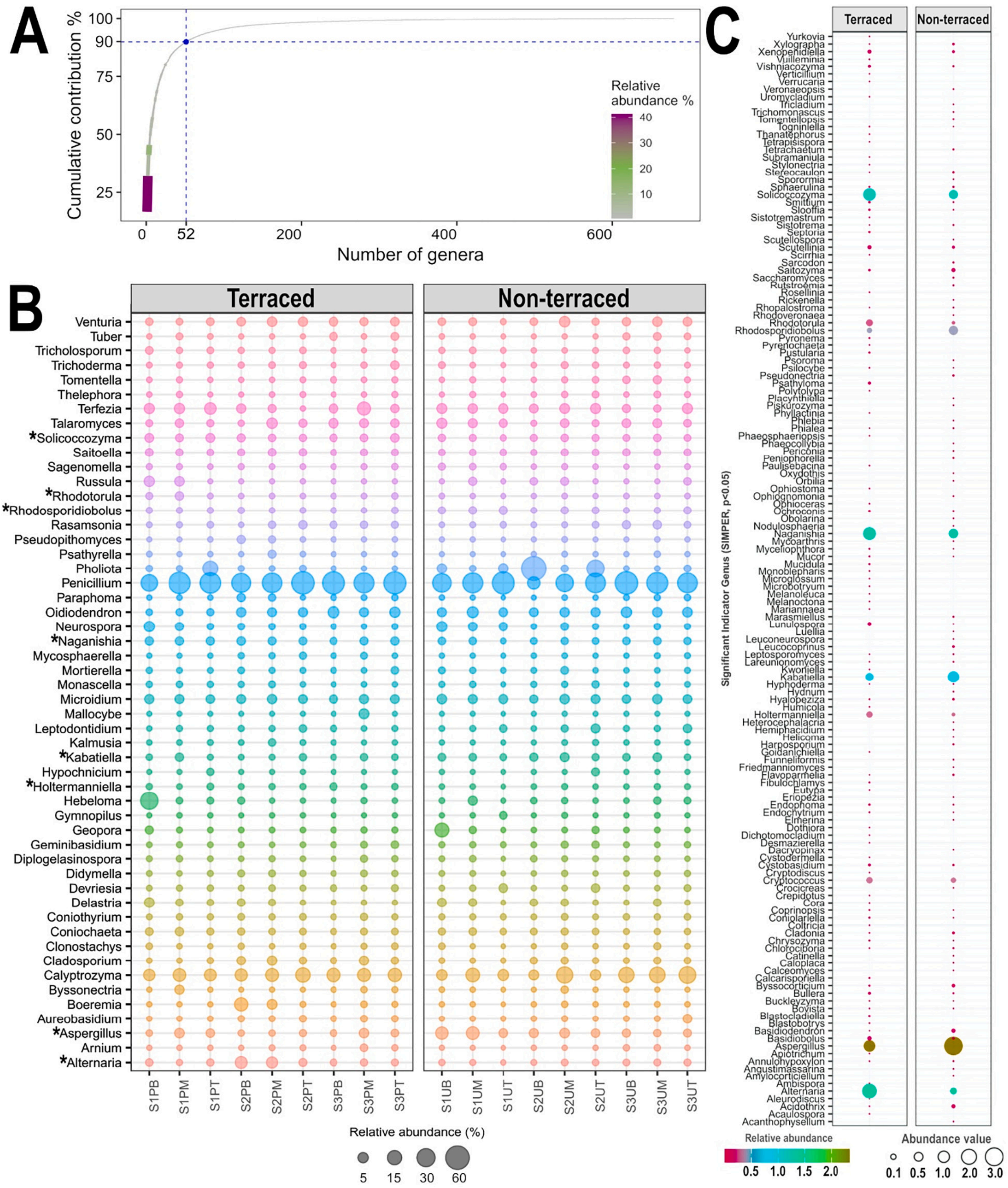

Fig. 3. SIMPER analysis and significant indicator genera for terraced and non-terraced plots. (A) The cumulative contribution plot with a defined threshold (90 %) to identify dominant genera. (B) Relative abundance of the 52 dominant genera, accounting for the 90 % threshold in the SIMPER analysis. (C) Significant indicator genera (SIMPER, $p < 0.05$) and their respective contributions for each treatment. Asterisks (*) denote significant indicator genera that were also highly dominant based on the 90 % threshold.

areas and the accumulation of OM (Cheng et al., 2025; O'Dea, 2007; Overby et al., 2015). However, evidence suggests that the recovery of grass at burned sites is a slow process (O'Dea, 2007). Thus, level-terrace plowing is emerging as a promising strategy for regenerating fungal niches associated with grasses under post-fire conditions (Cheng et al., 2025). Previous studies have demonstrated that grasses are closely linked to fungal activity, particularly the activity of saprotrophic and mycorrhizal species, so their concomitant recovery in parallel with fungal activity could promote the regeneration of biological niches (Fernández-Raga et al., 2021; O'Dea, 2007; Qi et al., 2020).

Qi et al. (2020) have previously demonstrated that level terraces in a *Pinus tabulaeformis* forest improved root distribution and soil nutritional characteristics. The authors attributed this effect to the reduction in slope, which allowed nutrients to accumulate and improved seedling

Table 3
Eight indicator genera that were particularly abundant (within the 90 % accumulated contribution) and significant according to a SIMPER analysis.

Indicator genera	Relative abundance (%)	Average relative contribution (%)	Abundance value		p value
			Terraced	Non-terraced	
Alternaria	1.37	1.0	2.21	0.34	0.002
Aspergillus	2.35	1.5	1.34	3.81	0.040
Holtermanniella	0.24	0.1	0.31	0.07	0.010
Kabatiella	0.81	0.5	0.51	1.25	0.030
Naganishia	1.26	0.4	1.64	0.80	0.002
Rhodosporidiobolus	0.41	0.3	0.19	0.78	0.006
Rhodotorula	0.20	0.2	0.39	0.05	0.020
Solicoccozyma	1.14	0.4	1.56	0.71	0.004

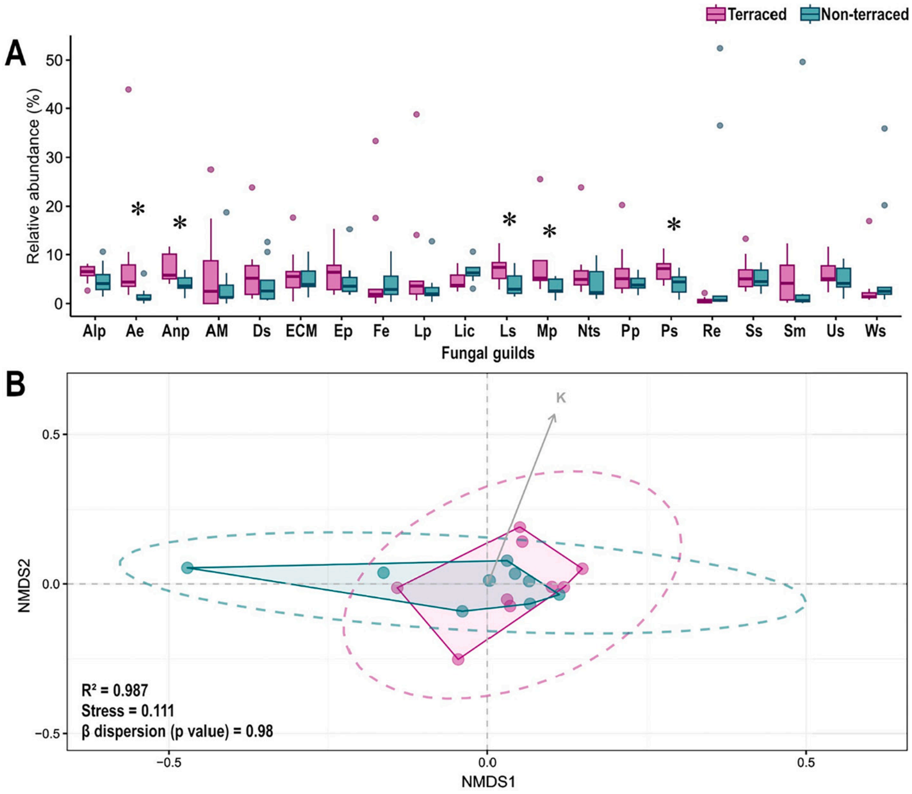

Fig. 4. Effect of treatments on fungal trophic guilds. (A) Relative abundance of trophic guilds, and (B) non-metric multidimensional scaling (NMDS) of trophic guild composition in terraced and non-terraced plots (solid-line polygons). Abbreviations: Alp, algal parasite; Ae, animal endosymbiont; Anp, animal parasite; AM, arbuscular mycorrhizal; Ds, dung saprotroph; ECM, ectomycorrhizal; Ep, epiphyte; Fe, foliar endophyte; Lic, lichenized; Ls, litter saprotroph; Mp, mycoparasite; Nts, nectar/tap saprotroph; Pp, plant pathogen; Ps, pollen saprotroph; Re, root endophyte; Ss, soil saprotroph; Sm, sooty mold; Us, unspecified saprotroph; Ws, wood saprotroph. Asterisks (*) indicate trophic guilds with significantly different relative abundances between treatments ($p < 0.05$). Dashed-line ellipses represent the 95 % confidence interval of observations within each group. The soil variable K correlated with the ordination is shown in gray.

Table 4
Indicator guilds with significant contributions to treatment differentiation based on a SIMPER analysis.

Fungal trophic guild	Relative abundance (%)	Average relative contribution (%)	Abundance value		*p* value
			Terraced	**Non-terraced**	
Animal endosymbiont	0.01	0.01	10.78	1.89	0.005
Animal parasite	0.50	0.16	282.78	159.00	0.010
Litter saprotroph	2.74	1.03	1552.89	861.44	0.040
Mycoparasite	0.56	0.27	357.44	137.44	0.008
Pollen saprotroph	0.18	0.06	98.56	57.44	0.030

survival by decreasing the dragging force of water. This finding aligns with Fernández-Raga et al. (2021), who suggested that the fertility of terraced soils stabilizes over time, even under post-fire conditions. These results are consistent with our findings of marginally higher N concentrations in the soil of terraced plowed plots than in unterraced plots and the significant regeneration of grass cover.

By contrast, Martins et al. (2023) concluded that, in the short term, terracing negatively affects soil fertility. Similarly, Martins et al. (2024) observed that terracing reduced vegetation cover and increased the proportion of stone-covered areas in forested regions of Portugal.

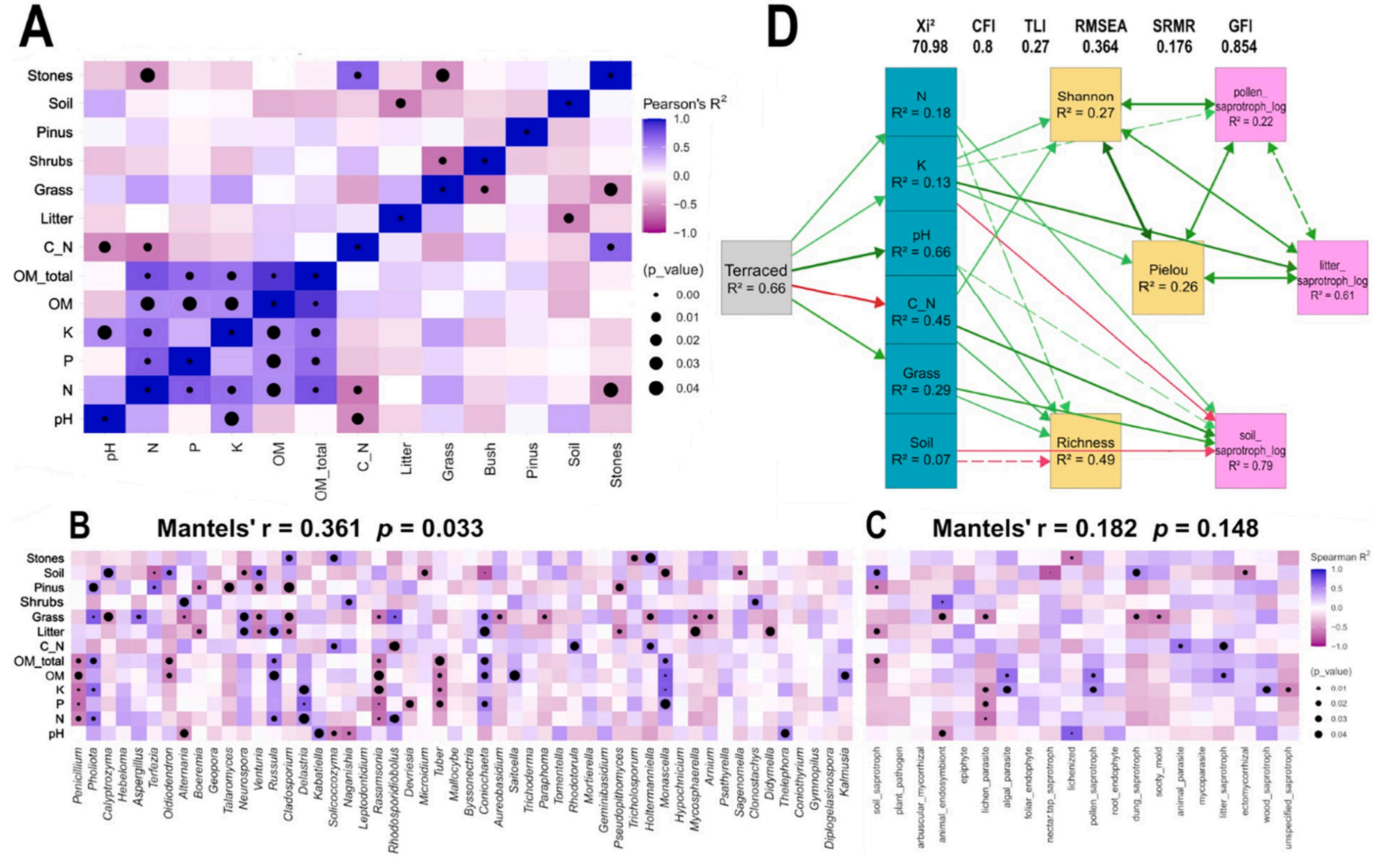

Fig. 5. Dynamics between soil characteristics and the fungal communities in terraced and non-terraced plots. (A) Pearson correlation analysis of soil chemical characteristics and soil cover. (B) Correlation between soil variables and significant fungal indicator genera (B) and trophic guilds (C). Black circles indicate statistically significant correlations ($p \leq 0.05$). (D) Structural equation modeling (SEM) depicting the direct effect of level-terrace plowing on soil characteristics and its indirect influence on fungal diversity and trophic guilds. Green arrows represent positive causal relationships; red arrows indicate negative causal relationships; solid arrows denote significant causal relationships ($p < 0.05$); dashed arrows represent marginal relationships ($p = 0.05$ to 0.09). The thickness and intensity of the arrows are proportional to the β coefficient. Abbreviations: OM, easily oxidizable organic matter; total OM, total organic matter; CFI, comparative fit index; TLI, Tucker–Lewis index; RMSEA, root mean square error of approximation; SMRM, standardized root mean squared residual; GFI, Goodness of fit index.

However, this study did not include post-fire conditions as a factor, which are crucial for understanding the significance of level-terrace plowing. Wildfires impact the ground cover and the soil chemical and biological characteristics equally at sites with and without terraces (Martins et al., 2023; Qi et al., 2020). However, terraced plots may be more suitable for the restoration of grass cover, which translates into new fungal niches.

Lucas-Borja et al. (2018) analyzed the effects of wildfires on soils with and without terraces. Although they concluded that terracing affects soil fertility before wildfires occur, post-fire conditions revealed that terraced sites exhibited higher organic matter levels and C/N ratios than non-burned terraced sites. Consistent with our findings, they did not identify significant differences in N concentrations between plots with and without terraces. In addition, terraced soils accumulated more K and Mg, suggesting that terracing may enhance the retention of certain nutrients. Furthermore, their study found no evidence that terraces significantly influenced microbial activity (CO_2 emissions) or enzymatic functions (urease, phosphatase, and β-glucosidase) in the soil.

4.2. Diversity and composition of fungal communities (RQ2)

Our findings partially supported our second hypothesis given that terraces did not significantly influence fungal richness and diversity but did affect the composition of fungal communities. This aligns with the findings of Espinosa et al. (2025), who suggested that wildfires can lead to significant changes in fungal community composition but not necessarily in changes in richness and diversity, even though these indicators are expected to decline after a fire. Moreover, Robinson et al. (2008) proposed that wildfires that do not severely impact fire-resistant fungal populations have variable effects on richness and diversity. Furthermore, fire is a selective factor for species with adaptations suited to post-fire environments (Fox et al., 2022; Glassman et al., 2016; Robinson et al., 2008; Salo et al., 2019). Thus, it is expected that sites frequently affected by wildfires sustain fungal communities dominated by fire-adapted species (Espinosa et al., 2025; Reazin et al., 2016).

Several studies have reported that wildfires alter the diversity of the soil microbiome. Although the effects of wildfire events vary depending on fire severity, high temperatures are generally lethal to various thermosensitive fungal populations. In addition, soil erosion and the loss of host plants lead to the depletion of biological niches (Espinosa et al., 2025; Fox et al., 2022). During megafires, many fungal niches are devastated; however, those niches that persist enable some fungi to remain without competition, creating microenvironmental conditions for fungal communities that are capable of rapidly proliferating in post-fire environments (Enright et al., 2022; Fox et al., 2022; Overby et al., 2015). Greenwood et al. (2023) highlighted that as plants recover, more niches that are suitable for fungal recolonization simultaneously become available, therefore, the success of fungal community restoration depends on the ability of fungi to acquire nutrients and to colonize available niches (Glassman et al., 2016; Salo et al., 2019). However, vegetation recovery after a fire is a gradual process, often taking more than two years (Fernández-González et al., 2024; O'Dea, 2007;

Robinson et al., 2008; Salo et al., 2019).

In the context of our study, the more rapid recovery of grass cover in terraced plots than in unterraced plots may have implications for the formation of new fungal niches and could explain why 50 of the 145 significant indicator genera showed exclusive associations with terraced plots, where grass cover was four times higher than in non-terraced plots. Several studies have reported that grasses play a fundamental role as key niches for the soil microbiome and have recognized their importance in the recovery of fungal communities and forest site restoration (Borowik et al., 2020; Durán et al., 2021; Eom et al., 1999). Furthermore, despite limited information on the role of grasses in post-fire contexts, some studies have suggested that grasses may function as reservoirs for fungal populations that are essential for the recovery of Mediterranean forest ecosystems affected by wildfires. For example, Espinosa et al. (2023) identified the genus *Naganishia* as directly associated with grasses in Mediterranean forest areas affected by wildfires, which is consistent with our findings. Moreover, the authors identified *Holtermanniella*, *Solicoccozyma*, and *Pyronema* as significant indicator taxa, which also agrees with other findings.

Pyronema is a pyrophilic saprotrophic genus that is extensively associated with post-fire ecosystems because it thrives in wildfire-affected areas and plays a key role in ecosystem recovery by aggregating and binding soil particles, which reduces soil erosion and improves water retention (Bruns et al., 2020; Enright et al., 2022; Filialuna and Cripps, 2021; Fischer et al., 2021). Yeasts belonging to the genera *Naganishia*, *Holtermanniella*, and *Solicoccozyma*, which belong to the class Tremellomycetes, are recognized for their ability to metabolize various carbon sources. The metabolic capabilities of these genera allow them to decompose recalcitrant carbon compounds generated under post-fire conditions, which gives them a competitive advantage over other fungi (Fischer et al., 2021; García-Carmona et al., 2024; Mašínová et al., 2017). Furthermore, *Naganishia* and *Holtermanniella* have previously been reported to be associated with grasses (Ricks et al., 2021).

Other indicator genera associated with grasses include the saprotrophs *Mucor* and *Mortierella*. However, unlike the previously mentioned taxa, these fungi prefer labile carbon sources, and have been linked to niches with higher resource availability (Praeg et al., 2020). This suggests that grass cover may enhance the availability of easily utilizable carbon, providing suitable conditions for the proliferation of less competitive saprotrophs.

AMF belonging to the genera *Acaulospora* and *Ambispora* were identified as significant indicator taxa. Although their abundance values were low, they were found exclusively in terraced plots. This suggests that the post-fire recovery of grass cover in terraced plots exerts a positive influence on certain species of AMF (Feng et al., 2024; Hewitt et al., 2023).

Overby et al. (2015), Bindell et al. (2021), and Yang et al. (2023) have reported that grasses can act as hotspots for AMF, such as *Acaulospora* and *Ambispora*, within ecosystems dominated by forest species, including areas managed with prescribed burns (Bindell et al., 2021). In this context, although our results did not show a significant effect at the guild level, the abundance of grass roots in the soil of terraced plots may have an ecological impact as a niche for specific fungal genera.

The ecological significance of AMF lies in their ability to enhance the resistance of various plant species to water stress within Mediterranean forest ecosystems affected by wildfires (Bellgard et al., 1994; Kyriazopoulos et al., 2014; Yang et al., 2023). Although evidence suggests that AMF are particularly susceptible to wildfires due to the loss of their plant mutualists (Bindell et al., 2021; Cheng et al., 2023; Ondik et al., 2023), their growth rate can be rapid when new hosts become available (Cheng et al., 2023). Therefore, the restoration of grass cover may be key to the recovery of grass–AMF interactions, which, in turn, could be fundamental for the regeneration of fire-affected ecosystems (Yang et al., 2023).

4.3. Composition of fungal trophic guilds (RQ3)

Contrary to our third hypothesis, no significant differences were found in trophic guild composition between treatments; nevertheless, our study identified five significant indicator guilds that were more associated with terraced plots. The litter saprotroph guild made the greatest average contribution and was nearly twice as abundant in terraced plots as it was in non-terraced plots.

Previous studies have reported that saprotrophs tend to increase in abundance in ecosystems affected by wildfires (Cuberos et al., 2024; Ondik et al., 2023). This pattern may be linked to environmental alterations such as elevated pH, reduced moisture retention, and a decrease in the availability of nutrients and carbon sources (Ondik et al., 2022, 2023; Salo et al., 2019). These changes act as selective pressure factors, favoring saprotrophs capable of acquiring energy and nutrients under adverse conditions over for other trophic guilds (Cuberos et al., 2024; Salo et al., 2019).

In our study, the increase in litter saprotrophic fungi may be linked to the effect of terraces. By transforming slopes into an artificial sequence of relatively flat segments (Deng et al., 2021), the slope length is reduced. The reduced angle improves soil moisture retention, enhances infiltration capacity, and prevents water erosion by mitigating the washing effect of runoff (Deng et al., 2021; Fernández-Raga et al., 2021). Collectively, these effects promote vegetation cover growth, root development, and leaf litter accumulation (Qi et al., 2020), creating a suitable niche for the soil microbiome in a challenging, fire-degraded environment.

Studies by Malvar et al. (2013), conducted in burned *Eucalyptus* forests, and Fernández et al. (2019), carried out in Mediterranean shrublands, showed that terraced sites were less susceptible to erosion, showed reduced sediment loss, and improved moisture retention. Their findings suggest that litter accumulation and the increase in grass cover may favor the proliferation of saprotrophic guilds under post-fire conditions.

Furthermore, Cuberos et al. (2024) observed that the accumulation of plant material following a wildfire can induce a significant increase in the abundance of litter saprotrophic fungi. This is because litter saprotrophs have the metabolic capability to extract energy from various recalcitrant carbon sources (Gołębiewski et al., 2019; Meng et al., 2024). For example, *Pyronema* and *Coniochaeta* have enzymatic capacities that allow them to process pyrolyzed organic matter produced during wildfires even though it contains aromatic compounds that are toxic to other fungi (Fischer et al., 2021; Nelson et al., 2022). Similarly relevant enzymatic capacities have been identified in other litter saprotrophic fungi, such as *Desmazierella*, which typically inhabits pine needles and can acquire phosphorus and nitrogen from these needles (Martinović et al., 2016; Meng et al., 2024). In our study, *Pyronema*, *Coniochaeta*, and *Desmazierella* were the indicator genera that were most strongly associated with terraced plots. Based on the aforementioned, in the context of our study, the increased abundance of litter saprotrophic fungi in the soil of terraced plots suggests that microenvironmental changes in soil chemistry and cover create favourable conditions for their post-fire proliferation (Cheng et al., 2025; Deng et al., 2021; Fernández et al., 2019; Malvar et al., 2013).

4.4. Dynamics between soil characteristics and the fungal community (RQ4)

Fire induces substantial changes in the soil, altering its physicochemical properties, biological dynamics, nutrient cycles, and fungal communities (Martins et al., 2023). The combustion of organic matter affects the availability of essential nutrients for biological activity and leads to an increase in recalcitrant pyrolyzed carbon concentrations, which act as selective factors for fungal communities with specific metabolic capabilities (Fischer et al., 2021; Meng et al., 2024). Given the reduction in vegetation cover and the physicochemical changes in the soil caused by the wildfire, slope reduction becomes particularly relevant, as it decreases runoff force and its erosive impact on the soil (Lucas-Borja et al., 2018). Moreover, reduced slopes allow for the accumulation of water-transported materials such as organic matter and ash (Bodí et al., 2014), which favours nutrient accumulation and may promote greater moisture retention and infiltration, which are two key factors for vegetation recovery after a wildfire (Lucas-Borja et al., 2018).

According to Zhang et al. (1998), a greater slope gradient increases soil erosion due to higher runoff velocity. Furthermore, the study by Wang et al. (2023) confirmed that the loss of soil sediments, such as organic matter and nutrients, especially nitrogen, increased with the slope and runoff intensity. In contrast, the meta-analysis by Holz and Augustin (2021) demonstrated that the sites with greater accumulation of runoff-transported sediments were more enriched with organic matter, nitrogen and carbon; moreover, Lei et al. (2025) found that terracing promotes the accumulation of nutrients such as N and K in the surface soil of terraces, thereby increasing soil fertility.

Based on the above, and considering the premise that slope reduction through terracing may favours the accumulation of organic matter and alluvial material (including viable fungal propagules) displaced by runoff, the observed nutrient dynamics and the strong correlations among pH, N, P, K, organic matter (OM), and the C/N ratio can be explained.

Our findings indicate that slope reduction associated with terracing is closely linked to edaphic nutrient accumulation and may play a key role in the regeneration of soil fertility and the recovery of both pioneer plant species and soil fungal communities following wildfire disturbance. This also explains the positive correlation between grass in soil cover and the accumulation of N, K, and litter.

On the other hand, if slope reduction favours nutrient accumulation and moisture retention, it is reasonable to expect that terraced sites enhance the reestablishment of biological niches more suitable for the development of fungal communities, compared to areas with steep slopes, especially under the severe conditions caused by wildfire. Lashermes et al. (2016) and Fox et al. (2022) concur that pH, nutrient availability, and the C/N ratio are key factors in fungal population restructuring and, hence, their post-fire variations often influence fungal community organization. Studies by (Ondik et al., 2022, 2023) support these perspectives and further highlight the importance of moisture retention in the recovery of fungal niches, such as pioneer vegetation (grass).

The negative correlation with the C/N ratio is a common feature in grasses and leaf litter. This suggests that the re-established ground cover actively influences the dynamics of carbon and nitrogen cycles, which may be related to an increase in fungal activity (Sullivan et al., 2022). In this context, Lashermes et al. (2016) and Ondik et al. (2022, 2023) have demonstrated that the C/N ratio is closely linked to fungal energy requirements and highlight a selective pressure favoring species with trophic capabilities directed toward the available carbon sources.

In this context, the retention of burned carbon, resulting from the incomplete pyrolysis of organic matter, can act as a reservoir of recalcitrant carbon that directly influences fungal activity (Fischer et al., 2021). The presence of pyrogenic carbon may be key to understanding the persistence of fungal species adapted to fire-affected ecosystems (Zhang et al., 2019). Examples such as *Pholiota*, *Pyronema*, *Coniochaeta*, and *Calyptrozyma*, which were detected in our study, have been recognized with the ability to metabolize fire-derived compounds and rapidly establish in environments enriched with pyrogenic carbon, and as early colonizers of burned soils (Filialuna and Cripps, 2021; Fischer et al., 2021; Nelson et al., 2022).

The SEM model integrates and schematically represents the previously described concepts in a coherent manner, allowing the identification of causal relationships among the analyzed variables. Specifically, it demonstrates that level-terrace plowing promotes the accumulation of nutrients, such as N and K (Lei et al., 2025), and these conditions significantly improve the soil capacity to support pioneer vegetation, such as grass patches in the ground cover. This vegetation cover, in turn, directly influences the C/N ratio (Ondik et al., 2022), creating a more favourable environment for microbial activity (Duponnois et al., 2011; Hewitt et al., 2023). The presence of grass and the values of the C/N ratio are positively correlated with fungal richness and diversity, suggesting that the re-established vegetation not only serves as an indicator of ecosystem recovery but also acts as a facilitating agent in the formation of biological niches suitable for the development of fungal communities. Furthermore, the model shows that grass and the C/N ratio positively influence the litter saprotroph and soil saprotroph guilds, while potassium exerts a positive effect on litter saprotrophs. These findings indicate that, although level-terrace plowing does not directly affect fungal diversity or trophic guilds, it does induce indirect effects through the improvement of edaphic conditions and pioneer vegetation, which together support the functional restructuring of fungal communities following wildfire disturbance.

Previous studies indicate that patches of grass contribute to nutrient accumulation, leading to their classification as “fertility islands” or “resource islands” (Duponnois et al., 2011; Garner and Steinberger, 1989; Schlesinger et al., 1996). In addition, multiple studies agree that grass can regulate soil microbial activity through the production of root exudates and secondary metabolites (Duponnois et al., 2011; Hewitt et al., 2023). Furthermore, Duponnois et al. (2011) suggests that grasses may act as “nurse plants” that promote the activity of fungi with relevant ecosystem functional capacities, facilitating the establishment of other dominant species in the primary ecosystem (Hewitt et al., 2023).

Overby et al. (2015) demonstrated that the native grass *Festuca arizonica* serves as a niche for the colonization of AMF in a forest in the USA, where plots were subjected to low-intensity prescribed burns and later mulched. *Bromus tectorum* has also been shown to provide a habitat for various rhizosphere and endophytic fungi, including the genus *Morchella*, which supports grass survival under post-fire conditions (Baynes et al., 2012). The grass patches create a favourable niche in the fire-altered environment, while the fungi restore nutrient flow from the soil to plant biota.

Our findings are consistent with our fourth hypothesis because they offer robust evidence that level-terrace plowing modifies soil microenvironmental conditions by promoting grass growth, with significant implications for soil fungal dynamics and relevant practical insights. This process contributes to the formation of fungal niches, facilitating the restructuring of essential ecosystem functions and aiding soil biological recovery. However, further research is needed to deepen our understanding of ecosystem functions associated with rhizospheric fungal communities in grasses enhanced by level-terrace plowing. Specifically, studies should explore how these fungi contribute to ecosystem recovery following megafires, such as the one that occurred in June 2022.

5. Conclusions

Our results show that level-terrace plowing significantly affected soil fungal composition, although it did not impact overall fungal richness or diversity. This suggests that although diversity remained relatively unchanged, the organization and distribution of fungal groups actively responded to changes induced by this soil management technique. In addition, a clear correlation was identified between fungal composition and edaphic variables such as vegetation cover (grass), pH, N, and the C/N ratio, reinforcing the importance of soil characteristics in post-fire microbiome dynamics.

One of the key findings of this study is the role of grass cover in regenerating fungal niches. Grass presence was notably higher in terraced plots, suggesting that this management technique can improve microenvironmental soil conditions for fungal recolonization, facilitating ecosystem recovery after megafires.

The analysis of interactions between edaphic factors and fungal communities revealed that variables such as the C/N ratio, N, and K exert an indirect influence on fungal diversity and certain trophic guilds. SEM confirmed these indirect effects, highlighting the significance of soil chemical properties and vegetation cover in regulating fungal populations after megafires.

Our findings provide strong evidence that level-terrace plowing contributes to the restoration of fire-affected ecosystems by enhancing grass cover and stabilizing soil conditions. Future studies could further explore the eco-physiological processes of ecologically relevant fungi, such as mycorrhizal and saprotrophic species, and their interactions with grass patches that act as nutrient islands or nurse plants during the recovery of ecosystems affected by megafires. This is particularly relevant in the current global context, where climate change and global warming are increasing the frequency and severity of wildfires.

From a management perspective, terracing represents a promising strategy not only for its ecological benefits but also for its potential in terms of cost-efficiency and scalability. Its implementation in moderately sloped terrain can significantly reduce nutrient loss, improve moisture retention, and support biological soil recovery without requiring external inputs. Therefore, assessing its economic viability and applicability across diverse geographic contexts should be a priority in future evaluations, especially in regions prone to recurrent wildfires.

CRediT authorship contribution statement

Jorge Víctor Maurice-Lira: Writing – original draft, Formal analysis, Data curation. **Claudia Prada-Polo:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Juan Andrés Oria-de-Rueda:** Supervision, Conceptualization. **Pablo Martín-Pinto:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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