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Research article

Organic amendments as a tool to restore soil microbial diversity after wildfires in native Mediterranean forests

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ABSTRACT

Wildfires are intensifying under climate change and increasingly compromising the resilience of Mediterranean ecosystems. Soil restoration through organic amendments has been proposed as an effective tool to mitigate soil degradation after fires, yet there is limited knowledge on how different typologies of organic amendments influence soil microbial communities and the recovery of microbial-mediated functions. This study evaluated contrasting organic amendments—straw mulch, compost, and fresh swine and poultry manures—on soil microbial diversity and enzymatic activity in burned native sclerophyllous, Mediterranean forest in central Chile, the earliest in its type experiencing effects of climate change. The study took place six months after amendment application and two years after a wildfire occurrence. Enzyme activities showed different responses according to organic amendments type: while manures strongly stimulate enzymes (urease, glucosidase, and phosphatase activities), compost and mulch promoted a gradual effect on nutrient cycling. Fungal biomass, reduced by fire, recovered best under compost and swine manure. However, organic amendments significantly reduced eukaryotic alpha diversity and differentiated communities from unburned soils and burned soils with no amendment. In contrast, only manures reduced alpha diversity in prokaryotes, while beta diversity analyses revealed that compost amended soils maintained communities closer to reference conditions. Overall, manures provided short-term functional improvements in burned soils, but compost supported a more balanced recovery, preserving microbial communities closer to unburned soils. Therefore, the compost amendment can represent a practical and ecologically safer strategy to accelerate post-fire soil restoration. Targeted application, for example through "fertile islands" in the most degraded areas, may enhance soil resilience while minimizing ecological risks in fire-sensitive landscapes.

1. Introduction

Climate change is altering forest fire regimes, making ecosystems with historical fire occurrences increasingly fragile and less resilient to such events (Moreira et al., 2020). Mediterranean ecosystems are particularly vulnerable, as increasing droughts and fire behaviour (e.g. frequency and intensity) are reshaping vegetation dynamics and soil processes, endangering their ecosystem stability and resilience (McLauchlan et al., 2020; Armenteras and de la Barrera, 2023). In Central Chile, recent megafires (summer 2016–2017) have exemplified

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how climate anomalies — over a decade of prolonged megadroughts (Garreaud et al., 2020)— accelerate ecosystem degradation (De la Barrera et al., 2018; Souza-Alonso et al., 2022). Indeed, Mediterranean ecosystem of central Chile, are among the world's most susceptible ecosystems to fires due to escalating droughts and the earliest in its type experiencing effects of climate anomalies (Miranda and Garreaud, 2023; Miranda and Garreaud, 2023a). Yet, the majority of research related to fire effects in South America is mainly focused on vegetation (Giorgis et al., 2021), while the implications for soils and their relationship with the recovery of ecosystems, remain comparatively less studied (Aponte et al., 2022; Fernández-García et al., 2021).

Mitigating soil degradation is central to the recovery of post-fire ecosystem, with soil microbial communities being critical to support vegetation reestablishment and nutrient cycling (Bouskill et al., 2022; Delgado-Baquerizo et al., 2016). Fires alter not only soil organic matter (SOM) dynamics but also key biogeochemical cycles, which, together with erosion events, modify soil fertility, delaying vegetation recovery and microbial mediated soil functions (Shakesby, 2011; Hudiburg et al., 2023). Organic amendments are an affective restoration tool to mitigate losses of SOM while promoting soil stability (Rojas et al., 2016; Shu et al., 2022); however, knowledge remains rather limited regarding how the organic application is expected to modify soil microbial diversity, composition, and functioning in natural, fire-disturbed ecosystems (García-Carmona et al., 2021; Guénon and Gros, 2016; Marín and Rojas, 2020). This consideration is particularly relevant given that most evidence on the implications of amendments on soil microbial communities are from agricultural soils (Luo et al., 2018; Shu et al., 2022). For example, certain copiotroph taxa are expected to be stimulated under organic addition, including those within the Proteobacteria, Firmicutes, Bacteroidetes, and Actinobacteria phyla, in detriment of oligotrophic bacteria adapted to nutrient-limited environments, such as Acidobacteria (Francioli et al., 2016; Ye et al., 2021). Moreover, using such organic materials might result in the introduction of exogenous taxa, some of them with the potential of being pathogens (Pérez-Valera et al., 2022; Sun et al., 2020). It remains to be revealed whether these patterns will be observed in native burned forests, and what their ecological implications or potential threats might be.

The selection of organic amendments is critical for effective soil restoration strategy, as the biochemical recalcitrance of organic inputs significantly influence the microbial response and decomposition rate, and consequently, the time required for effective results to emerge (Diacono and Montemurro, 2011; González-Ubierna et al., 2012). Substrate availability and quality associated with the organic materials applied are known to drive substantial variations in microbial community composition in amended agricultural soils (Shu et al., 2022; Zhang et al., 2021); thus, similar effects are expected in fire-affected soils. Moreover, the choice of organic amendment not only directly affects the microbial community structure but also indirectly affects physicochemical properties, such as pH and carbon (C) and nitrogen availability (Clocchiatti et al., 2020; Luna et al., 2016), properties already disturbed by wildfires. Fresh materials (e.g., manures), provide high proportions of labile C fractions that result in rapid increases in microbial biomass and plant establishment. However, despite these rapid responses, some disadvantages are reported for fresh amendments affecting the microbial long-term recovery, including autochthonous soil organic carbon mineralization, increases in salinity or acidity, nitrogen immobilization, or the introduction of potential pathogens (Bernal et al., 2009; Kowaljow and Mazzarino, 2007; Pérez-Valera et al., 2022). By contrast, stable materials release nutrients gradually and contribute to long-term fertility and soil organic carbon storage (Bernal et al., 2009; García-Carmona et al., 2021).

This study aimed to address these research gaps by testing contrasting organic amendments, such as straw mulch, compost, and fresh swine and poultry manures, in burned sclerophyllous forests in central Chile. Microbial community diversity and composition (prokaryotes and eukaryotes) and their functional response (enzymatic activities) were evaluated two years after the 2016–2017 megafire occurrence and six months after amendment application. By integrating community and functional responses, this work provides new insights into the potential of different organic amendments as a restoration tool for soil microbial communities in a native Mediterranean forest affected by a megafire without any recent fire history. The main hypothesis was that organic amendments would significantly modify microbial phylogenetic and functional responses compared to unamended soils, with effects driven by differences in nutrient availability and soil physicochemical conditions induced by each material (as reported in García-Carmona et al., 2021). Specifically, it was anticipated that: (i.) fresh organic amendments (manures) would strongly enhance microbial abundance and activity, causing significant shifts in community composition due to the release of labile nutrients, favoring copiotrophic taxa but also with an increased risk of introducing potential soil pathogens; and (ii.) stable amendments (straw, compost) would induce moderate effects on microbial communities, promoting gradual nutrient release and longer-term stability. Overall, it was expected that all organic amendments would stimulate microbial-mediated soil functions, contributing to post-fire ecosystem recovery.

2. Materials and methods

2.1. Study area and experimental design

This study was conducted in the Mediterranean climate area of Central Chile, in the O'Higgins administrative region, the second most affected region during the summer megafires in 2016–2017 with close to 105,000 ha out of the 547,000 ha affected in the country (CONAF, 2017). The research site, with no fire records within the last 30 years until 2017, is in the Pumanque commune (34°36.502′S, 71°42.281′W; 130 m a.s.l.), and is mainly used by small farmers for livestock pasture and wood charcoal production. The average annual precipitation in the area is 451 mm and the average temperature is 15.4 °C (29.9 °C in summer, 5.3 °C in winter). Vegetation at the site is characterized by native sclerophyll forest species, dominated by *Quillaja saponaria* Molina, *Lithraea caustica* Hook. & Arn., and *Peumus boldus* Molina in the canopy, and *Trevoa trinervis* Miers, *Azara serrata* Ruiz & Pav., and *Colliguaja odorifera* Molina in the understory. Soils are classified as Aquic Dystroxerepts (Soil Survey Staff, 2014) with a low depth (~40 cm), and a sandy loam texture (58 % sand, 34 % silt, and 8 % clay), on a 10 % slope facing south (Aponte et al., 2022; García-Carmona et al., 2021).

The experimental set up and soil sampling have been previously described by García-Carmona et al. (2021). Briefly, the experiment was established in June 2018, approximately one and a half years after the wildfire of January 2017, which had affected the site with low to moderate severity. Soil samples were collected in January 2019, corresponding to six months after amendment application (two years after the fire). This six-month interval was chosen to evaluate soil biochemical properties and microbial responses to the amendments within the context of post-fire dynamics (including microbial nutrient uptake, leaching, volatilization, and plant recolonization).

Six treatments were established in the field experiment. T0 corresponded to the reference unburned soils, T1 to burned soils without organic amendment (control), T2 to burned soils with straw mulch, T3 to burned soils with compost (200 m^3 ha^{-1}; 78.77 t dry weight ha^{-1}), T4 to burned soils with poultry manure (200 m^3 ha^{-1}; 150 t dry weight ha^{-1}), and T5 to burned soils with swine manure (200 m^3 ha^{-1}; 95.67 t dry weight ha^{-1}). Although it is expected that constant-volume application of amendments results in unequal dry mass and nutrient inputs across amendments, this approach was chosen to simulate common restoration practices in the field. Each treatment was replicated in four plots of 3 m × 1.5 m within a burned area of approximately 50 m × 50 m, while the unburned reference area (T0) corresponded to a native sclerophyll forest located 500 m away. In addition, plots receiving compost and both manures (T3, T4, T5) were covered with a mulch layer composed of a wheat and oat straw mix.

A total of 96 surface soil sub-samples samples (0–6 cm depth) were randomly collected from the field experiment (six treatments × four plots per treatment × four soil sampling points per plot). From these, 24 soil samples were selected and included in the present study (six treatments × four samples per treatment, randomly chosen). Samples collected in the field were transported to the laboratory under refrigerated conditions (4 °C). Upon arrival, samples were sieved at 2 mm, one part frozen (−20 °C) for DNA extraction and another kept refrigerated (4 °C) for enzyme activity and phospholipid fatty acid analyses (PLFA). The soil physico-chemical properties of, previously published (García-Carmona et al., 2021), are presented in the Supporting Materials (SM1, Table S.M.1).

2.2. Soil biochemical and microbial analyses

Soil enzyme activities were determined using standard colorimetric methods by UV–Vis spectroscopy (Unicam UV 500 UV–Visible Spectrometer). Dehydrogenase activity was measured following García et al. (1997), based on the reduction of INT (2-p-iodophenyl-3-p-nitrophenyl-5-phenyltetrazolium chloride) to INTF (iodonitrotetrazolium formazan). Urease and protease activities were determined by quantifying the NH_4^+ released after the addition of urea or BAA (N-α-benzoyl-l-arginine amide) substrates, respectively (Nannipieri et al., 1981). β-glucosidase and alkaline phosphatase activities were determined by measuring the formation of PNP (p-nitrophenol) after soil incubation with PNG (p-nitrophenyl-β-d-glucopyranoside) (Tabatabai, 1983) and PNPP (p-nitrophenyl phosphate disodium) (Naseby and Lynch, 1997), respectively.

Microbial biomass was estimated by phospholipid fatty acid analysis (PLFA) following Bossio et al. (1998). Lipids were extracted with a chloroform-methanol-phosphate buffer mixture and then separated from neutral and glycolipid fatty acids in a solid phase extraction column (0.58 Si; Supelco Inc., Bellefonte, PA, USA). After mild alkaline methanolysis, samples were analyzed by gas chromatography-mass spectrometry with a 25 m Ultra 2 (5 % phenyl)-methylpolysiloxane column (Hewlett Packard 6890 Gas Chromatograph, J and W Scientific, Folsom, CA, USA). Fungal biomass (eukaryotic) was determined by the combined contents of c18:2ω6t and c18:2ω6c, while bacterial biomass (prokaryotic) based on the sum of contents of 16:1ω9, cy17:0, 18:1ω9t, 18:1ω9c cy19:0, 16:1ω9, cy17:0, 18:1ω9t, 18:1ω9c cy19:0, 10Me16:0, and 10Me18:0 (Federle, 1986; Olsson et al., 1995; Zelles et al., 1994). Total microbial biomass was estimated by the sum of all the extracted PLFAs.

2.3. DNA extraction, amplicon metabarcoding, and bioinformatic processing

DNA was isolated using the DNeasy PowerSoil Kit (QIAGEN GmnH, Hilden, Germany), following the manufacturer's instructions. Quality and quantity of DNA were checked using a Nanodrop spectrophotometer (Thermo Scientific, Waltham, MA, USA). DNA extracts were delivered to the University of Tartu Institute of Genomics Core Facility (Tartu, Estonia) for sequencing.

For library preparation, primers 515F (Parada et al., 2016) and 806R (Apprill et al., 2015) were used to amplify the 16S rRNA region, targeting the Prokaryotic community (Bacteria and Archaea). For the Eukaryotic community, the 18S rRNA region was amplified using primers 1391_F (Amaral-Zettler et al., 2009) and EukBr_R (Stoeck et al., 2010), focusing mainly on fungi, along with other protists and microfauna. PCR was carried out in two sequential reactions: first, the amplicon PCR (24 cycles) with the region-specific primers and partial sequencing adapters; the second, with index PCR (7 cycles), which was used to ligate sequencing adapters and Nextera XT (Illumina) sample identifying indices. PCR reactions contained 0.4 μM of each primer and 2x KAPA HiFi HotStart ReadyMix in a final volume of 25 μl for the amplicon PCRs and 30 μl for the index PCRs. Next, 30 ng of DNA sample was used in the amplicon PCR and 50 ng of the purified amplicon was used in the index PCR reaction. The amplicon PCR cycling conditions were: a period of 3 min at 95 °C followed by 24 cycles of 30 s at 95 °C, 30 s at 55 °C, and 30 s at 72 °C, followed by a 5 min period at 72 °C; samples were stored at 4 °C. Index PCR cycling conditions were the same as the amplicon PCR, but 7 cycles were used instead of 24. Negative controls were included in all PCR reactions. Products of the PCR reactions were then purified with the Agencourt AMPureXP Kit (Beckman Coulter, Inc.). The samples were eluted in EB Buffer (10 mM Tris-Cl, pH 8.5; QIAGEN Inc.). The DNA concentration of the purified amplicons was measured using a Qubit 2.0 Fluorometer (ThermoFisher Scientific). The fragment size of the amplicon libraries was determined by the Agilent TapeStation DNA Screentape. Thereafter, libraries were equimolarly pooled. The amplicon library pool was quantified by the Applied Biosystems 7900HT Fast Real-Time PCR System using the KAPA Library Amplification Kit, and sequenced with an Illumina MiSeq v2 Nano sequencing kit for 2 x 250 bp.

Sequencing data underwent analysis using a tailored workflow primarily derived from the "VSEARCH" tool v-2.14 (https://github.com/Yoelvis13/16s-and-18s-rRNA-Bioinformatic-pipeline-Vsearch/tree/main). The PhiX reads, and primer sequences were trimmed using Bowtie2 v-2.5.5 and Cutadapt v-3.4, respectively (Langmead and Salzberg, 2012; Martin, 2011). The paired-end reads were merged using the *fastq_mergepairs* algorithm and filtered with a *conda deacrimaximum* expected error of 1 using *fastq_filter* in "VSEARCH" (Edgar and Flyvbjerg, 2015). The merged and quality-filtered sequences were dereplicated using the *derep_fulllength* algorithm in "VSEARCH," and the UNOISE algorithm was employed to recover Amplicon Sequencing Variants (ASVs) (Edgar, 2016). Chimeric ASVs were identified and removed using the *uchime* algorithm implemented in "VSEARCH" (Edgar et al., 2011). The verification of non-target sequences for the 16S and 18S rRNA genes in the remaining ASVs was performed using Metaxa2 v-2.2.3 (Bengtsson-Palme et al., 2013). The final ASV table was obtained by mapping the filtered sequences against the verified ASV centroids using the *usearch_global* algorithm in "VSEARCH". Taxonomic classification was performed using a naive Bayesian classifier *Sintax* (Edgar, 2016) by mapping the ASVs against the non-redundant Silva v132 database for 16S rRNA (Quast et al., 2013) and Silva 18sv123 for 18s rRNA. To ensure data quality and minimize noise, three filtering thresholds were applied to the ASV dataset. First, ASVs with a relative abundance lower than 0.001 % across the entire dataset were removed to exclude extremely low-abundance taxa that may result from sequencing errors or contamination. Second, ASVs present in fewer than nine samples were excluded to eliminate highly localized taxa that lack sufficient representation across the dataset. Third, ASVs with an abundance ratio exceeding 0.1 between the most abundant and the second most abundant sample were considered potential outliers and removed to prevent single-sample anomalies from distorting community structure analyses. These thresholds were chosen to enhance the robustness of downstream ecological interpretations while preserving. The filtered ASV table was normalized using an iterative rarefaction approach with 100 iterations, applying the *rrarefy* function from the **vegan** package v-2.6.8 in R. In each iteration, the dataset was subsampled to match the minimum sequencing depth observed across samples, ensuring uniform coverage. The resulting rarefied matrices were compiled into a three-dimensional array, and the median abundance of each ASV across all iterations was calculated to obtain a robust estimate of relative abundance. This approach minimized stochastic sampling effects while preserving biologically meaningful diversity and mitigating biases associated with uneven sequencing depth (Oksanen et al., 2020). Rarefied sequencing data sets were used to determine alpha diversity indexes (observed richness, Shannon diversity index, inverse Simpson index, and Pielou's evenness) using the *diversity* function in the "vegan" package (v-2.6.8).

2.4. Statistical analysis

Statistical analyses were performed using RStudio version 2023.09.0 (RStudio Team, 2023). For enzyme activities (dehydrogenase, urease, protease, β-glucosidase, phosphatase), PLFAs and alpha diversity indexes, linear models with treatment as a fixed effect were fitted (lm in R). Initially linear mixed models (identity link) with plot as a random intercept (lmer, package lme4) were evaluated to account for potential pseudoreplication (two sub-samples per plot), but likelihood-ratio tests and singular-fit diagnostics indicated negligible among-plot variance; therefore, after AIC tests, final inference relies on linear models (Supplementary Table S.M.2-1). Model assumptions were checked via residual diagnostics and Shapiro–Wilk tests. Hypothesis tests are reported as Type II ANOVA (package car) and pairwise contrasts using the TukeyHSD function from (“agricolae” package) (Supplementary Table S.M.2-2). To evaluate the overall effect of treatments in alpha diversity indexes across correlated indices, a MANOVA was ran first. Given the significance of the multivariate test, ANOVAs were subsequently conducted for each alpha index to identify the specific sources of variation. Holm’s correction was applied to control for Type I error across multiple tests, and pairwise comparisons were performed using estimated marginal means with Tukey adjustment (emmeans) (Supplementary Table S.M.2-2; S.M.2-3).

Because amendments were applied at a constant volume but differed in dry matter and nutrient contents, complementary dose sensitivity analyses within the organic-amendment subset were conducted (T3–T5: compost, poultry and swine manures). These models included the initial total nitrogen input (N input, kg ha^{-1}, dry basis) as a continuous predictor. N inputs were prioritized over dry matter due to their strong collinearity ($r \approx 0.98$ within T3–T5) and the direct link of N with microbial responses. Material × dose interactions were explored but are not identifiable with the present design because N input does not vary within materials; therefore, we report simple dose models as sensitivity checks (Supplementary Table S.M.2-4).

For beta diversity, differences in microbial community structure were evaluated using PERMANOVA (*adonis2*, Bray–Curtis, 4999 permutations). Two models were tested: one without blocking and another with permutation strata = block to account for spatial dependence among plots. The blocked model provided a better fit and was used for final interpretation. Detailed PERMANOVA results are presented in Supplementary Table SM2-5., and homogeneity of multivariate dispersions was examined via PERMADISP with *betadisper* function (“vegan” package). Canonical Analysis of Principal Coordinates (CAP), based on Bray-Curtis distance, was conducted using *CAPdiscrim* function (“BiodiversityR” package v-2.17; Kindt and Coe, 2005), and Distance-Based Redundancy Analysis (dbRDA) based on Bray-Curtis distance (*dbrda* and *envfit* functions, vegan) to constrain community variation by soil physicochemical properties. To identify the physicochemical variables driving the structure of prokaryotic and eukaryotic communities, a permutation-based analysis of variance with 4999 permutations was applied to assess the significance of these variables in explaining variance within the dissimilarity matrix. Multicollinearity among predictor variables was evaluated using the variance inflation factor (VIF), calculated with the *vif.cca* function from the “vegan” package. Predictor variables with VIF values below ten were considered acceptable. Full model formulas are provided in Supplementary Table SM2-6.

3. Results

3.1. Soil enzyme activity and microbial biomass

Enzyme activities exhibited different responses according to the use of contrasting organic amendments and fire occurrence (Fig. 1). Dehydrogenase activity increased significantly in all amended soils compared to both the reference (T0) and control burned soils (T1). The enzyme activities related to the N cycle (urease and protease) showed significant

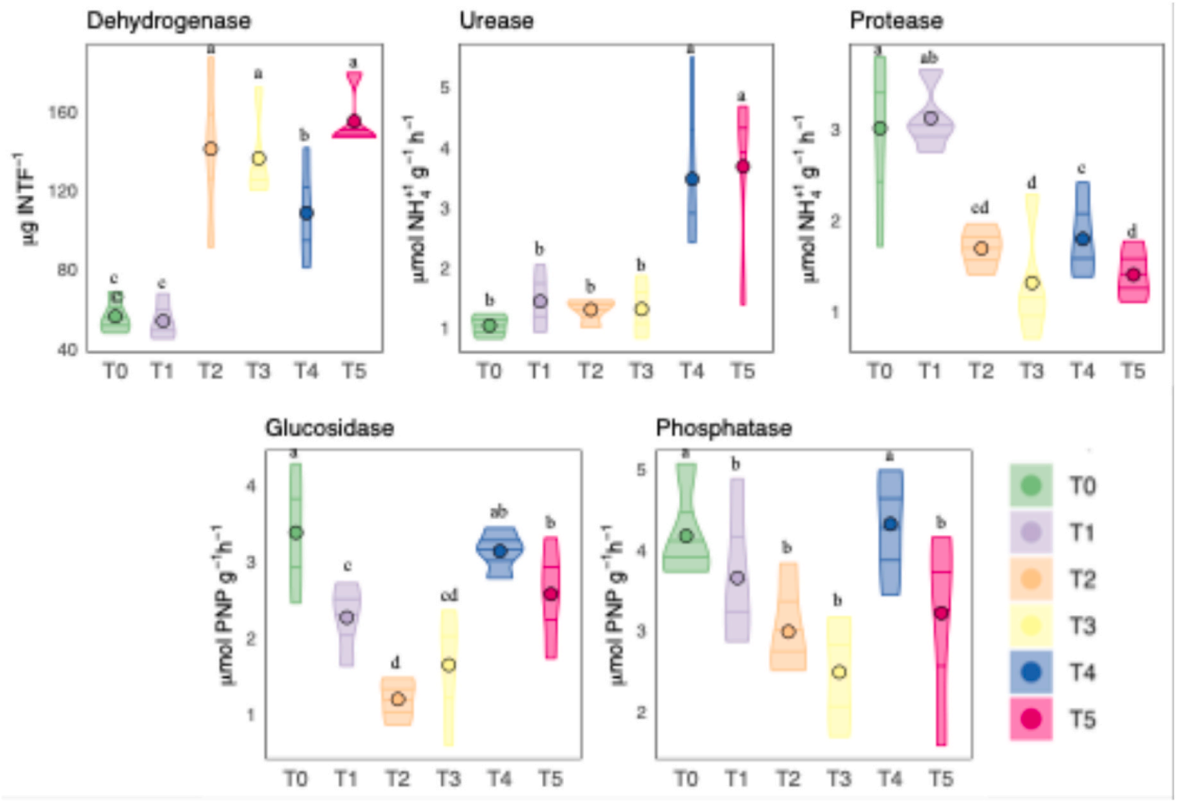

Fig. 1. Dehydrogenase, urease, protease, β-glucosidase, and phosphatase levels for each treatment. Lowercase letters indicate significant differences among treatments (p-value <0.05, Tukey test). T0, unburned; T1, control burned; T2, mulch; T3, compost; T4, poultry manure; and T5, swine manure.

differences between the reference (T0) and control burned soils (T1) when compared to poultry manure (T4) and swine manure (T5) amended soils, but in opposite directions. Urease activity, related to the microbial ammonium utilization, positively and exclusively responded to the manure application (T4 and T5), and was significantly activated in soils under their application. In contrast, protease activity, related to organic forms of nitrogen (peptides), was significantly higher in reference soils, followed by control burned soils, and showed a lower response to the application of organic amendments. Regarding biogeochemical cycles related to soil organic carbon, evaluated here by β-glucosidase activity as an indicator of available labile carbon substances in soils, this was significantly lower in T1 compared to T0; thus, it was affected by fire and sensitive to the different organic amendments applied. Phosphatase activity registered a significant reduction in burned soils, except poultry manure amended soils, which showed the highest values among treated soils, comparable to the reference condition. Dose sensitivity analyses (T3–T5) regressing enzyme activities against initial N input (kg ha^{-1}) by the amendment yielded modest associations that did not alter the treatment patterns from the main models (Supplementary Table SM2-54).

Total microbial biomass, determined by PLFA, showed no lasting effects of fire and did not vary among treatments (Table 1). Similarly, bacteria biomass followed the trend observed in total PLFA biomass, showing no significant differences among treatments. In contrast, fungi biomass responded significantly to fire occurrence and organic amendments. Control burned soils exhibited the lowest value of fungal biomass (1.60 nmol g^{-1}), while the highest values were evidenced in compost and swine manure treated soils (2.82 and 2.61 nmol g^{-1}, respectively). Dose sensitivity analyses restricted to T3–T5 (regressing PLFAs against initial N input, kg ha^{-1}) yielded weak associations and did not change treatment contrasts, indicating that material quality rather than N supply drives the observed differences (Supplementary Table SM2-54).

3.2. *Soil alpha and beta diversity*

Alpha diversity indices showed strong treatment effects (MANOVA results, Supplementary Table S.M.1-2), and revealed contrasting responses to treatments between prokaryotic and eukaryotic communities (Fig. 2, Supplementary Table S.M.1–3, S.M.2-3). In prokaryotic communities, while no fire legacies were detected (comparable results in T0 and T1), a strong negative response was observed in manure soils for all alpha diversity indices, particularly in T5 compared to T4 (Fig. 2A). In contrast, soils treated with compost (T3) and mulch only (T2) maintained diversity levels similar to those in control soils. An exception was observed for the Simpson index, where mulch treated soils (T2) showed significantly lower values, indicating less influence of dominant species. In eukaryotic communities, all amended soils showed markedly lower diversity values across all alpha diversity indices compared to unburned (T0) and burned control (T1) soils (Fig. 2B). Higher values for compost (T3) and poultry manure (T4) compared to mulch soils (T2) were generally observed, with swine manure (T5) in between these treatments. When conditioning on initial N inputs in the amendment subset (T3–T5) with dose sensitivity analyses, α-diversity patterns remained the same, indicating limited explanatory power of dose relative to amendment quality (Supplementary Table SM2-4).

Table 1

Microbial abundances (mean and standard deviation) for the total microbial community, fungal, bacterial, and the ratio fungal to bacteria communities, based on the PLFAs abundances (nmol g^{-1}). Lowercase letters indicate significant differences among treatments (p-value <0.05, Tukey test). Letters are only shown when statistical significance is observed. T0, unburned; T1, control burned; T2, mulch; T3, compost; T4, poultry manure; and T5, swine manure.

Treatments	Total	Fungi	Bacteria	Fungi/Bacteria
T0	11.9 ± 2.4	2.11 ± 0.44 ab	7.19 ± 1.79	0.30 ± 0.06
T1	10.1 ± 0.8	1.60 ± 0.22 b	5.71 ± 0.91	0.29 ± 0.07
T2	11.0 ± 1.7	2.42 ± 0.33 ab	6.32 ± 0.89	0.38 ± 0.03
T3	12.8 ± 2.2	2.82 ± 0.50 a	7.16 ± 1.26	0.40 ± 0.07
T4	10.3 ± 1.4	2.11 ± 0.38 ab	5.78 ± 0.68	0.36 ± 0.03
T5	11.9 ± 1.4	2.61 ± 0.44 a	6.81 ± 0.97	0.39 ± 0.08

Microbial community structure shows a profound effect in response to organic amendments and the fire effects on both prokaryotic and eukaryotic communities (Fig. 3A and B, perMANOVA results in Supplementary Table SM1-3; SM2-5). In the prokaryotic community (Fig. 3A), treatments resulted in high dissimilarity, with the unburned control soils (T0) clearly separated from all other treatments (upper part Y-axis), especially from the manure treated soils, which clustered in the lower part of the plot. The communities in manure soils showed notable differentiation along the X-axis, indicating variability among these treatments. In particular, poultry manure soils (T4) showed a marked divergence from other treated soils, suggesting a unique microbial composition. In contrast, eukaryotic communities showed a different response (Fig. 3B). Soils treated with organic amendments clustered closely together, indicating a high degree of similarity in microbial composition. These amended soils were highly dissimilar to both the unburned (T0) and burned control (T1) soils, which were also clearly separated from each other (Y-axis). The significant dissimilarity between the two control soils indicates the persistent influence of the fire occurrence on the eukaryotic community structure.

Shifts in microbial community composition were explained by changes in selected soil physicochemical properties following organic amendments (Fig. 3C and D; Supplementary Table S.M.1-4). Soil variables included in the dbRDA models (pH, Cu, Pb, Cd, and carbohydrates) were chosen from an initial set of 10 physicochemical parameters (Supplementary Table SM1-1) after checking for multicollinearity using VIF (threshold <10). In the prokaryotic community (Fig. 3C), the increase in soil pH in compost soils (7.48, Supplementary Table S.M1-1) strongly affected the community composition, along with the increase in Cu content. In contrast, the communities in soils treated with manures were mainly driven by the increase in Pb, in the case of T4, and Cd for both manures. Similar trends were observed for the eukaryotic community (Fig. 3D), where Pb and Cd were main drivers in manure treated soils, while pH was the dominant factor in compost soils (T3).

3.3. *Soil prokaryotic and eukaryotic community composition*

In the prokaryotic community, control soils, both unburned (T0) and burned without amendment (T1), showed similar relative abundances of dominant phyla and genera (Fig. 4A). The most notable fire legacy was the significant increase in Firmicutes, particularly the genus *Bacillus*, which persisted in amended soils. Except for the elevated Firmicutes, mulch treated soils (T2) were similar to the control soils in terms of dominant taxa, revealing low effects from mulch. In contrast, organic amendments (compost T3, and manures T4 and T5) significantly influenced microbial composition. These three amendments increased the dominance of Bacteroidetes at the phylum level, while Arthrobacter (Actinobacteria) consistently increased across amendments, and Solirubrobacter (Actinobacteria) decreased. Both compost and manure amendments were also associated with an increase in Proteobacteria, particularly Sphingomonas, in detriment of Acidobacteria. Differences emerged between compost and manure treatments: compost (T3) uniquely promoted an increase in Microvirga (Proteobacteria), while manure-treated soils showed notable increases in Nocardioides (Actinobacteria) and Flavobacterium (Bacteroidetes). Swine manure (T5) stands out with an exceptionally high increase in Sphingomonas (Fig. 4C).

In the eukaryotic community, fire and organic amendments led to significant changes at both the phylum and genus levels (Fig. 4B, Table S.M.2). A distinct fire legacy effect was observed with an increase in Chytridiomycota in burned control soils (T1) and mulch treated soils (T2), an effect that was presumably mitigated by organic amendments addition (T3-T5), where the abundance decreased. At the genus level,

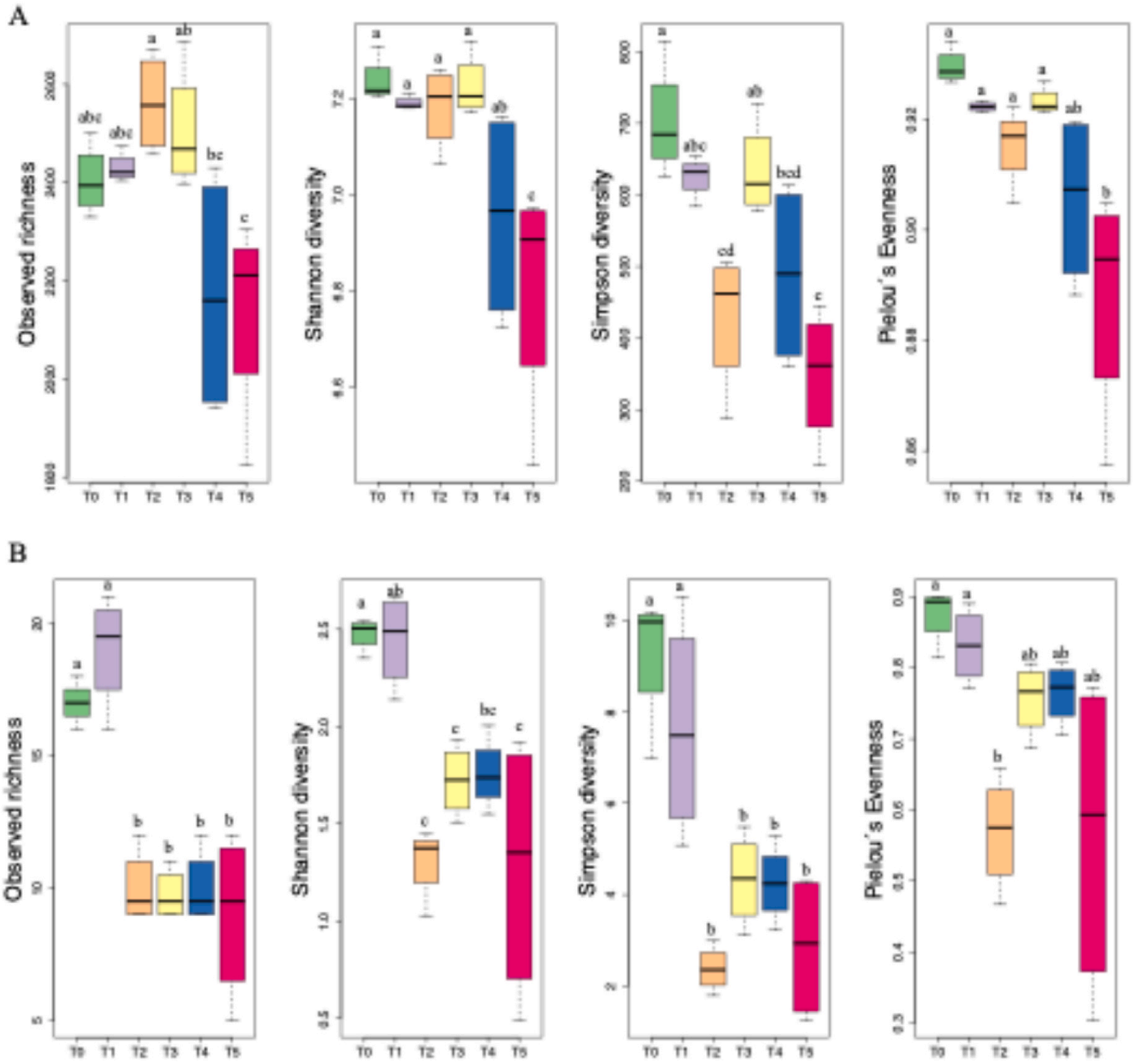

Fig. 2. Box plots of alpha diversity (mean ± standard deviation) of prokaryotic (A) and eukaryotes (B) communities for treatments, showing the effect of organic amendments in burned soils. Lowercase letters indicate significant differences among treatments (p-value <0.05, Tukey test). T0, unburned; T1, control burned; T2, mulch; T3, compost; T4, poultry manure; and T5, swine manure.

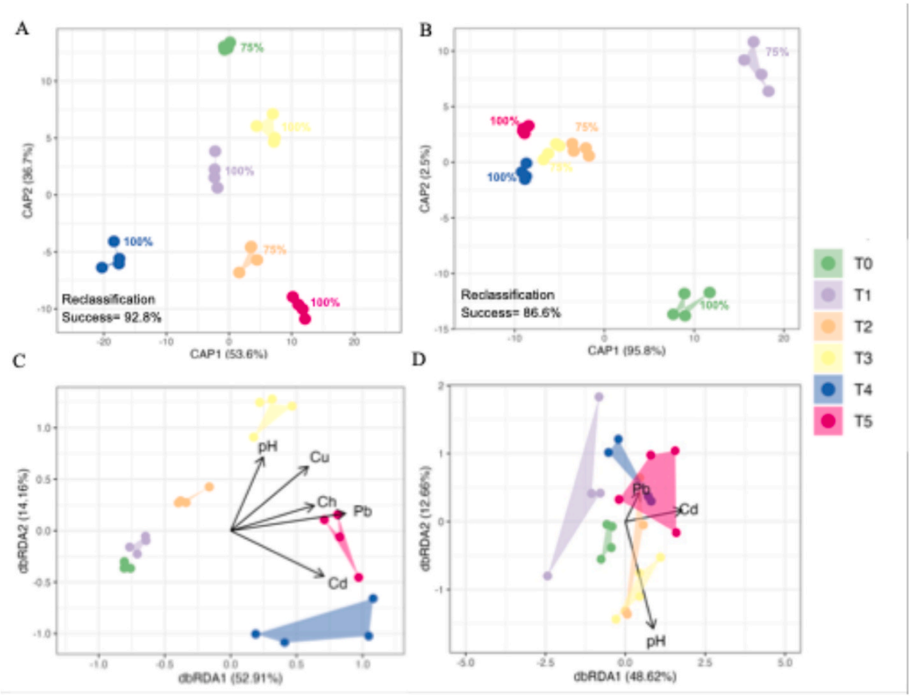

Fig. 3. Beta diversity analysis for communities treated with organic amendments. In the upper part, canonical analysis of principal coordinates (CAP) based on Bray-Curtis dissimilarities for prokaryotes (A) and eukaryotes (B). In the bottom part, distance-based redundancy analysis (dbRDA) based on Bray-Curtis dissimilarities, constrained by soil physicochemical properties (pH, Cu, Pb, Cd, and Ch as carbohydrates) for prokaryotes (C) and eukaryotes (D).

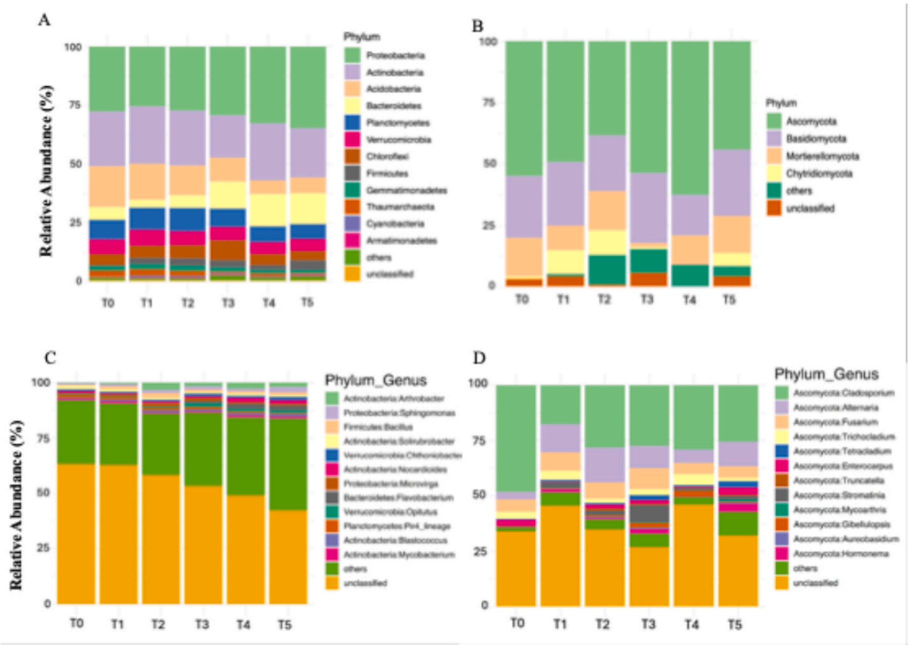

Fig. 4. Bar plots show the relative abundance of phylum-level taxonomic assignments for prokaryotic (A) and eukaryotic (B) ASVs, and genus-level assignments for prokaryotic (C) and eukaryotic (D) ASVs. The “Others” group in prokaryotic and eukaryotic plots represents taxa with low relative abundance. T0, unburned; T1, control burned; T2, mulch; T3, compost; T4, poultry manure; and T5, swine manure.

Alternaria showed a notable increase in fire-affected soils. Organic amendments also stimulated a range of less abundant taxa, as reflected by the increase in the “other” category (i.e., taxa making less that 0.1 of relative abundance) in all amended soils, increasing the diversity within the community compared to control soils (T0 and T1). Compared to control burned soils (T1), amendments with compost and manure increased Ascomycota, with Cladosporium responding positively to organic inputs after initially declining with fire occurrence. The compost addition (T3) showed a unique effect, with a selective inhibition of Mortierellomycota abundance, and a relative increase in Stromatinia at the genus level. Both manure types also significantly reduced the abundance of Fusarium. Poultry manure (T4) showed a distinct pattern with a relative increase in Trichocladium and decreases in Tetracladium and Enterocarpus, suggesting favorable conditions to certain genera within Ascomycota (Fig. 4D).

4. Discussion

4.1. Differentiated responses of prokaryotes and eukaryotes to organic amendments

The type of organic amendment emerged as a major dominant of post-fire microbial trajectories. Prokaryotic communities were particularly sensitive to amendment typology, whereas eukaryotic communities experienced a loss in diversity and a trend toward homogeneous assemblages regardless of amendment type. These contrasting patterns suggest that prokaryotes quickly react to nutrient and pH shifts, a mechanism commonly highlighted in post-fire dynamics, while fungi show a more constrained recovery, consistent with their life cycles and higher fire sensitivity (Pressler et al., 2019; Whitman et al., 2019).

Fresh manures induced the strongest shifts in the microbial community, reflecting the immediate availability of labile nutrients that stimulates copiotrophic taxa (Zhang et al., 2018). This stimulation enhanced microbial activity and fungi biomass, particularly under swine manure, consistent with previous findings emphasizing its potential to accelerate nutrient mineralization (García-Carmona et al., 2021). However, the boost in activity was accompanied by a loss in alpha diversity, suggesting that manures promote microbial activity at expense of community complexity. Dissimilarities between communities in poultry and swine manure soils may be explained by differences in carbon profiles and the content of trace metals, since heavy metals are known to be long-term stressors for microbes (Shuaib et al., 2021).

In contrast, compost induced a balanced microbial response, enhancing activity and fungal biomass while maintaining prokaryotic diversity more similar to control soils (unburned and untreated burned). This balanced response reflects the gradual release of nutrients from stable organic matter, a mechanism reported as beneficial for microbial communities under long-term compost application (Francioli et al., 2016; Ros et al., 2003). Additionally, the associated increase in pH, a well-stablished modulator of microbial community structure (Morris and Blackwood, 2024; Li et al., 2019), further explain the compositional changes in both prokaryotic and eukaryotic communities; emphasizing the role of soil pH as master variable in edaphic ecosystems.

Straw mulch induced only moderate shifts in microbial communities, likely due to the slower decomposition rate of plant materials that lead to accumulation of recalcitrant carbon in soils (Bao et al., 2020; Siedt et al., 2021). Unlike manure or compost, straw mulch might exert more pronounced long-term effects, consistent with observations in burned semiarid Mediterranean ecosystems where it is described to increase soil multifunctionality over time (Lucas-Borja et al., 2019).

Organic amendments had a stronger impact on eukaryotic communities, which exhibited reduced diversity and a homogenized structure after six months, irrespective of amendment type. This pattern is consistent with the idea that nutrient pulses and pH strong shifts favor competitively dominant sapiotrophic taxa over low-nutrient and stable conditions, adapted taxa, a mechanism reported in agricultural soils under long-term organic amendment application (Sun et al., 2020; Vida et al., 2020). Similar trends have been observed in burned Mediterranean soils, where wood mulch addition led to temporal fungal homogenization (García-Carmona et al., 2023). Given their role in carbon and nutrient cycling (Taylor and Bhatnagar, 2024), and their slower recovery than bacteria after fires (Dove and Hart, 2017; Holden et al., 2016), a short-term loss of diversity may temporarily limit these functions. Nonetheless, the high functional redundancy among saprotrophic species (Baldrian, 2017), and the migration from nearby refugia (Averill et al., 2022), suggest that a single amendment application is unlikely to cause permanent disruption to fungal communities. Even so, increasing fire severity and frequency could amplify the loss of diversity and would require particular caution in fire-prone environments.

4.2. Legacy effects of fire

The strong effects of organic amendments on microbial communities overlapped with the persistent fire legacies that remained evident nearly two years post-disturbance. Phylogenetic shifts, such as the increase in Firmicutes and the genus Arthrobacter, are consistent with common post-fire responses in Mediterranean soils (Aponte et al., 2022; Fernández-González et al., 2017; Prendergast-Miller et al., 2017), highlighting the resilience of fire-adapted taxa. However, fungal biomass and eukaryotic structure revealed persistent fire effects, consistent with their greater heat sensitivity and slower recolonization than bacteria (Mataix-Solera et al., 2009). In Mediterranean ecosystems, fire-induced alterations in the quantity and quality of organic matter, pH, water repellency, and aggregate stability, are major drivers of long-lasting changes in microbial diversity and functionality (González-Pérez et al., 2004; Pérez-Valera et al., 2019). In Chilean sclerophyll forests, however, the resilience of soil microbiota remains understudied, raising concerns given the predicted increase in fire frequency with climate change in the region (Armenteras et al., 2020). Recent evidence from the 2017 megafire at the same site showed that prokaryote composition remained profoundly altered almost three years post-fire, despite the stabilization of soil physicochemical properties, with organic matter mineralization and nitrogen availability emerging as key driver of structural shifts, revealing the long-lasting effects of fires in microbial diversity (Aponte et al., 2022). Given the generalized decrease in soil organic matter after fire events across South America (Giorgis et al., 2021), organic matter replenishment through amendments could represent an effective management strategy to mitigate the loss of soil functionality, stimulating microbial processes associated with organic matter turnover in soils that buffer fire legacies and accelerate ecosystem recovery.

4.3. Recovery of soil functions through enzyme activity

Organic amendments influenced soil enzymes differently, suggesting diverse pathways for restoring nutrient cycling related to C, N, and P cycles. Dehydrogenase activity consistently increased across treatments, confirming that amendments generally stimulate microbial metabolism (Bastida et al., 2008), as reported in other recently burned Mediterranean soils (Guénon and Gros, 2015). Fresh manures strongly enhanced urease, β-glucosidase, and phosphatase activities, indicating ongoing nutrient mineralization and effective utilization of labile nutrients. By contrast, compost and mulch led to more moderate enzyme activity levels, reflecting slower nutrient release rates and potentially longer-term stability (Luna et al., 2016; Wang et al., 2022). Interestingly, high enzymatic activity persisted even when microbial diversity declined, suggesting that functional redundancy buffered the diversity loss, taxonomic shifts across amendments (Pérez-Valera et al., 2019).

Because amendments were applied at constant volume, initial loads differed among materials; however, by six months material quality and stoichiometry more plausibly govern enzyme patterns than dose. Fresh manures, rich in readily mineralizable C and N, tend to produce short-lived enzymatic surges (rapid ammonification and copiotrophic blooms), whereas compost, with more polymerized organic matter, promotes slower release kinetics and steadier functions. In parallel, saturation of microbial–enzymatic processes and subsequent abiotic losses (leaching, volatilization, sorption), together with plant–microbial uptake, progressively diminish the imprint of the initial dose. Consistent with this mechanism, the dose sensitive models (in T3–T5, conditioning on initial N input) produced only modest, enzyme-specific slopes and did not alter treatment contrasts, reinforcing that material composition rather than initial load alone explains the observed biochemical recovery over six months.

4.4. Shifts in specific microbial taxa related to copio- and oligotrophic strategists

Organic amendments promoted clear taxonomic shifts, favoring fast-growing and nutrient-responsive taxa over those adapted to resource-limited conditions (Goldfarb et al., 2011; Ye et al., 2021). These changes suggest that the main driver for those shifts was nutrient availability rather than the establishment of exogenous microbes, that tend to be outcompeted by native communities in post-fire environments characterized by lower moisture, higher pH, and nutrient limitations (Hueso et al., 2011; Pérez-Valera et al., 2022).

In the prokaryotic community, organic amendments promoted copiotrophic taxa, such as Proteobacteria (notably Sphingomonas), while reducing the relative abundance of oligotrophic groups like Acidobacteria, a pattern consistent with previous findings (Francioli et al., 2016; Goldfarb et al., 2011; Naether et al., 2012). These shifts were pronounced in manure-treated soils, with an increase in Nocardioides (Actinobacteria) and Flavobacterium (Bacteroidetes), taxa associated with nutrient-rich environments and organic matter degradation (Neher et al., 2020; Sun et al., 2019), the dominance of Sphingomonas under swine manure highlights a selective enrichment of decomposer genera compared to poultry manure (Cheng et al., 2023). Compost supported taxa associated with more stable carbon pools, such as Microvirga, indicating a sustained pathway to nutrient cycling (Araujo et al., 2023; Mayerhofer et al., 2021).

Eukaryotic communities showed similar changes driven by the amendments, with organic inputs favoring Ascomycota, a group of saprotrophic taxa that thrive on organic amended soils (Ye et al., 2021), while fire legacies were evident in the persistence of Chytridiomycota (Smith et al., 2017). The significant increase in less dominant or rare taxa probably indicates a diversification effect due to the availability of diverse substrates, suggesting that organic amendments support a wider range of saprotrophic fungi, which may translate into an increase in soil multifunctionality (Chen et al., 2020). However, the profile of the organic inputs plays a key role in determining specific saprotrophic taxa stimulation (Clocchiatti et al., 2020), as seen with different responses between compost and manure additions. Unique to the compost treatment, Mortierellomycota decreased, as observed in long-term composted soils (Liu et al., 2024). Stromatinia also increased in compost soils, but while it was present in all soils, its increase should be monitored as a specific species, *S. cepivora*, is pathogenic to crops like onions. A reduction in Fusarium in manure soils, a genus that includes saprophytic but also pathogenic species in agricultural systems, may be linked to the increase of Actinobacteria that can suppress pathogens with actinomycins secretion (Yang et al., 2020).

4.5. Implications for soil restoration

A key question in post-fire restoration is whether organic amendments can enhance microbial recovery in fire-affected soils. The results confirmed the main hypothesis, showing that amendments altered microbial communities within six months of application, favoring fast-growing decomposers compared to the nutrient-limited native communities. In terms of functionally, manures provided a short-term boost in nutrient cycling enzymes, while compost and mulch promoted slower but more stable effects. Importantly, compost maintained prokaryotic communities closer to reference conditions, whereas manures induced stronger shifts and reduced microbial diversity.

These findings suggest that organic amendments can contribute to post-fire soil resilience, but their effectiveness depends on the type of material applied. In practical terms, compost emerges as a more balanced and ecologically safer amendment for supporting microbial functions while minimizing disruption to community structure. Manures may be useful when rapid functional recovery is required, but their potential risks, including nutrient imbalances, pollution with heavy metals or pathogen introduction, require careful monitoring.

In Mediterranean sclerophyll forests of Chile, where fire frequency is increasing under climate change, targeted applications of compost as “fertile islands” in the most degraded patches (Rojas et al., 2016; Varela et al., 2011), could accelerate ecosystem recovery while reducing ecological risks. This study, together with previous work at the same site (García-Carmona et al., 2021), constitutes one of the few efforts assessing soil restoration strategies in these ecosystems, where the microbiome remains largely understudied (Aponte et al., 2022). Expanding research on the use of organic amendments in non-agricultural, fire-prone ecosystems is critical to refine restoration practices and anticipate responses to changing fire regime. Overall, these insights underscore the need to select appropriate organic inputs to foster soil functional resilience and ecosystem recovery in a Mediterranean ecosystem highly vulnerable to climate change, with implications for fire-prone regions worldwide.

CRediT authorship contribution statement

Minerva García-Carmona: Writing – original draft, Visualization, Validation, Formal analysis. **Yoelvis Sulbaran-Bracho:** Writing – review & editing, Visualization, Validation, Formal analysis, Data curation. **César Marín:** Writing – review & editing, Validation. **Jonathan E. Maldonado:** Validation, Data curation. **Fuensanta García-Orenes:** Writing – review & editing, Funding acquisition. **Claudia Rojas:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Claudia Rojas reports financial support and administrative support were provided by Universidad de O’Higgins. Claudia Rojas reports a relationship with University of O’Higgins - Colchagua Campus that includes: employment. If there are other authors, they 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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.128261.

Data availability

Data will be made available on request.

References

Amaral-Zettler, L.A., McCliment, E.A., Ducklow, H.W., Huse, S.M., 2009. A method for studying protistan diversity using massively parallel sequencing of V9 hypervariable regions of small-subunit ribosomal RNA genes. PLoS One 4, e6372. https://doi.org/10.1371/JOURNAL.PONE.0006372.

Aponte, H., Galindo-Castañeda, T., Yáñez, C., Hartmann, M., Rojas, C., 2022. Microbial community-level physiological profiles and genetic prokaryotic structure of burned soils under Mediterranean sclerophyll forests in central Chile. Front. Microbiol. 13, 824813. https://doi.org/10.3389/FMICB.2022.824813/BIBTEX.

Apprill, A., McNally, S., Parsons, R., 2015. Minor revision to V4 region SSU rRNA 806R gene primer greatly increases detection of SAR11 bacterioplankton. Aquat. Microb. Ecol. 75, 129–137. https://doi.org/10.3354/ame01753.

Araujo, A.S.F., Rocha, S.M.B., Pereira, A.P. de A., Melo, V.M.M., Oliveira, F.A.S., de Alcantara Neto, F., de Medeiros, E.V., Araujo, F.F., Mendes, L.W., 2023. Responses of bacterial and archaeal communities to nitrogen fertilization in a compost-amended soil. Pedobiologia 101, 150915. https://doi.org/10.1016/J.PEDOBI.2023.150915.

Armenteras, D., de la Barrera, F., 2023. Landscape management is urgently needed to address the rise of megafires in South America. Commun. Earth Environ. 4, 1–4. https://doi.org/10.1038/s43247-023-00964-6.

Armenteras, D., González, T.M., Ríos, O.V., Elizalde, M.C.M., Oliveras, I., 2020. Fire in the ecosystems of northern South America: advances in the ecology of tropical fires in Colombia, Ecuador and Peru. Caldasia 42, 1–16. https://doi.org/10.15446/CALDASIA.V42N1.77353.

Averill, C., Anthony, M.A., Baldrian, P., Finkbeiner, F., van den Hoogen, J., Kiers, T., Kohout, P., Hirt, E., Smith, G.R., Crowther, T.W., 2022. Defending Earth's terrestrial microbiome. Nat. Microbiol. 1–9. https://doi.org/10.1038/s41564-022-01228-3.

Baldrian, P., 2017. Forest microbiome: diversity, complexity and dynamics. FEMS (Fed. Eur. Microbiol. Soc.) Microbiol. Rev. 41, 109–130. https://doi.org/10.1093/FEMSRE/FUW040.

Bao, Y., Feng, Y., Stegen, J.C., Wu, M., Chen, R., Liu, W., Zhang, J., Li, Z., Lin, X., 2020. Straw chemistry links the assembly of bacterial communities to decomposition in paddy soils. Soil Biol. Biochem. 148, 107866. https://doi.org/10.1016/J.SOILBIO.2020.107866.

Bastida, F., Zsolnay, A., Hernández, T., García, C., 2008. Past, present and future of soil quality indices: a biological perspective. Geoderma 147, 159–171. https://doi.org/10.1016/j.geoderma.2008.08.007.

Bengtsson-Palme, J., Ryberg, M., Hartmann, M., Branco, S., Wang, Z., Godhe, A., De Wit, P., Sánchez-García, M., Ebersberger, I., de Sousa, F., Amend, A., Jumpponen, A., Unterseher, M., Kristiansson, E., Abarenkov, K., Bertrand, Y.J.K., Sanli, K., Eriksson, K.M., Vik, U., Veldre, V., Nilsson, R.H., 2013. Improved software detection and extraction of ITS1 and ITS2 from ribosomal ITS sequences of fungi and other eukaryotes for analysis of environmental sequencing data. Methods Ecol. Evol. 4, 914–919. https://doi.org/10.1111/2041-210X.12073.

Bernal, M.P., Alburquerque, J.A., Moral, R., 2009. Composting of animal manures and chemical criteria for compost maturity assessment. A review. Bioresour. Technol. 100, 5444–5453. https://doi.org/10.1016/j.biortech.2008.11.027.

Bossio, D.A., Scow, K.M., Gunapala, N., Graham, K.J., Ecol, M., 1998. Determinants of soil microbial communities: effects of agricultural management, season, and soil type on phospholipid fatty acid profiles. Microb. Ecol. 36, 1–12.

Bouskill, N.J., Mekonnen, Z., Zhu, Q., Grant, R., Riley, W.J., 2022. Microbial contribution to post-fire tundra ecosystem recovery over the 21st century. Commun. Earth Environ. 3, 1–15. https://doi.org/10.1038/s43247-022-00356-2, 2022.

Chen, Q.L., Ding, J., Zhu, D., Hu, H.W., Delgado-Baquerizo, M., Ma, Y.B., He, J.Z., Zhu, Y. G., 2020. Rare microbial taxa as the major drivers of ecosystem multifunctionality in long-term fertilized soils. Soil Biol. Biochem. 141, 107686. https://doi.org/10.1016/j.soilbio.2019.107686.

Cheng, L., Wang, L., Wang, X., Ou, Y., Liu, H., Hou, X., Yan, L., Li, X., 2023. The various effect of cow manure compost on the degradation of imazethapyr in different soil types. Chemosphere 337, 139325. https://doi.org/10.1016/J.CHEMOSPHERE.2023.139325.

Clocchiatti, A., Hannula, S.E., van den Berg, M., Korthals, G., de Boer, W., 2020. The hidden potential of saprotrophic fungi in arable soil: patterns of short-term stimulation by organic amendments. Appl. Soil Ecol. 147, 103434. https://doi.org/10.1016/J.APSOIL.2019.103434.

CONAF, 2017. Número De Incendios Forestales Y Superficie Afectada a La Fecha. Ministerio de Agricultura, Santiago [WWW Document]. https://www.conaf.cl/incendios-forestales/incendio.

De la Barrera, F., Barraza, F., Favier, P., Ruiz, V., Quense, J., 2018. Megafires in Chile 2017: monitoring multiscale environmental impacts of burned ecosystems. Sci. Total Environ. 637, 1526–1536. https://doi.org/10.1016/j.scitotenv.2018.05.119.

Delgado-Baquerizo, M., Maestre, F.T., Reich, P.B., Jeffries, T.C., Gaitan, J.J., Encinar, D., Berdugo, M., Campbell, C.D., Singh, B.K., 2016. Microbial diversity drives multifunctionality in terrestrial ecosystems. Nat. Commun. 7, 1–8. https://doi.org/10.1038/ncomms10541.

Diacono, M., Montemurro, F., 2011. Long-term effects of organic amendments on soil fertility. Sustain. Agri. 2, 761–786. https://doi.org/10.1007/978-94-007-0394-0_34.

Dove, N.C., Hart, S.C., 2017. Fire reduces fungal species richness and in situ mycorrhizal colonization: a meta-analysis. Fire Ecol. 13, 37–65. https://doi.org/10.4996/fireecology.130237746.

Edgar, R.C., 2016. UNOISE2: improved error-correction for Illumina 16S and ITS amplicon sequencing. bioRxiv, 081257. https://doi.org/10.1101/081257.

Edgar, R.C., Flyvbjerg, H., 2015. Error filtering, pair assembly and error correction for next-generation sequencing reads. Bioinformatics 31, 3476–3482. https://doi.org/10.1093/BIOINFORMATICS/BTV401.

Edgar, R.C., Haas, B.J., Clemente, J.C., Quince, C., Knight, R., 2011. UCHIME improves sensitivity and speed of chimera detection. Bioinformatics 27, 2194–2200. https://doi.org/10.1093/bioinformatics/btr381.

Federle, T.W., 1986. Microbial distribution in soil—new techniques. In: Megusar, F., Gantar, M. (Eds.), Perspectives in Microbial Ecology. Proceedings of the Fourth International Symposium on Microbial Ecology. Slovene Society for Microbiology, Ljubljana, Slovenia, pp. 493–498.

Fernández-García, V., Marcos, E., Huerta, S., Calvo, L., 2021. Soil-vegetation relationships in Mediterranean forests after fire. Forest Ecosys. 8, 1–13. https://doi.org/10.1186/S40663-021-00295-Y/FIGURES/6.

Fernández-González, A.J., Martínez-Hidalgo, P., Cobo-Díaz, J.F., Villadas, P.J., Martínez-Molina, E., Toro, N., Tringe, S.G., Fernández-López, M., 2017. The rhizosphere microbiome of burned holm-oak: potential role of the genus Arthrobacter in the recovery of burned soils. Sci. Rep. 7, 1–12. https://doi.org/10.1038/s41598-017-06112-3.

Francioli, D., Schulz, E., Lentendu, G., Wubet, T., Buscot, F., Reitz, T., 2016. Mineral vs. organic amendments: microbial community structure, activity and abundance of agriculturally relevant microbes are driven by long-term fertilization strategies. Front. Microbiol. 7, 215318. https://doi.org/10.3389/FMICB.2016.01446/BIBTEX.

García, C., Hernandez, T., Costa, F., 1997. Potential use of dehydrogenase activity as an index of microbial activity in degraded soils. Commun. Soil Sci. Plant Anal. 28, 123–134. https://doi.org/10.1080/00103629709369777.

García-Carmona, M., Lepinay, C., Mataix-Solera, J., Baldrian, P., Arcenegui, V., Cajthaml, T., García-Orenes, F., 2023. Post-fire wood mulch negatively affects the moss biocrust cover and its positive effects on microbial diversity in a semi-arid Mediterranean forest. Appl. Soil Ecol. 191. https://doi.org/10.1016/j.apsoil.2023.105026.

García-Carmona, M., Marín, C., García-Orenes, F., Rojas, C., 2021. Contrasting organic amendments induce different short-term responses in soil abiotic and biotic properties in a fire-affected native Mediterranean Forest in Chile. J. Soil Sci. Plant Nutr. 21, 2105–2114. https://doi.org/10.1007/S42729-021-00506-Z/TABLES/2.

Garreaud, R.D., Boisier, J.P., Rondanelli, R., Montecinos, A., Sepúlveda, H.H., Veloso-Aguila, D., 2020. The Central Chile Mega Drought (2010–2018): a climate dynamics perspective. Int. J. Climatol. 40, 421–439. https://doi.org/10.1002/joc.6219.

Giorgis, M.A., Zeballos, S.R., Carbone, L., Zimmermann, H., Von Wehrden, H., Aguilar, R., Ferreras, A.E., Tecco, P.A., Kowaljow, E., Barri, F., Gurvich, D.E., Villagra, P., Jaureguiberry, P., 2021. A review of fire effects across South American ecosystems: the role of climate and time since fire. Fire Ecol. https://doi.org/10.1186/s42408-021-00100-9, 17–11.

Goldfarb, K.C., Karaoz, U., Hanson, C.A., Santee, C.A., Bradford, M.A., Treseder, K.K., Wallenstein, M.D., Brodie, E.L., 2011. Differential growth responses of soil bacterial taxa to carbon substrates of varying chemical recalcitrance. Front. Microbiol. 2, 1–10. https://doi.org/10.3389/fmicb.2011.00094.

González-Pérez, J.A., González-Vila, F.J., Almendros, G., Knicker, H., 2004. The effect of fire on soil organic matter - a review. Environ. Int. 30, 855–870. https://doi.org/10.1016/j.envint.2004.02.003.

González-Ubierna, S., Jorge-Mardomingo, I., Carrero-González, B., Teresa de la Cruz, M., Ángel Casermeiro, M., 2012. Soil organic matter evolution after the application of high doses of organic amendments in a Mediterranean calcareous soil. J. Soils Sediments 12, 1257–1268. https://doi.org/10.1007/s11368-012-0516-y.

Guénon, R., Gros, R., 2016. Soil microbial functions after Forest fires affected by the compost quality. Land Degrad. Dev. 27, 1391–1402. https://doi.org/10.1002/ldr.2393.

Guénon, R., Gros, R., 2015. Increasing the maturity of compost used affects the soil chemical properties and the stability of microbial activity along a mediterranean post-fire chronosequence. Eur. J. Soil Biol. 66, 1–10. https://doi.org/10.1016/j.ejsobi.2014.11.002.

Holden, S.R., Rogers, B.M., Treseder, K.K., Randerson, J.T., 2016. Fire severity influences the response of soil microbes to a boreal forest fire. Environ. Res. Lett. 11, 035004. https://doi.org/10.1088/1748-9326/11/3/035004.

Hudiburg, T., Mathias, J., Bartowitz, K., Berardi, D.M., Bryant, K., Graham, E., Kolden, C. A., Betts, R.A., Lynch, L., 2023. Terrestrial carbon dynamics in an era of increasing wildfire. Nat. Clim. Change. https://doi.org/10.1038/s41558-023-01881-4.

Hueso, S., Hernández, T., García, C., 2011. Resistance and resilience of the soil microbial biomass to severe drought in semiarid soils: the importance of organic amendments. Appl. Soil Ecol. 50, 27–36. https://doi.org/10.1016/J.APSOIL.2011.07.014.

Kindt, R., Coe, Richard, 2005. Tree Diversity Analysis: A Manual and Software for Common Statistical Methods for Ecological and Biodiversity Studies. World Agrofirestry Centre.

Kowaljow, E., Mazzarino, M.J., 2007. Soil restoration in semiarid Patagonia: chemical and biological response to different compost quality. Soil Biol. Biochem. 39, 1580–1588. https://doi.org/10.1016/j.soilbio.2007.01.008.

Langmead, B., Salzberg, S.L., 2012. Fast gapped-read alignment with Bowtie 2. Nat. Methods 9 (4 9), 357–359. https://doi.org/10.1038/nmeth.1923, 2012.

Li, W., Niu, S., Liu, X., Wang, J., 2019. Short-term response of the soil bacterial community to differing wildfire severity in Pinus tabulaeformis stands. Sci. Rep. 9, 1–10. https://doi.org/10.1038/s41598-019-38541-7.

Liu, Q., Tang, L., Sun, H., Kong, X., Jiao, Y., Wu, W., Li, S., Shen, Y., 2024. Responses of the fungal-bacterial community and network to surface mulching and nitrogen fertilization in the Loess Plateau. Plant Soil 494, 111–126. https://doi.org/10.1007/S11104-023-06260-8/FIGURES/4.

Lucas-Borja, M.E., Plaza-Álvarez, P.A., Ortega, R., Miralles, I., González-Romero, J., Sagra, J., Moya, D., Zema, D.A., De Las Heras, J., 2019. Short-term changes in soil functionality after wildfire and straw mulching in a Pinus halepensis M. forest. For. Ecol. Manag. 457, 117700. https://doi.org/10.1016/j.foreco.2019.117700.

Luna, L., Pastorelli, R., Bastida, F., Hernández, T., García, C., Miralles, I., Solé-Benet, A., 2016. The combination of quarry restoration strategies in semiarid climate induces different responses in biochemical and microbiological soil properties. Appl. Soil Ecol. 107, 33–47. https://doi.org/10.1016/j.apsoil.2016.05.006.

Luo, G., Li, L., Friman, V.-P., Guo, J., Guo, S., Shen, Q., Ling, N., 2018. Organic amendments increase crop yields by improving microbe-mediated soil functioning of agroecosystems: a meta-analysis. Soil Biol. Biochem. 124, 105–115. https://doi.org/10.1016/j.soilbio.2018.06.002.

Marín, C., Rojas, C., 2020. Early responses of soil health indicators to organic amendments and plant establishment at a fire-affected sclerophyllous forest. Agro Sur 48, 17–27. https://doi.org/10.4206/agrosur.2020.v48n2-03.

Martin, M., 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. EMBnet.J. 17, 10–12. https://doi.org/10.14806/EJ.17.1.200.

Mataix-Solera, J., Guerrero, C., García-Orenes, F., Bárcenas, G., Torres, M.P., 2009. Forest fire effects on soil microbiology. In: Cerdá, A., Robichaud, P.R. (Eds.), Fire Effects on Soils and Restoration Strategies. CRC Press, pp. 133–175. https://doi.org/10.1201/9781439843338-c5.

Mayerhofer, J., Thuerig, B., Oberhaensli, T., Enderle, E., Lutz, S., Ahrens, C.H., Fuchs, J. G., Widmer, F., 2021. Indicative bacterial communities and taxa of disease-suppressing and growth-promoting composts and their associations to the rhizoplane. FEMS (Fed. Eur. Microbiol. Soc.) Microbiol. Ecol. 97. https://doi.org/10.1093/FEMSEC/FIAB134.

McLauchlan, K.K., Higuera, P.E., Miesel, J., Rogers, B.M., Schweitzer, J., Shuman, J.K., Tepley, A.J., Varner, J.M., Veblen, T.T., Adalsteinsson, S.A., Balch, J.K., Baker, P., Batllori, E., Bigio, E., Brando, P., Cattau, M., Chipman, M.L., Coen, J., Crandall, R., Daniels, L., Enright, N., Gross, W.S., Harvey, B.J., Hatten, J.A., Hermann, S., Hewitt, R.E., Kobziar, L.N., Landesmann, J.B., Loranty, M.M., Maezumi, S.Y., Mearns, L., Moritz, M., Myers, J.A., Pausas, J.G., Pellegrini, A.F.A., Platt, W.J., Roozeboom, J., Safford, H., Santos, F., Scheller, R.M., Sherriff, R.L., Smith, K.G., Smith, M.D., Watts, A.C., 2020. Fire as a fundamental ecological process: research advances and frontiers. J. Ecol. 108, 2047–2069. https://doi.org/10.1111/1365-2745.13403.

Miranda, A., Garreaud, R., 2023. Climate-induced large-scale browning in Chilean Mediterranean forest. Nat. Plants 9, 1785–1786. https://doi.org/10.1038/s41477-023-01546-2.

Moreira, F., Ascoli, D., Safford, H., Adams, M.A., Moreno, J.M., Pereira, J.M., Catry, F.X., Armesto, J., Bond, W., González, M.E., Curt, T., 2020. Wildfire management in Mediterranean-type regions: paradigm change needed. Environ. Res. Lett. 15, 011001. https://doi.org/10.1088/1748-9326/ab541e.

Morris, S.J., Blackwood, C.B., 2024. The ecology of soil biota and their function. In: Paul, E., Frey, S. (Eds.), Soil Microbiology, Ecology and Biochemistry. Elsevier, pp. 275–302. https://doi.org/10.1016/B978-0-12-822941-5.00010-7.

Naether, A., Foesel, B.U., Naegele, V., Wüst, P.K., Weinert, J., Bonkowski, M., Alt, F., Oelmann, Y., Polle, A., Lohaus, G., Gockel, S., Hemp, A., Kalko, E.K.V., Linsenmair, K.E., Pfeiffer, S., Renner, S., Schöning, I., Weisser, W.W., Wells, K., Fischer, M., Overmann, J., Friedrich, M.W., 2012. Environmental factors affect acidobacterial communities below the subgroup level in grassland and forest soils. Appl. Environ. Microbiol. 78, 7398–7406. https://doi.org/10.1128/AEM.01325-12/SUPPL_FILE/ZAM999103757SO1.PDF.

Nannipieri, P., Ceccanti, B., Cervelli, S., Matarese, E., 1981. Extraction of phosphatase, urease, proteases, organic carbon, and nitrogen from soil. Soil Sci. Soc. Am. J. 45. https://doi.org/10.2136/sssaj1981.03615995004500020048x. NP-NP.

Naseby, D.C., Lynch, J.M., 1997. Rhizosphere soil enzymes as indicators of perturbations caused by enzyme substrate addition and inoculation of a genetically modified strain of Pseudomonas fluorescens on wheat seed. Soil Biol. Biochem. 29, 1353–1362. https://doi.org/10.1016/S0038-0717(97)00061-8.

Neher, D.A., Limoges, M.A., Weicht, T.R., Sharma, M., Millner, P.D., Donnelly, C., 2020. Bacterial community dynamics distinguish poultry compost from dairy compost and non-amended soils planted with spinach. Microorganisms 8. https://doi.org/10.3390/MICROORGANISMS8101601. Page 1601 8, 1601.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O’hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H, 2020. vegan: Community Ecology Package. R package version 2.5-6. 2019.

1995, U Olsson, P., Bååth, E., Jakobsen, I., Research, B.S.-M., 1995. The use of phospholipid and neutral lipid fatty acids to estimate biomass of arbuscular mycorrhizal fungi in soil. Mycol. Res. 99, 623–629.

Parada, A.E., Needham, D.M., Fuhrman, J.A., 2016. Every base matters: assessing small subunit rRNA primers for marine microbiomes with mock communities, time series and global field samples. Environ. Microbiol. 18, 1403–1414. https://doi.org/10.1111/1462-2920.13023.

Pérez-Valera, E., de Melo Rangel, W., Elhottová, D., 2022. Cattle manure application triggers short-term dominance of Acinetobacter in soil microbial communities. Appl. Soil Ecol. 176, 104466. https://doi.org/10.1016/J.APSOIL.2022.104466.

Pérez-Valera, E., Goberna, M., Verdú, M., 2019. Fire modulates ecosystem functioning through the phylogenetic structure of soil bacterial communities. Soil Biol. Biochem. 129, 80–89. https://doi.org/10.1016/j.soilbio.2018.11.007.

Prendergast-Miller, M.T., de Menezes, A.B., Macdonald, L.M., Toscas, P., Bissett, A., Baker, G., Farrell, M., Richardson, A.E., Wark, T., Thrall, P.H., 2017. Wildfire impact: natural experiment reveals differential short-term changes in soil microbial communities. Soil Biol. Biochem. 109, 1–13. https://doi.org/10.1016/j.soilbio.2017.01.027.

Pressler, Y., Moore, J.C., Cotrufo, M.F., 2019. Belowground community responses to fire: meta-analysis reveals contrasting responses of soil microorganisms and mesofauna. Oikos 128, 309–327. https://doi.org/10.1111/oik.05738.

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., Glöckner, F.O., 2013. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. Nucleic Acids Res. 41, D590–D596. https://doi.org/10.1093/NAR/GKS1219.

Rojas, C., Gutierrez, R.M., Bruns, M.A., 2016. Bacterial and eukaryal diversity in soils forming from acid mine drainage precipitates under reclaimed vegetation and biological crusts. Appl. Soil Ecol. 105, 57–66. https://doi.org/10.1016/j.apsoil.2016.03.012.

Ros, M., Hernandez, M.T., García, C., 2003. Soil microbial activity after restoration of a semiarid soil by organic amendments. Soil Biol. Biochem. 35, 463–469. https://doi.org/10.1016/S0038-0717(02)00298-5.

RStudio Team, 2023. Rstudio: Integrated Development for R. RStudio, Inc., Boston, MA. URL. http://www.rstudio.com/.

Shakesby, R.A., 2011. Post-wildfire soil erosion in the Mediterranean: review and future research directions. Earth Sci. Rev. 105, 71–100. https://doi.org/10.1016/j.earscirev.2011.01.001.

Shu, X., He, J., Zhou, Z., Xia, L., Hu, Y., Zhang, Yulin, Zhang, Yanyan, Luo, Y., Chu, H., Liu, W., Yuan, S., Gao, X., Wang, C., 2022. Organic amendments enhance soil microbial diversity, microbial functionality and crop yields: a meta-analysis. Sci. Total Environ. 829, 154627. https://doi.org/10.1016/j.scitotenv.2022.154627.

Shuaib, M., Azam, N., Bahadur, S., Romman, M., Yu, Q., Xuexiu, C., 2021. Variation and succession of microbial communities under the conditions of persistent heavy metal and their survival mechanism. Microb. Pathog. 150, 104713. https://doi.org/10.1016/J.MICPATH.2020.104713.

Siedt, M., Schäffer, A., Smith, K.E.C., Nabel, M., Roß-Nickoll, M., van Dongen, J.T., 2021. Comparing straw, compost, and biochar regarding their suitability as agricultural soil amendments to affect soil structure, nutrient leaching, microbial communities, and the fate of pesticides. Sci. Total Environ. 751, 141607. https://doi.org/10.1016/J.SCITOTENV.2020.141607.

Smith, J.E., Kluber, L.A., Jennings, T.N., McKay, D., Brenner, G., Sulzman, E.W., 2017. Does the presence of large down wood at the time of a forest fire impact soil recovery? For. Ecol. Manag. 391, 52–62. https://doi.org/10.1016/J.FORECO.2017.02.013.

Souza-Alonso, P., Saiz, G., García, R.A., Pauchard, A., Ferreira, A., Merino, A., 2022. Post-fire ecological restoration in Latin American forest ecosystems: insights and lessons from the last two decades. For. Ecol. Manag. 509, 120083. https://doi.org/10.1016/J.FORECO.2022.120083.

Stoeck, T., Bass, D., Nebel, M., Christen, R., Jones, M.D.M., Breiner, H.W., Richards, T.A., 2010. Multiple marker parallel tag environmental DNA sequencing reveals a highly complex eukaryotic community in marine anoxic water. Mol. Ecol. 19, 21–31. https://doi.org/10.1111/J.1365-294X.2009.04480.X.

Sun, H., Narihiro, T., Ma, X., Zhang, X.X., Ren, H., Ye, L., 2019. Diverse aromatic-degrading bacteria present in a highly enriched autotrophic nitrifying sludge. Sci. Total Environ. 666, 245–251. https://doi.org/10.1016/J.SCITOTENV.2019.02.172.

Sun, R., Chen, Y., Han, W., Dong, W., Zhang, Y., Hu, C., Liu, B., Wang, F., 2020. Different contribution of species sorting and exogenous species immigration from manure to soil fungal diversity and community assemblage under long-term fertilization. Soil Biol. Biochem. 151, 108049. https://doi.org/10.1016/J.SOILBIO.2020.108049.

Tabatabai, M.A., 1983. Soil enzymes. In: Methods of Soil Analysis: Part 2 Chemical and Microbiological Properties, pp. 903–947.

Taylor, D.L., Bhatnagar, J.M., 2024. Fungi in soil: a rich community with diverse functions. In: Paul, E., Frey, S. (Eds.), Soil Microbiology, Ecology and Biochemistry. Elsevier, pp. 75–129. https://doi.org/10.1016/B978-0-12-822941-5.00004-1.

Varela, S.A., Gobbi, M.E., Laos, F., 2011. Can biosolids compost improve, in the short term, native vegetation and soils fertility in burned Nothofagus pumilio forest in Patagonia, Argentina? Bosque 32, 267–278. https://doi.org/10.4067/S0717-92002011000300008.

Vida, C., de Vicente, A., Cazorla, F.M., 2020. The role of organic amendments to soil for crop protection: induction of suppression of soilborne pathogens. Ann. Appl. Biol. 176, 1–15. https://doi.org/10.1111/AAB.12555.

Wang, C., Ning, P., Li, J., Wei, X., Ge, T., Cui, Y., Deng, X., Jiang, Y., Shen, W., 2022. Responses of soil microbial community composition and enzyme activities to long-term organic amendments in a continuous tobacco cropping system. Appl. Soil Ecol. 169, 104210. https://doi.org/10.1016/J.APSOIL.2021.104210.

Whitman, T., Whitman, E., Woolet, J., Flannigan, M.D., Thompson, D.K., Parisien, M.A., 2019. Soil bacterial and fungal response to wildfires in the Canadian boreal forest across a burn severity gradient. Soil Biol. Biochem. 138, 107571. https://doi.org/10.1016/j.soilbio.2019.107571.

Yang, Y., Li, X., Liu, J., Zhou, Z., Zhang, T., Wang, X., 2020. Fungal community structure in relation to manure rate in red soil in southern China. Appl. Soil Ecol. 147, 103442. https://doi.org/10.1016/J.APSOIL.2019.103442.

Ye, G., Banerjee, S., He, J.Z., Fan, J., Wang, Z., Wei, X., Hu, H.W., Zheng, Y., Duan, C., Wan, S., Chen, J., Lin, Y., 2021. Manure application increases microbiome complexity in soil aggregate fractions: results of an 18-year field experiment. Agric. Ecosyst. Environ. 307, 107249. https://doi.org/10.1016/J.AGEE.2020.107249.

Zelles, L., Bai, Q.Y., Ma, R.X., Rackwitz, R., Winter, K., Beese, F., 1994. Microbial biomass, metabolic activity and nutritional status determined from fatty acid patterns and poly-hydroxybutyrate in agriculturally-managed soils. Soil Biol. Biochem. 26, 439–446. https://doi.org/10.1016/0038-0717(94)90175-9.

Zhang, S., Fang, Y., Luo, Y., Li, Yongchun, Ge, T., Wang, Y., Wang, H., Yu, B., Song, X., Chen, J., Zhou, J., Li, Yongfu, Chang, S.X., 2021. Linking soil carbon availability, microbial community composition and enzyme activities to organic carbon mineralization of a bamboo forest soil amended with pyrogenic and fresh organic matter. Sci. Total Environ. 801. https://doi.org/10.1016/j.scitotenv.2021.149717.

Zhang, Y., Hao, X., Alexander, T.W., Thomas, B.W., Shi, X., Lupwayi, N.Z., 2018. Long-term and legacy effects of manure application on soil microbial community composition. Biol. Fertil. Soils 54, 269–283. https://doi.org/10.1007/S00374-017-1257-2/TABLES/5.