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Soil nutrient availability and stoichiometry shape microbial community composition 2 years after wildfire

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Introduction: The response of soil microbial communities to fire-induced changes in nutrients is a key determinant of post-fire ecosystem dynamics. In *Pinus sylvestris* forests, we investigated how bacterial and fungal communities are shaped by nutrient availability and soil stoichiometric relationships 2 years after wildfire across a gradient of fire severity.

Methods: We analyzed soils from unburned, low-severity, and high-severity fire conditions. Soil carbon fractions, including total, organic, inorganic, and pyrogenic carbon, nitrogen, available phosphorus, and stoichiometric ratios (C:N, C:P, and N:P) were quantified. Bacterial and fungal communities were characterized using 16S rRNA gene and ITS amplicon sequencing, respectively.

Results: Available phosphorus and nutrient stoichiometric ratios were key drivers of microbial community composition 2 years after fire. Fungal taxa associated with nutrient concentrations or ratios showed balanced responses, with similar proportions of fungal communities being positively and negatively affected. In contrast, several prokaryotic taxa showed positive associations with post-fire nutrient conditions and appeared to benefit from them, including Microbacteriaceae, Geodermatophilaceae, and Sphingomonadaceae.

Discussion: The identification of specific microbial families linked to nutrient availability highlights their potential as indicators of soil recovery. These findings demonstrate the importance of soil stoichiometric relationships in shaping microbial communities in post-fire ecosystems and contribute to a better understanding of soil recovery processes by linking nutrient dynamics with microbial changes after fire.

KEYWORDS

bacterial community, fungal community, post-fire soil, soil nutrients, stoichiometric ratios

1 Introduction

Wildfires are natural disturbances that play a central role in shaping the structure and functioning of terrestrial ecosystems. They impact soil and biological communities, influencing vegetation dynamics, nutrient cycling, and ecosystem services (Agbeshie et al., 2022; Fernández-Guisuraga et al., 2020; Rocas-Díaz et al., 2022). In recent decades, wildfire regimes have intensified in many regions due to climate change and land-use change (Harrison et al., 2021; Moreira et al., 2011; Pausas and Fernández-Muñoz, 2012). Among fire regime

parameters, fire severity is one of the main drivers of ecosystem responses because it determines the magnitude of ecological change following fire (Fernández-García et al., 2018a). High-severity fires can substantially reduce soil organic matter and disrupt biogeochemical processes, whereas low-severity fires often promote vegetation regeneration and short-term increases in nutrient availability (Agbeshie et al., 2022; Kardol et al., 2023; Certini, 2005).

Soil microbial communities, comprising bacteria, archaea, and fungi, are essential for nutrient cycling and maintaining ecosystem stability. Fire can alter microbial communities by reducing biomass and diversity and by providing competitive advantages to fire-adapted or opportunistic taxa (Dooley and Treseder, 2012; Sáenz de Miera et al., 2020). In addition to these direct effects, post-fire recovery processes indirectly shape microbial communities through changes in soil properties and nutrient availability (Adkins et al., 2020).

Among soil chemical properties, carbon (C) and nitrogen (N) are key elements governing post-disturbance processes in forest soils. Fire can strongly modify soil carbon pools through losses of labile organic matter and the formation of more resistant pyrogenic carbon, while also altering the quantity and quality of organic matter inputs (Sawyer et al., 2018; Babur et al., 2022; Girona-García et al., 2019). Nitrogen dynamics are also highly sensitive to fire severity: low-severity fires may temporarily increase N availability through ash inputs and partially combusted litter, whereas high-severity fires often reduce total soil N pools (Huerta et al., 2020). Following fire, mineralization processes can generate transient ammonium pulses that may subsequently be oxidized to nitrate through microbial nitrification, while losses through leaching and denitrification influence net N availability (Knicker, 2007).

While total nutrient concentrations are fundamental for understanding post-fire soil recovery, nutrient ratios provide additional insights into soil processes and biological responses. Stoichiometric relationships, particularly the C:N ratio, have been shown to influence vegetation regrowth, plant community composition, and cascading ecological effects (Bui and Henderson, 2013; Fernández-García et al., 2021; Vogels et al., 2024). These findings indicate that ecosystem responses to disturbance depend not only on nutrient availability but also on the proportional balance among key elements regulating soil and biological processes.

Although most studies have focused on nutrient–vegetation relationships (Fernández-García et al., 2021), nutrients are also key determinants of microbial community structure (Smithwick et al., 2012). Microbial activity can in turn influence nutrient availability through processes such as mineralization, nitrification, and organic matter decomposition, highlighting bidirectional interactions between soil nutrients and microorganisms. Despite increasing knowledge about microbial dynamics and nutrient cycling after fire, important gaps remain regarding how nutrient stoichiometry influences microbial community reassembly and how bacterial and fungal taxa respond to post-fire nutrient conditions. Addressing these questions is essential for improving our understanding of soil functioning and resilience after fire, as post-fire ecosystem recovery depends not only on vegetation regrowth but also on the restoration of soil processes influenced by fire severity and interactions among ecosystem components. Consequently, investigating relationships between microbial communities and environmental variables such as soil pH, moisture, nutrient availability, and vegetation cover is critical for understanding the mechanisms shaping post-fire soil functioning (Adkins et al., 2020).

Despite the ecological relevance of interactions between microbes and soil chemistry, relatively few studies have simultaneously

examined microbial community composition and soil nutrient pools in post-fire environments (Adkins et al., 2020; Muñoz-Rojas et al., 2016; Smithwick et al., 2012). Most metataxonomic studies that integrate soil and microbial parameters focus on high taxonomic levels or broad groups (e.g., phylum), whereas studies exploring nutrient–microbial relationships at lower taxonomic levels remain limited.

A better understanding of how microbial communities respond to and interact with changes in soil chemistry caused by fire is essential for predicting ecosystem trajectories and elucidating the role of microbial communities in post-fire scenarios. To address this gap, we assessed soil bacterial and fungal communities in a *Pinus sylvestris* ecosystem 2 years after a forest fire, quantifying nitrogen, phosphorus, and different forms of carbon across a gradient of fire severity and relating these soil chemical properties to microbial community composition and structure. We hypothesize that soil nutrient availability and stoichiometric ratios are key drivers of microbial community structure after fire. Furthermore, we expect differences in the response patterns of fungal and bacterial communities, with certain nutrients or stoichiometric relationships playing a more prominent role in structuring one group over the other.

2 Materials and methods

2.1 Study area and field sampling

The study area was located within a large wildfire that occurred during the summer of 2022 in the Sierra de la Culebra (Zamora, northwestern Spain). The wildfire took place between June 15 and 19, burning a total of 25,228 ha. Elevation ranges from 747 to 1,205 m above sea level, with an average slope of 11.8% and a maximum of 60.7%, indicating a heterogeneous terrain—mostly gently sloping but with interspersed steep areas, reflecting marked local topographic variation. The region has a Mediterranean climate with dry summers (Rivas-Martínez et al., 2017), a mean annual temperature of 11 °C, and a mean annual precipitation of 750 mm (Ninyerola et al., 2005). Further details on the fire event are provided in Fernández-Guisuraga and Calvo (2025).

Soils are acidic and primarily derived from quartzite (GEODE, 2024; ITACyL, 2024). According to the Harmonized World Soil Database v2.0 (FAO and IIASA, 2023), soils are classified as Chromic Luvisols and Dystric Regosols. The landscape mosaic affected by the wildfires was dominated by heathlands (*Erica arborea*, *Erica australis*) and rockroses (*Cistus ladanifer*), as well as woodlands composed of *Quercus pyrenaica*, *Quercus ilex*, and planted stands of *Pinus pinaster* and *Pinus sylvestris*. Stands of *P. sylvestris* accounted for around 12% (3,028 ha) of the total burned area.

Immediately after the wildfire, sampling sites were established in burned and nearby unburned areas. Site selection was based on ensuring comparability in pre-fire ecosystem type (*Pinus sylvestris* plantations), soil parent material, slope range, and vegetation characteristics, using pre-fire vegetation maps, available soil surveys, and *in situ* field inspection. Fire severity was classified based on visual assessment following the criteria of the modified Composite Burn Index (CBI) (Fernández-García et al., 2018b). Two years after the wildfire (2024), a total of 21 soil samples were collected. Within the burned perimeter, sampling was distributed across different burned patches to capture landscape heterogeneity while maintaining homogeneous and

consistent fire severity levels, resulting in two burned severity classes: low fire severity (L) and high fire severity (H), with seven composite samples per class. Additionally, seven composite samples were collected in an adjacent unburned area selected to match pre-fire conditions. All sampling sites were separated by at least 80 m. At each site, one composite soil sample was obtained by homogenizing soil collected from four subpoints. The uppermost 3 cm of mineral soil were collected after removing the litter layer and surface debris, which represents the layer strongly affected by fire. Each soil sample was divided into two subsamples: one for microbial community analysis (DNA extraction) and the other for chemical analyses. Samples were stored under refrigerated conditions during fieldwork. Upon arrival at the laboratory, samples for DNA extraction were frozen at -20°C , and those for chemical analysis were air-dried and sieved to a 2 mm.

2.2 Chemical analyses, DNA extraction, and sequence processing

Total carbon (C) and total nitrogen (N) were measured using the Dumas combustion method (Dumas, 1831) with an elemental analyzer (EuroVector EA3000; EuroVector SpA, Rodano, Italy). Total organic carbon (TOC) was quantified using the same analytical procedure after the removal of inorganic carbon by acidification prior to combustion. Total C and total N concentrations were expressed in mg g^{-1} dry soil to allow stoichiometric calculations, whereas TOC and total inorganic carbon (TIC; calculated as the difference between total C and TOC) were expressed as percentages of dry soil mass (% w/w). Available phosphorus (P) was extracted using 0.5 M NaHCO_3 at pH 8.5 following the Olsen method (Olsen et al., 1954) and quantified spectrophotometrically at 882 nm (UV Mini 1,240, UV/Vis spectrophotometer; Shimadzu). P concentrations were expressed in mg g^{-1} dry soil. Stoichiometric ratios (C:N, C:P, and N:P) were calculated using nutrient concentrations expressed on a mass basis. Pyrogenic carbon (Pyr_C) was determined using the weak nitric acid and hydrogen peroxide digestion method described by Kurth et al. (2006) and expressed as a percentage of total C (% of total C). Following the modifications proposed by DeLuca et al. (2020), high-organic-matter samples were processed using a reduced soil mass (0.05 g instead of 1 g) and pretreated with 30% H_2O_2 for 24 h before digestion. Stoichiometric ratios of C:N, C:P, and N:P were calculated from total C, N, and available P concentrations to assess nutrient balance.

For microbial community analysis, both prokaryotic and fungal taxa were considered. DNA was extracted from soil samples using the DNeasy PowerSoil Pro Kit (QIAGEN, Hilden, Germany). DNA quantity and purity were assessed using a NanoDrop spectrophotometer (Thermo Fisher Scientific, Waltham, USA) and a Qubit 2.0 fluorometer (Invitrogen, Carlsbad, USA), and DNA integrity was evaluated by agarose gel electrophoresis. The V3–V4 region of the bacterial 16S rRNA gene was amplified using primers 341F (5'-CCTAYGGGRBGCAS-3') and 806R (5'-GGACTACNNGGTATCTAAT-3') (Yu et al., 2005), while the ITS1 region of the fungal rRNA operon was amplified using primers ITS5F (5'-GGAAGTAAAGTCGTAACAAGG-3') and ITS2R (5'-GCTGCGTTCTTCATCGATGC-3') (Usyk et al., 2017). Amplicon libraries were generated using a LightCycler480 thermal cycler (Roche, Basel, Switzerland) and sequenced using 2×250 bp paired-end reads on an Illumina platform (Illumina Inc., San Diego, USA).

Bioinformatic processing of raw reads was performed using VSEARCH v2.29 (Rognes et al., 2016). Paired-end reads were merged and quality filtered, including the removal of short reads, sequences with insufficient overlap, and chimeric sequences. Minimum length thresholds were set at 350 bp for prokaryotic and 150 bp for fungal reads. Operational Taxonomic Units (OTUs) were clustered at 97% sequence similarity using the *cluster_size* function implemented in VSEARCH. Taxonomic classification of OTUs was performed using the *assignTaxonomy* function in DADA2 v1.16 (Callahan et al., 2016), applying a minimum bootstrap confidence of 50. Prokaryotic OTUs were classified against the SILVA v138 reference database (McLaren and Callahan, 2021), while fungal OTUs were assigned using the UNITE database (Abarenkov et al., 2024). Post-classification filtering included the removal of (i) OTUs unassigned at the kingdom or phylum level, (ii) OTUs identified as chloroplasts, and (iii) sequences not corresponding to prokaryotic or fungal taxa. Samples were normalized to 100,000 reads prior to downstream analyses to account for differences in sequencing depth among samples.

2.3 Statistical analyses

To assess whether microbial community composition was structured by nutrient concentrations and their stoichiometric ratios, redundancy analysis (RDA) was performed independently for prokaryotic and fungal communities. OTU tables were Hellinger-transformed using the *decostand()* function from the *vegan* package (Oksanen et al., 2022). In the case of prokaryotes, the OTU table was filtered to retain taxa representing approximately 90% of the total read abundance, to reduce the number of OTUs and computational load. For each community, an initial RDA model was constructed, including all environmental variables (after excluding those with high collinearity, assessed via variance inflation factors using *vif.cca()*). A stepwise model selection was then performed using bidirectional permutation tests (*ordistep()* function, 999 permutations). The statistical significance of the final RDA model, individual explanatory variables, and canonical axes was evaluated using a permutation-based analysis of variance (999 permutations) implemented via *anova.cca()* from the *vegan* package.

To investigate specific associations between microbial taxa and soil nutrients, a global correlation network was constructed using Spearman's rank correlations between the relative abundances of family-level taxa (normalized to 100,000 reads) and soil nutrient variables measured across the 21 sampling points (including unburned, low, and high severity points). Only strong correlations were retained in the network ($\rho > 0.7$, $p < 0.05$). These associations were represented in an undirected weighted network. Changes in taxon abundances and nutrients across severity levels were statistically evaluated using Kruskal–Wallis tests followed by Dunn's post-hoc tests with Benjamini–Hochberg adjustment for multiple comparisons when appropriate (Benjamini and Hochberg, 1995; Dunn, 1964; Kruskal and Wallis, 1952). Network visualization and analysis were performed using Cytoscape (Shannon et al., 2003). All statistical analyses were conducted in R (R Core Team, 2025), employing base and specialized packages including FSA for post-hoc testing (Ogle et al., 2025).

3 Results

The amplicon analysis yielded 1,505,093 reads for the prokaryotic community and 1,841,179 for the fungal community after bioinformatic processing and quality filtering, before normalization. On average, each sample contained $2,789 \pm 570$ OTUs (mean $\pm$ standard deviation) in the prokaryotic community and $2,315 \pm 137$ in the fungal community. Within the prokaryotic community, a total of 31 phyla, 68 classes, 166 orders, 236 families, and 549 genera were identified, whereas the fungal community comprised 13 phyla, 46 classes, 117 orders, 259 families, and 488 genera.

Redundancy analysis (RDA) (Table 1 and Figure 1) revealed a significant association between prokaryotic community composition and soil nutrient variables (global model: $F = 4.89$, $p = 0.001$). Stepwise model selection identified C:N ratio, P and TOC as the best explanatory variables. These accounted for 46.3% of the total variance in prokaryotic community composition (constrained inertia = 0.1827; total inertia = 0.3946). Within the constrained fraction, the first and second canonical axes explained 79.6 and 12.9% of the variance, respectively; however, only the first canonical axis was statistically significant (Table 1). Among the selected predictors, C:N and P were significantly correlated with shifts in community structure ($p < 0.05$), whereas TOC showed no significant independent effect. For the fungal community, the selected variables were C:N ratio, C:P ratio, and N. Among them, C:N and C:P were significant predictors, whereas N showed a marginal, non-significant effect (global model: $F = 3.23$, $p = 0.001$). These variables explained 36.3% of the total variance in fungal community composition (constrained inertia = 0.21; total inertia = 0.60). The first two canonical axes explained 76.8 and 10.1% of the constrained variance, respectively, but again only the first axis was significant (Table 1), indicating that the contribution of N should be interpreted with caution. The first RDA axis separated microbial communities from burned (low and high fire severity) and unburned

areas, particularly in relation to the C:N ratio. OTUs from unburned soils were associated with higher C:N values in both prokaryotic and fungal communities.

Analysis of soil nutrients and stoichiometric ratios (Table 2) showed that nutrient ratios were more sensitive to fire disturbance than absolute nutrient concentrations. Significant differences in all three stoichiometric ratios (C:N, C:P, and N:P) were found between burned (low and high severity) and unburned soils, whereas no significant differences were detected between the two fire severity levels. Among individual nutrients, P concentrations were approximately 2.5–3 times higher in burned soils (0.019 mg g^{-1} in both low- and high-severity plots) than in unburned soils (0.007 mg g^{-1}), with differences being statistically significant ($p < 0.01$). Regarding carbon forms, TIC concentrations were very low overall but decreased markedly under high fire severity, with values approximately five- to six-fold lower in high-severity plots ($0.05\% \text{ w/w}$) compared to unburned ($0.28\% \text{ w/w}$) and low-severity plots ($0.33\% \text{ w/w}$). Differences were significant between low- and high-severity plots ($p = 0.04$) and marginally significant between unburned and high-severity plots ($p = 0.05$).

The Spearman correlation networks (Figures 2, 3) reveal a stronger influence of stoichiometric nutrient ratios (C:N, N:P, and C:P) compared to total nutrient concentrations or carbon forms. All three ratios displayed significant correlations with several bacterial and fungal classes and families, indicating that relative nutrient availability plays a key role in structuring microbial communities. P was the only absolute nutrient variable shared between the two networks, and it showed predominantly positive associations with multiple microbial taxa. In both prokaryotic and fungal networks, P was correlated with taxa that were more abundant in burned plots (low and high severity), suggesting that phosphorus availability is likely a key factor promoting the activity or growth of post-fire microbial taxa. An important contrast between the two networks is found in the sign of the correlations. In the prokaryotic network, most significant associations with nutrients were negative, whereas in the fungal network, positive correlations were predominant. Another relevant difference concerns the distribution of nutrient-associated taxa across fire severity levels. In the prokaryotic network, most correlated taxa were more abundant in burned plots, while in the fungal network, they were more frequently associated with unburned plots. Finally, the prokaryotic network showed greater overall connectivity, with several families associated with multiple nutrient variables. In contrast, the fungal network was sparser, with fewer connections per node.

The prokaryotic correlation network (Figure 2; Supplementary Table S1) showed predominantly positive associations between P and families within the classes Alphaproteobacteria, Actinobacteria, and Gammaproteobacteria. In contrast, the stoichiometric ratios C:N and C:P were mostly associated with negative correlations. Several families exhibited positive correlations with P and negative correlations with C:N or C:P. Among the most abundant families, Acidothermaceae and Mycobacteriaceae showed negative correlations with P and positive correlations with C:P. Both were more abundant in unburned plots, with Mycobacteriaceae showing significant differences between unburned and burned samples (p [UB–L] = 0.01; p [UB–H] = 0.009; p [L–H] > 0.05). In contrast, Microbacteriaceae (p [UB–L] = 0.009; p [UB–H] = 0.002; p [L–H] > 0.05), Geodermatophilaceae (p [UB–L] = 0.004; p [UB–H] = 0.002; p [L–H] > 0.05), and Sphingomonadaceae (p [UB–L] = 0.008; p [UB–H] = 0.001; p [L–H] > 0.05) were positively

TABLE 1 Redundancy analysis (RDA) results for prokaryotic and fungal community composition.

Prokaryotic community	<i>F</i>	<i>p</i> -value
General model	4.89	0.001
C:N	9.66	0.001
P	3.20	0.01
TOC	1.79	0.081
Axis 1	11.67	0.001
Axis 2	1.88	0.065

Fungal community	<i>F</i>	<i>p</i> -value
General model	3.23	0.001
C:N	5.58	0.001
C:P	2.24	0.027
N	1.88	0.056
Axis 1	6.85	0.001
Axis 2	1.58	0.130

F and *p*-values are shown for the global RDA models, selected explanatory variables, and canonical axes. N, total nitrogen; P, available phosphorus; TOC, total organic carbon; C:N, carbon-nitrogen ratio; C:P, carbon-phosphorus ratio.

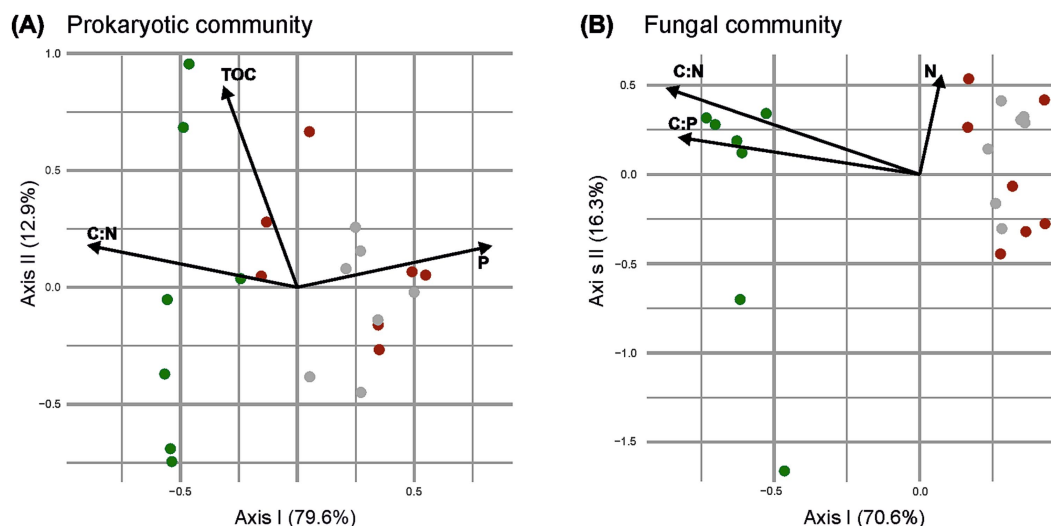


FIGURE 1

Redundancy analysis (RDA) ordination plots of (A) prokaryotic and (B) fungal community composition in relation to selected soil nutrients and stoichiometric ratios. Points are colored according to fire severity class: unburned plots (UB, green), low fire severity plots (L, red), and high fire severity plots (H, gray). Axis labels indicate the percentage of constrained variation explained by each canonical axis.

TABLE 2 Soil nutrient concentrations, carbon forms, and stoichiometric ratios across fire severity classes.

Variable	units	UB	L	H	KW	UB-L	UB-H	L-H
C	mg g ⁻¹ dry soil	79.3 ± 94.7	100.35 ± 44.9	62.11 ± 24.34	0.483			
N	mg g ⁻¹ dry soil	2.33 ± 2.59	4.3 ± 1.70	3.28 ± 0.99	0.361			
P	mg g ⁻¹ dry soil	0.007 ± 0.003	0.019 ± 0.013	0.019 ± 0.006	0.002	0.003	0.005	0.931
TOC	% w/w	7.65 ± 8.75	9.38 ± 4.24	6.21 ± 2.47	0.522			
TIC	% w/w	0.28 ± 0.78	0.33 ± 0.27	0.05 ± 0.06	0.032	0.89	0.05	0.04
Pyr_C	% of total C	2.10 ± 1.30	1.94 ± 1.04	3.78 ± 2.30	0.251			
C:N	–	34.04 ± 6.08	23.17 ± 3.33	22.42 ± 1.72	0.027	0.060	0.030	1.000
C:P	–	12,316 ± 6,649	4,065 ± 3,053	2869.59 ± 1259.30	0.007	0.038	0.007	0.413
N:P	–	361.80 ± 161.58	187.12 ± 107.57	138.61 ± 47.97	0.010	0.116	0.008	0.212

Values for UB, L, and H are shown as median ± standard deviation. KW indicates the p-value from the Kruskal–Wallis test. UB-L, UB-H, and L-H indicate Benjamini–Hochberg-adjusted p-values from pairwise comparisons. C, total carbon; N, total nitrogen; P, available phosphorus; TOC, total organic carbon; TIC, total inorganic carbon; Pyr_C, pyrogenic carbon; C:N, carbon-nitrogen ratio; C:P, carbon-phosphorus ratio; N:P, nitrogen-phosphorus ratio.

correlated with P and showed higher relative abundances in burned plots. Geodermatophilaceae and Sphingomonadaceae were negatively correlated with N:P and C:P. Similarly, Micrococcaceae (p [UB-L] = 0.002; p [UB-H] = 0.004; p [L-H] > 0.05), Gemmatimonadaceae (p [UB-L] = 0.009; p [UB-H] = 0.007; p [L-H] > 0.05), and Comamonadaceae (p [UB-L] = 0.008; p [UB-H] = 0.003; p [L-H] > 0.05) displayed positive correlations with P and negative correlations with C:N and C:P. Oxalobacteraceae followed a similar pattern, with positive correlation with P and negative with C:P (p [UB-L] = 0.003; p [UB-H] = 0.003; p [L-H] > 0.05). Additional nutrient associations were observed for Polyangiaceae, negatively correlated with Pyr C, and Ktedonobacteriaceae, negatively associated with N.

The fungal correlation network (Figure 3; Supplementary Table S2) showed predominantly negative associations between P and families within the Agaricomycetes, which were generally more abundant in

unburned plots. Significant differences were observed between unburned and both low- and high-severity plots, as in the case of Hydnaceae (p [UB-L] = 0.002; p [UB-H] = 0.006; p [L-H] > 0.05). In contrast, several families displayed positive correlations with P and were characterized by higher relative abundances in burned plots. Among these, Helotiaceae (p [UB-L] = 0.003; p [UB-H] = 0.004; p [L-H] > 0.05) was one of the most abundant families in the network. Other positively correlated taxa included members of the classes Dothideomycetes and Tremellomycetes. Several families showed positive correlations with P, including multiple members of the class Agaricomycetes, with Hydnaceae being among the most abundant. Mortierellaceae (Mortierellomycota) correlated negatively with P and was significantly more abundant in unburned plots (p [UB-L] = 0.004; p [UB-H] = 0.002; p [L-H] > 0.05). Regarding nutrient stoichiometric ratios, several Agaricomycetes families showed positive correlations with C:N, C:P, and N:P. Families within Sordariomycetes also

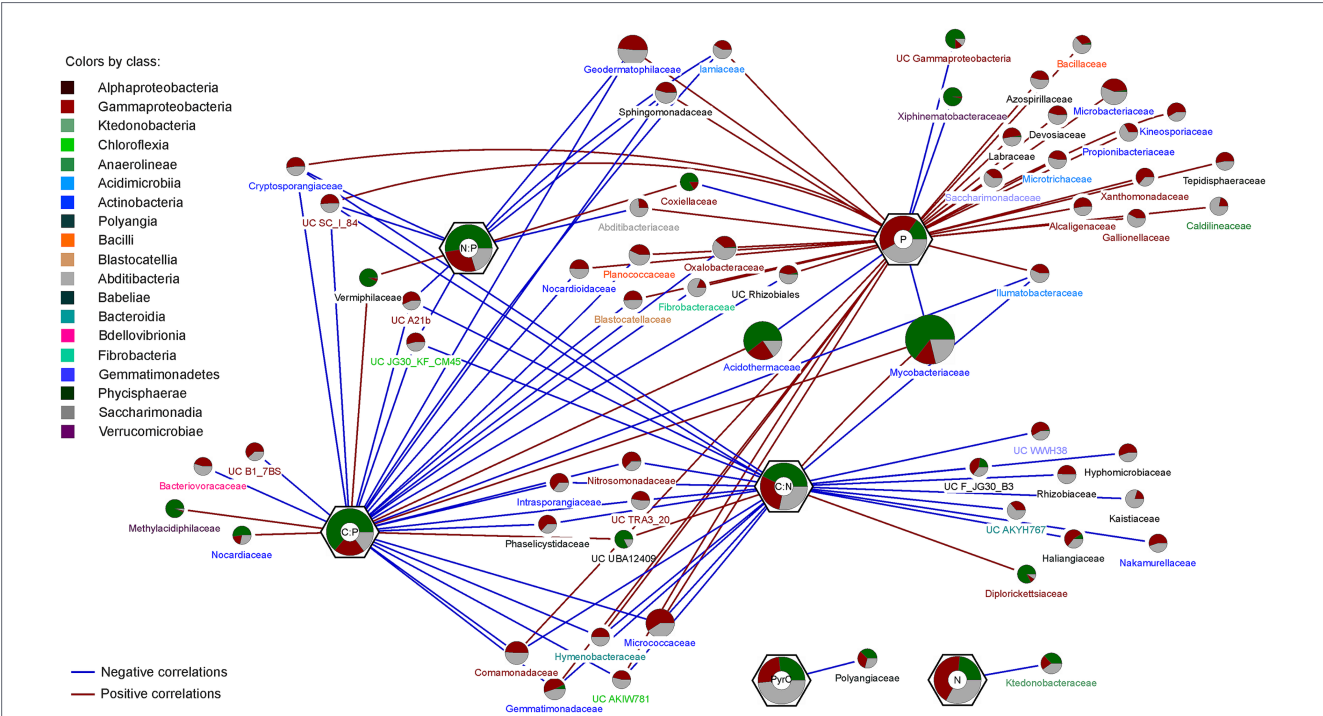


FIGURE 2
Spearman correlation network between prokaryotic families and soil nutrient variables. The network includes only strong and statistically significant correlations, defined as $|\text{Spearman's } \rho| > 0.7$ and $p < 0.05$. The colors of taxon labels indicate the taxonomic class to which each family belongs, whereas edge colors indicate the sign of the correlation: red = positive and blue = negative. Taxon node size reflects total relative abundance, calculated as the sum of median relative abundances across UB, L, and H. Pie charts show the distribution of relative abundance among fire severity classes: UB, green; L, red; and H, gray. Nutrient-node sizes were fixed. The prefix "UC" indicates unclassified clades.

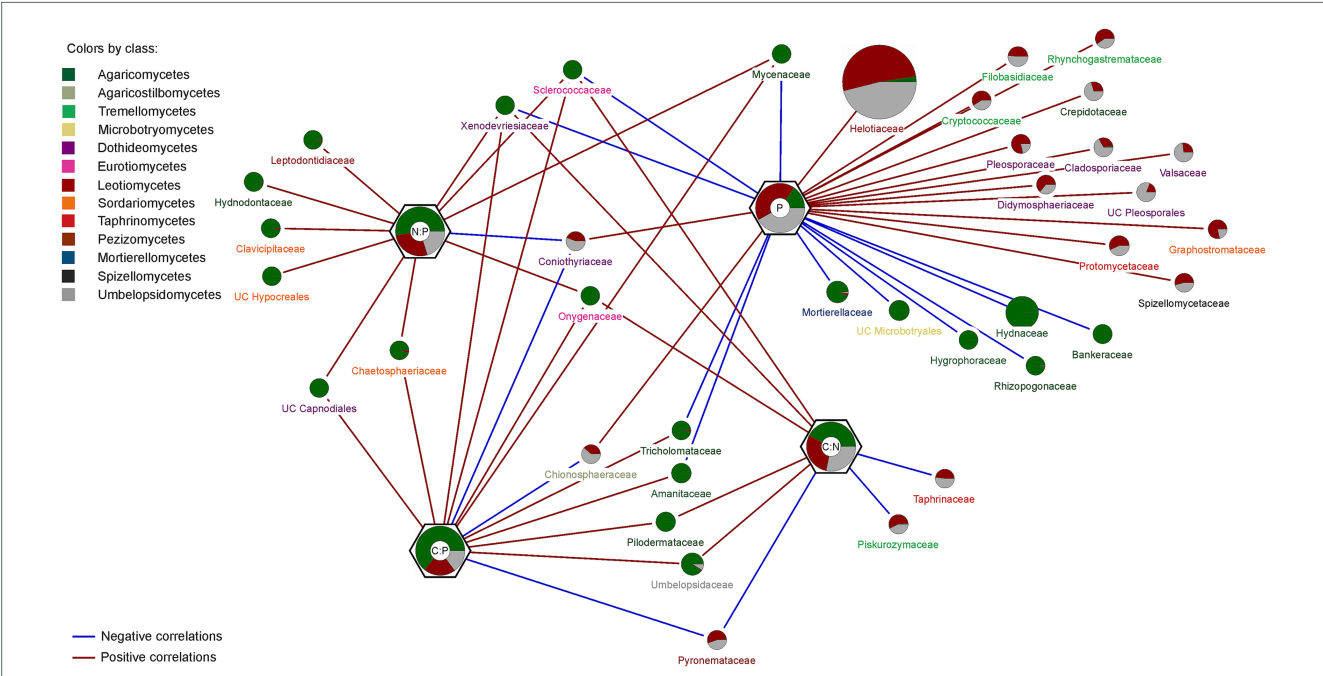


FIGURE 3
Spearman correlation network between fungal families and soil nutrient variables. The network includes only strong and statistically significant correlations, defined as $|\text{Spearman's } \rho| > 0.7$ and $p < 0.05$. The colors of taxon labels indicate the taxonomic class to which each family belongs, whereas edge colors indicate the sign of the correlation: red, positive and blue, negative. Taxon node size reflects total relative abundance, calculated as the sum of median relative abundances across UB, L, and H. Pie charts show the distribution of relative abundance among fire severity classes: UB, green; L, red; and H, gray. Nutrient-node sizes were fixed. The prefix "UC" indicates unclassified clades.

exhibited positive correlations with N:P and C:P. Similarly, Umbelopsidaceae (phylum Mucoromycota) displayed positive correlations with both C:N and C:P and was significantly more abundant in unburned plots (p [UB–L] = 0.008; p [UB–H] = 0.046; p [L–H] > 0.05). Additionally, Pyronemataceae, a taxon typically associated with burned habitats, exhibited negative associations with the stoichiometric ratios C:P and C:N.

4 Discussion

The results of this study support our hypothesis that soil nutrient availability and stoichiometric ratios are key drivers of microbial community structure after fire, particularly through the influence of C:N, C:P, and N:P ratios. This hypothesis is confirmed both at the level of OTUs and at the level of taxonomic families. Moreover, consistent with our second prediction, differentiated responses between prokaryotic and fungal communities were observed, reflecting functional and ecological differences between these two groups.

The OTU level analysis showed that the C:N ratio is a key factor structuring both microbial communities, as demonstrated by Barreiro et al. (2016), where changes in C:N induced by the addition of different high C:N mulch materials modified the structure and abundance of fungal and prokaryotic communities. In our work, no significant changes in C, TOC, and N were detected, but there was a significant increase in P, consistent with observations in north-western Iberian Mediterranean pine forests (Fernández-García et al., 2019). These changes resulted in a significant decrease in calculated ratios, particularly when comparing unburned and high severity samples. Bui and Henderson (2013) demonstrated the importance of nutrient stoichiometry in various Australian plant ecosystems, highlighting the role of P and the interactions between vegetation—through litter stoichiometry—and soil. Our results suggest a link between fire-induced stoichiometric changes (C:N, C:P and N:P ratios) and microbial community composition. Such changes are expected to modify nutrient-cycling dynamics and, consequently, alter plant–soil feedback. Indeed, by reshaping the structure, composition and functional potential of both prokaryotic and fungal communities, fire can disrupt the reciprocal interactions that regulate ecosystem productivity and resilience, as illustrated by Kardol et al. (2023).

P was strongly related to variations in both prokaryotic and fungal communities, reinforcing the hypothesis that post-fire nutrient availability plays a key role in structuring microbial communities. In the prokaryotic community, this was observed through a direct positive correlation with P concentration in burned areas. In fungi, the response was also positive but appeared to be primarily driven by variations in the C:P ratio rather than by total P availability, particularly in unburned soils. These patterns are consistent with previous studies that emphasize the role of P and nutrient stoichiometry in post-fire microbial dynamics (Cleveland and Liptzin, 2007; Hou et al., 2025; Oliverio et al., 2020). Intra-treatment variability in community composition was also detected in both groups: TOC explained part of this variation in prokaryotic communities, while N was relevant for fungi. This small-scale heterogeneity is likely driven by spatial differences in vegetation structure and post-fire recovery, which affect the quantity and quality of organic inputs to the soil (Hart et al., 2005; Ling et al., 2021).

Moreover, spatial patterns in soil organic matter dynamics have been linked to fire severity and time since disturbance (Cui et al., 2014), reinforcing the idea that both direct fire effects and vegetation-mediated processes contribute to the observed microbial responses.

Correlation network analysis revealed that both stoichiometric ratios and P were strongly associated with taxonomic associations at the family level in both prokaryotic and fungal communities, highlighting their role in post-fire recovery (Fernández-García et al., 2021). In general, most prokaryotic groups represented in the network ($\rho > 0.7$, $p < 0.05$) are more abundant in areas affected by fire, showing a positive effect on these groups of post-fire soil properties. However, most fungal groups exhibit higher levels of abundance in samples that have remained unaffected by fire, with a few exceptions such as the Helotiaceae, Tremellomycetes, and Dothideomycetes groups. These general differences corroborate the findings of preceding studies, which demonstrated a more pronounced negative impact of fire on the fungal community than on the prokaryotic community (Pulido-Chávez et al., 2023). These differences also suggest that the bacterial community may exhibit a more complex and structured pattern of nutrient association, possibly reflecting functional differentiation or redundancy, while fungal responses appear more selective and constrained.

Within the prokaryotic network Mycobacteriaceae and Acidothermaceae (Actinobacteria) showed negative correlations with P and were more abundant in unburned plots. Mycobacteriaceae—typical of acidic, oligotrophic soils—exhibit slow growth and the ability to metabolize recalcitrant compounds (Falkinham, 2009; Walsh et al., 2019). Acidothermaceae includes acidophilic, cellulolytic taxa (Berry et al., 2014) that decline with increasing P (Fu et al., 2021), likely due to ash-derived nutrient enrichment (Pereira et al., 2012), favoring copiotrophic competitors.

Conversely, Microbacteriaceae, Geodermatophilaceae, and Sphingomonadaceae were positively correlated with P and enriched in burned plots. Microbacteriaceae includes copiotrophic taxa such as *Curtobacterium*, known for phosphate solubilization (Evtushenko and Takeuchi, 2006; Chu et al., 2025). Geodermatophilaceae includes taxa tolerant of variable nutrient conditions and elevated P availability (Berry et al., 2014; Chen et al., 2024), while Sphingomonadaceae contains metabolically versatile taxa linked to mineral weathering and P solubilization (Glaeser and Kämpfer, 2014; He et al., 2023).

Other families, including Micrococcaceae, Gemmatimonadaceae, and Oxalobacteraceae, showed positive correlations with P and negative with C:P and/or C:N ratios. Micrococcaceae (Actinobacteria), particularly the genus *Pseudarthrobacter*, is abundant in burned soils and degrades aromatic compounds (Seo et al., 2009; Adkins et al., 2020; Sáenz de Miera et al., 2020) and has been linked to increased soil N and P (Ortiz-Cornejo et al., 2017; Wang et al., 2024). Gemmatimonadaceae includes oligotrophic taxa involved in N cycling and P solubilization (Hanada and Sekiguchi, 2014; Liang et al., 2020), while Oxalobacteraceae (Pseudomonadota), mainly represented by *Massilia* in our samples, colonizes burned soils and solubilizes P (Sáenz de Miera et al., 2020; Pulido-Chávez et al., 2023; Samaddar et al., 2019).

Polyangiaceae and Ktedonobacteraceae showed no significant P correlations. Polyangiaceae includes predatory bacteria producing bioactive metabolites (García and Müller, 2014), while Ktedonobacteraceae (Chloroflexota) forms filamentous mycelia

(Yabe et al., 2017) and may influence N₂O emissions (Bi et al., 2024).

Correlation network analysis revealed P as a key driver structuring the fungal community. Helotiaceae (Ascomycota), dominated by *Calyptrozyma*, correlated positively with P and was enriched in burned soils (Day et al., 2019; Maurice-Lira et al., 2025). Likewise, Dothideomycetes and Tremellomycetes increased with P and after fire, consistent with their roles as early decomposers and saprotrophic yeasts (Zhang et al., 2017; Buscardo et al., 2015; Weiss et al., 2014). In contrast, Agaricomycetes, particularly Hydnaceae (*Sistotrema*), declined, reflecting ectomycorrhizal sensitivity to fire-altered nutrients (Di Marino et al., 2008). Mortierellaceae were also reduced and negatively correlated with P, consistent with adaptation to P limitation and phosphate solubilization ability (Telagathoti et al., 2021; Ni et al., 2025; Ning et al., 2020; Osorio and Habte, 2015).

Several families were more related to nutrient ratios than to P directly. Within Sordariomycetes, Clavicipitaceae and unclassified Hypocreales correlated positively with N:P, and Chaetosphaeriaceae with both N:P and C:P. These taxa are linked to N and P dynamics (Li et al., 2023; Xiao et al., 2020). Clavicipitaceae—including endophytes and entomopathogens producing secondary metabolites—has been proposed as an indicator of soil health (Torres and White, 2009; Schlatter et al., 2022). Chaetosphaeriaceae, mainly saprotrophic, benefits from labile C and N sources (Liu et al., 2023).

Other groups reflected contrasting stoichiometric responses: Umbelopsidaceae (*Umbelopsis*) was more abundant in unburned soils and correlated with C:N and C:P, consistent with its oligotrophic saprotrophic lifestyle (Richardson, 2009; Pawłowska et al., 2019); whereas Pyronemataceae, dominated by thermotolerant *Pyronema*, was enriched in burned soils and negatively correlated with C:N and C:P, reflecting adaptation to nutrient-enriched post-fire conditions (Fox et al., 2022; Pulido-Chávez et al., 2023).

Overall, these results support our hypothesis that post-fire changes in soil nutrient availability and stoichiometric ratios (C:N, C:P, N:P) contribute to structuring both prokaryotic and fungal communities 2 years after wildfire. Several bacterial families (Microbacteriaceae, Geodermatophilaceae, and Sphingomonadaceae) and fungal taxa (Helotiaceae, Tremellomycetes, and Dothideomycetes) were associated with higher P availability and were more abundant in burned plots. In contrast, other bacterial families (Acidothermaceae and Mycobacteriaceae) and fungal groups, including families within the class Agaricomycetes as well as Mortierellaceae and Sordariomycetes, showed reduced relative abundance in burned soils where P concentrations were higher. These patterns reflect correlational relationships between post-fire soil nutrient conditions and microbial community composition and should not be interpreted as direct responses to P availability alone, as additional factors related to fire effects on vegetation and organic matter dynamics may also contribute to microbial community reassembly (Hart et al., 2005; Cui et al., 2014; Ling et al., 2021).

Our results are consistent with previous studies highlighting the role of phosphorus and stoichiometric relationships in soil microbial dynamics and decomposition (Bergkemper et al., 2016; Oliverio et al., 2020; Purahong et al., 2016). These results also align with evidence that changes in nutrient availability and stoichiometric ratios

are important not only for plant or invertebrate communities (Fernández-García et al., 2021; Mulder and Elser, 2009) but are also influenced in microbial structure and composition, which may in turn affect nutrient cycling and plant–soil feedbacks, potentially impacting ecosystem productivity and resilience (Kardol et al., 2023).

The observed correlations between phosphorus and nutrient ratios with certain microbial families 2 years after fire suggest that nutrient effects on microbial communities in pine ecosystems can persist well beyond the immediate post-fire stage (Mikita-Barbato et al., 2015). This may be related to habitat restructuring via ash deposition, potentially initiating medium- to long-term niche differentiation (Hou et al., 2025). These findings highlight the importance of ecosystem type in shaping microbial resilience: while shrubland ecosystems often exhibit high resilience, forested ecosystems appear more vulnerable to fire effects on microbial communities (Pinto et al., 2023), both directly and indirectly, through changes in nutrient availability and competitive interactions.

Nevertheless, this study is based on observational correlations; thus, experimental manipulation work is required to confirm causal relationships between specific microbial families and the observed variations in stoichiometry and phosphorus. Temporal approaches could further elucidate the directionality of the relationships between nutrient stoichiometry and microbial community dynamics. Our findings emphasize the importance of stoichiometric relationships and phosphorus as key drivers of post-fire microbial dynamics and highlight that the functions of many bacterial and fungal families remain poorly understood, limiting comprehensive insight into ecosystem recovery processes after fire. However, this study identifies candidate families for future functional investigations and provides a foundation for broader research across diverse ecosystems and geographic regions to identify general patterns in microbial responses to fire.

5 Conclusion

This study demonstrates the importance of stoichiometry in structuring soil microbial communities, highlighting phosphorus as a key factor in post-fire dynamics in *Pinus sylvestris* pine forests 2 years after fire. Several microbial taxa showed differential responses to phosphorus and stoichiometric ratios. Among prokaryotes, families such as Microbacteriaceae, Geodermatophilaceae, and Sphingomonadaceae were positively affected, while Acidothermaceae and Mycobacteriaceae showed negative responses to post-fire conditions. In fungal communities, some taxa (e.g., Agaricomycetes, Mortierellaceae) responded negatively to post-fire phosphorus availability, whereas others (e.g., Helotiaceae, Tremellomycetes, or Dothideomycetes) were positively affected. Overall, bacterial communities appeared to benefit from the post-fire conditions, whereas fungal responses were more heterogeneous.

The identification of key microbial families and the main nutritional drivers provide valuable insights into the mechanisms underlying microbial reorganization after fire. These findings expand our understanding of soil recovery dynamics in post-fire situations by linking microbial community structure to nutrient

availability, with important implications for ecosystem resilience and nutrient cycling.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary material](#), further inquiries can be directed to the corresponding author.

Author contributions

RP: Formal analysis, Writing – original draft, Data curation, Conceptualization, Methodology, Investigation. GA: Supervision, Writing – review & editing, Methodology, Investigation, Conceptualization. LC: Supervision, Conceptualization, Methodology, Investigation, Writing – review & editing, Funding acquisition. VJ: Writing – review & editing, Funding acquisition, Supervision, Methodology. LS: Methodology, Supervision, Data curation, Conceptualization, Writing – review & editing, Investigation.

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Supplementary material

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