



Plant species modulates fire-effects and post-fire temporal dynamics on soil microbial communities in Andean dry shrublands (Arequipa, Perú)

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Abstract

Background and Aims Wildfires in high-altitude dry shrublands of the Peruvian Andes are increasingly becoming a significant ecological threat, with substantial and potentially persistent impacts on soils. This study investigated how fire affects soil microbial communities and functions beneath two dominant shrub species, *Berberis lutea* and *Parastrephia*

quadrangularis, which differ in biomass and fuel structure and therefore in the intensity of combustion that their soils are exposed to. We hypothesized that fire would modify microbial community composition, biomass and functional activity, leading to distinct recovery trajectories beneath the two shrub species due to their contrasting fuel characteristics.

Methods We conducted a medium-term assessment (3–4 years post-fire) of soil microbial structure and activity using phospholipid fatty acids (PLFA), microbial respiration, microbial biomass carbon and enzyme activities.

Results Fire effects on soils were species-specific. Soils beneath *P. quadrangularis* showed greater potential for bacterial and fungal communities recovery, while those under *B. lutea* soils were more severely affected, likely due to higher aboveground biomass. Despite these differences, both species experienced a strong and persistent reduction in enzymatic activities, indicating long-lasting impacts on soil functionality. In addition, soil properties such as aggregate stability and water repellency were identified as key factors associated with microbial recovery.

Conclusions The results reveal the high vulnerability of Andean dryland soils to wildfire and highlight the role of vegetation type in determining post-fire microbial recovery. Incorporating soil biological indicators into post-fire restoration planning and soil vulnerability assessment may help reduce long-term degradation risks in these fragile high-altitude ecosystems.

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Introduction

The Andean region is a global biodiverse hotspot, comprising high-montane ecosystems such as cloud forests, high-altitude grasslands (puna and páramo) and dry shrublands (Myers et al. 2000). The historical use of these highlands for agriculture and grazing has intensified in recent decades (Buytaert et al. 2006; Vélez-Mora et al. 2022), and together with climate change, is reshaping vegetation composition and fuel continuity across the landscape (Zimmermann et al. 2009; Abatzoglou et al. 2019). While human-induced fires are frequent in Andean grasslands and grass-shrublands (e.g., páramo and pajonales) (MINAM 2015), fire has historically been rare in high-altitude dry shrublands, where low rainfall and low biomass productivity limit fuel accumulation with low horizontal and vertical connectivity, resulting in natural fire intervals exceeding 200 years (Oliveras et al. 2014). However, novel fire regimes, where human-induced ignitions are interacting with prolonged droughts and vegetation shifts, are now driving rapid structural and functional ecosystem shifts (Bush et al. 2015; Armenteras et al. 2020). In the Peruvian Andes, official records report a shift in fire occurrence, with an increase from 37.2 fires per year in 2003–2012 to over 1,000 in 2020 (CENEPRED 2020). Increasing fire incidence in arid environments has strong negative effects, limiting shrub recovery and degrading soils, through losses of fertility and water retention capacity and increased erosion risk, and disrupting soil microbial communities that support nutrient cycling and soil stability (Pratt et al. 2014; Giorgis et al. 2021; Coleine et al. 2024). These ecological impacts can, in turn, feed back to human land use by compromising soil functions essential for pastoral and agricultural livelihoods (Chartier and Rostagno 2006; Casillo et al. 2012). Understanding how Andean dry shrublands respond to wildfire and the factors that control their recovery trajectories is therefore critical for both ecosystem resilience and land management.

Dry shrublands are characterized by a mosaic of vegetation patches and intershrub spaces. This strong spatial heterogeneity structures soil fertility and ecosystem

functionality, as soils beneath shrub canopies contain higher organic matter, moisture, and microbial activity compared with the nutrient-poor open interspaces (Schlesinger et al. 1996; Ravi et al. 2007; Bachar et al. 2011). The greater fuel accumulation in those shrub patches leads to stronger fire intensity and thus, potentially higher soil severity (Keeley 2009; Stephan et al. 2010), making them particularly sensitive to fire effects and key microsites for assessing soil recovery trajectories. At fine scales, subtle variations in shrub structure, including both intrinsic plant traits (fuel chemistry or bark thickness) and extrinsic properties related to size and shape (surface to volume ratio or spatial arrangement), modulate combustion dynamics and the extent of soil heating (Pyne et al. 1996; Hollis et al. 2011; O'Brien et al. 2018). As a result, specific variation in fuel traits can produce heterogeneous transformations of soil organic matter (Knicker 2007; Pellegrini et al. 2018), microbial biomass decline (Hart et al. 2005; Bárcenas-Moreno et al. 2011), and alterations in soil physical properties such as changes in aggregate stability or induced water repellency (Mataix-Solera et al. 2011). Understanding how different shrub species influence local fire effects on soils might be important for predicting species-specific fire legacies in dry shrublands.

Evidence from semi-arid shrublands worldwide, such as chaparral (Vourlitis et al. 2022), sagebrush steppe (Nichols et al. 2021), and mountainous dry shrublands in northern Iran (Kooch et al. 2024), reports post-fire declines in soil organic matter, porosity, aggregate stability, and nutrient availability, as well as in microbial activity, with impacts persisting for more than a decade. In South America, however, most research on fire effects in drylands has focused on the fire-prone Cerrado and Gran Chaco savannas (Giorgis et al. 2021), leaving the Andean dry shrublands mostly unexplored. Yet, in these environments, wildfires typically result in the depletion of soil organic carbon and an increase in bulk density (Giorgis et al. 2021), coupled with reduced aggregation and enhanced hydrophobicity (González et al. 2024; Coaguila et al. 2025). Such responses to fire are further modulated by the inherent properties of soils (Agbeshie et al. 2022). In recent volcanic montane areas under arid climate, soil development is limited, resulting in sandy soils with low organic matter content and poor aggregation (Mataix-Solera et al. 2021). These characteristics make them highly vulnerable to degradation, such that even moderate fire intensities

can trigger cascade effects, compromising the potential of soils for post-fire recovery (Agbeshie et al. 2022).

The recovery of dry shrublands may largely depend on the response of soil microbial communities, which regulate post-fire organic matter decomposition, nutrient cycling and plant regeneration (Semenova-Nelsen et al. 2019; Pérez-Valera et al. 2020; Dove et al. 2021). In arid ecosystems, microbial communities are phylogenetically and functionally unique (Neilson et al. 2017; Coleine et al. 2024), reflecting adaptations to water and nutrient scarcity (Delgado-Baquerizo et al. 2018; Tian et al. 2022). Fire directly reduces microbial biomass and alters the soil environment by modifying the substrate availability, soil moisture and temperature dynamics, and nutrient balance (Dooley and Treseder 2012; Zhou et al. 2025). The changes alter the microbial community structure, favoring heat-resistant or fast-growing taxa while suppressing oligotrophic groups (Ferrenberg et al. 2013; Pulido-Chavez et al. 2021). The trajectory of microbial recovery is expected to reflect the degree of soil alteration, with fire-induced changes in organic matter, nutrients, soil structure, or water repellency mediating microhabitat conditions and nutrient availability (Muñoz-Rojas et al. 2016; Adkins et al. 2020). However, the mechanisms linking microbial recovery to plant-soil interactions after fire remain poorly understood in Andean dry shrublands, where nutrient-poor, weakly aggregated, sandy soils may constrain resilience (Doherty et al. 2016; Coaguila et al. 2025). Understanding the plant-soil-microbial interactions during the early recovery period can help identify priority areas for intervention and develop effective restoration strategies in an increasingly fire-prone Andes (Souza-Alonso et al. 2022; Oliveras et al. 2025).

We evaluated both structural (PLFA) and functional (enzyme activities, microbial respiration, microbial biomass carbon) responses of microbial communities to fire disturbance at a medium-term recovery stage (three and four years after the fire event). Given the different influence of shrub species on post-fire soil physicochemical properties (Coaguila et al. 2025), we examined soils beneath two dominant Andean shrubs, *Berberis lutea* Ruiz & Pav. and *Parastrephia quadrangularis* (Meyen) Benth. & Hook.fil. Specifically, we tested the following hypotheses: 1) fire alters microbial community structure and

reduce microbial biomass, resulting in medium-term functional impacts on soil nutrient cycling; 2) microbial recovery trajectories differ between soils beneath the two shrub species, reflecting differences in shrub traits that may influence localized fire severity; 3) soil properties related to soil structure and soil organic matter mediate the resilience of microbial communities after fire.

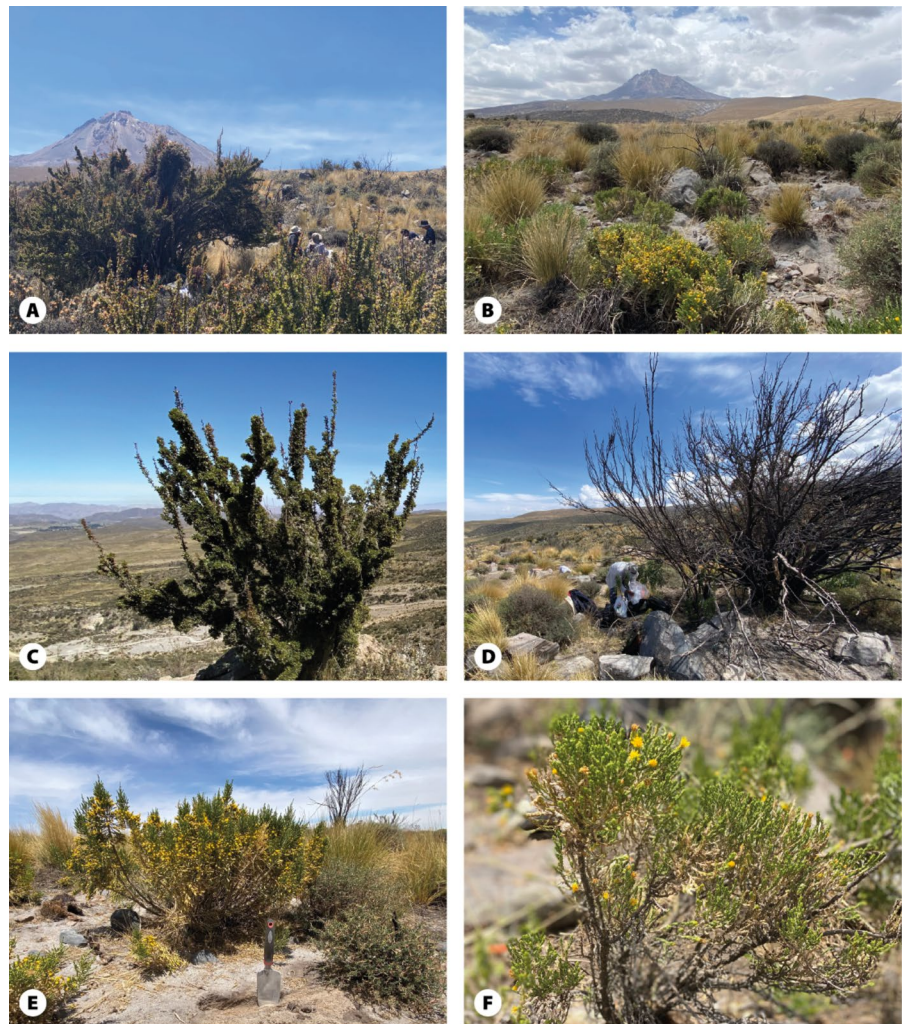
Material and Methods

Study area, wildfire and sampling strategy

The study was conducted in the Pichu Pichu volcano mountain in the Arequipa region (Perú), at an altitude of 3700 m a.s.l. The study area is part of the high-altitude Andean dry shrublands, characterized by sparse woody vegetation adapted to arid high mountain climate (MINAM 2015). The climate is classified as cold desert (BWk), with an average annual precipitation of 385 mm concentrated in three to four months. The landscape consists of a sparse shrubland dominated by shrub species less than 4 m tall, interspaced with open patches of herbaceous cover. The dominant shrub species are *Berberis lutea* Ruiz & Pav. and *Parastrephia quadrangularis* (Meyen) Benth. & Hook. fil., accompanied by the herbaceous *Stipa ichu* (Ruiz & Pav.) Kunth and less abundant species such as *Chuquiraga spinosa* Less. and *Adesmia spinosissima* Meyen ex Vogel. Soils in the area have a loamy sand texture with low clay values (<5%), acidic pH (5.2), soil organic matter (<5.3%), and low total aggregation (<30%) (Coaguila et al. 2025).

In September 2018, a wildfire burned 1992 ha of this shrubland landscape on the slopes of the Pichu Pichu volcano. The burning reached moderate to high fire severity according to Keeley et al. (2009): complete charring or consumption of understory vegetation, consumption of fine twigs on the soil surface, and the presence of charred logs and a layer of grey ash covering the soil. In the years following the fire, the area exhibited symptoms of soil degradation, the pronounced interannual rainfall variability typical of arid climates being a trigger for soil erosion processes (Coaguila et al. 2025). Total rainfall in 2020 reached 572.3 mm, more than double the totals recorded in 2021 (248.8 mm) and 2022 (272.2 mm). Extreme

Fig. 1 (A–B) High Andean dry shrubland landscape showing the two dominant shrub species in the front: *Berberis lutea* (A) and *Parastrephia quadrangulata* (B). (C) *Berberis lutea* individual in an unburned control area; (D) *Berberis lutea* individual three years after the wildfire; (E) *Parastrephia quadrangulata* individual in an unburned area; (F) *Parastrephia quadrangulata* individual burned during the 2018 wildfire, displaying signs of resprouting



rainfall events, such as 36 mm in two hours on one day in February 2020, exacerbated soil erosion risks.

The samplings were performed in soils affected by the burning of the two dominant shrub species, *B. lutea* and *P. quadrangulata*, to explore potential species-specific soil responses to fire (Fig. 1). The species differ in biomass and fuel structure (i.e., arrangement), among other traits. *B. lutea* grows to a higher height (~2 m in this area), has a fragmented canopy and develops dense, tall branches with thorns, with a fuel bed of ~1 cm. *P. quadrangulata* has a smaller in biomass, is compact but not dense (with fine, superimposed branches), is resinous, and typically reaches a height of ~1 m at high altitudes (Gowda and Raffaele 2004; SERFOR 2024; Heim 2025). While the fuel load was not directly quantified, these contrasting physical

and structural traits suggest that the two species experience different fire combustion (Fig. 2). To evaluate the post-fire soil status and its recovery trajectory over time, two soil samplings were conducted in September 2021 and September 2022, representing 3 and 4 years after the 2018 fire event. During each sampling, a total of 40 soil samples were collected from the top 5 cm of mineral soil, 20 samples from burned areas and 20 from unburned control areas, with samples collected separately beneath each of the two shrub species to assess potential species-specific effects. For the PLFA analyses, 24 samples were randomly selected from the total dataset (2 sampling years $\times$ 2 fire treatments $\times$ 2 species $\times$ 3 replicates). The remaining samples were used for complementary analyses of soil biochemical properties.

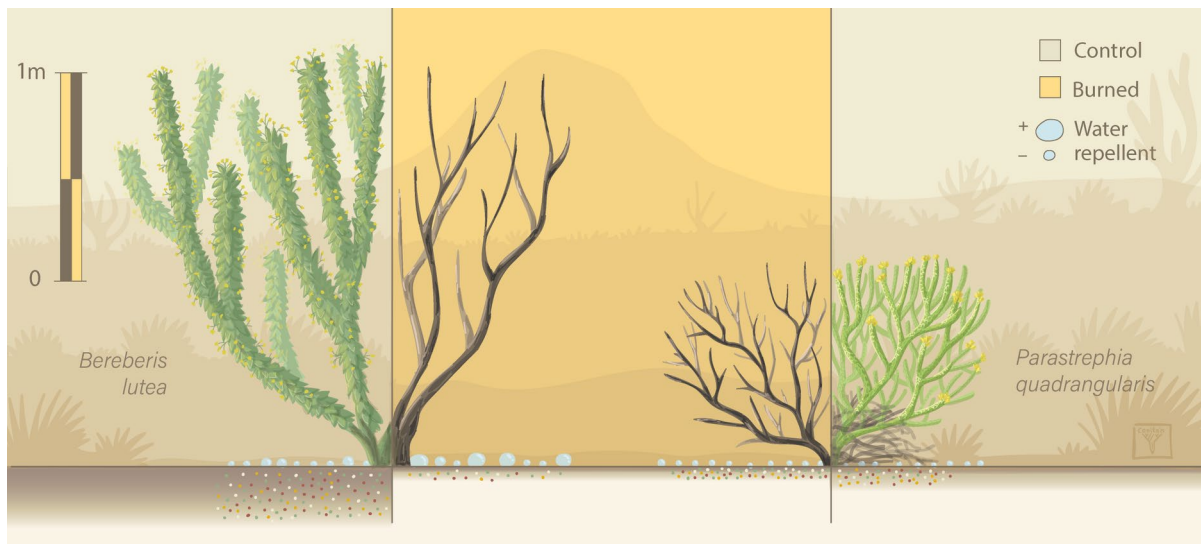


Fig. 2 Conceptual illustration of the two dominant shrub species (*Berberis lutea* and *Parastrephia quadrangularis*) and their contrasting fuel structures. The figure highlights differences in plant height and fuel arrangement that influence com-

bustion intensity. The associated soils represent fire-induced changes, including organic matter consumption, the development of water repellency and reduction in microbial biomass

Biological and biochemical soil properties analyses

The composition of the soil microbial community structure and biomass was inferred from the relative abundance of specific phospholipid fatty acid (PLFA) biomarkers, 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, the fatty acid methyl esters were identified by gas chromatography (flame ionization detector) by the relative retention times of the fatty acids, using methyl nondecanoate (19:0) as internal standard. Individual fatty acids were assigned to major microbial groups according to established indicators: fungal biomass (eukaryotic) was determined by the combined contents of c18:2 ω 6t and c18:2 ω 6c, while bacterial biomass (prokaryotic) based on the sum of contents of 16:1 ω 9, cy17:0, 18:1 ω 9t, 18:1 ω 9c, cy19:0, 16:1 ω 9, cy17:0, 18:1 ω 9t, 18:1 ω 9c, cy19:0, 10Me16:0, 10Me18:0 (Federle 1986; Zelles et al. 1994; Olsson et al. 1995). Total microbial biomass was estimated as the sum of all the extracted PLFAs (total PLFAs).

Soil enzyme activity was evaluated by dehydrogenase activity following the procedure described by (García, et al. 1997), measuring the reaction product INTF (iodonitrotetrazolium formazan), which is formed by the reduction of the substrate INT (2-p-iodophenyl-3-p-nitrophenyl-5-phenyltetrazolium chloride), as an indicator of overall microbial oxidative activity. Additionally, 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), reflecting nitrogen mineralization and protein degradation processes. β -glucosidase and acid 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, as indicators of carbon and phosphorous cycling potential. Enzymes activities were determined colorimetrically using UV–Vis spectroscopy.

Basal soil respiration was measured using an automated impedance-meter (BacTrac 4200 Microbiological Analyser, Sylab, Austria), based on changes in the impedance of a KOH solution (2%) after CO_2

emissions by soil microorganisms incubated at 30 °C. Microbial biomass carbon was estimated, also using an impedance-meter, as the substrate-induced respiration using glucose (3 mg per gram of soil) as carbon substrate, according to Anderson and Domsch (1978).

Other soil physicochemical properties mentioned in this study are already described and profoundly studied in the previous work (Coaguila et al. 2025). Briefly, pH and EC were measured in aqueous extracts, texture was determined using the Bouyoucos method, and organic carbon was assessed by the Walkley and Black method. Water repellency was measured using the water drop penetration time test, and aggregate stability was evaluated with a rainfall simulator following Roldán et al. (1994), based on (Benito, and Díaz-Fierros, 1989). This method quantified the stability of macroaggregates (4–0.25 mm) by exposing them to artificial rainfall of controlled energy and intensity; aggregates stability is then the percentage of macroaggregates that remain intact after the simulated rainfall event.

Statistical analysis

All statistical analyses were performed using R (R Core Team 2025) and RStudio (Version 4.5.1; Posit Team, 2025).

To assess the effects of study factors on microbial community represented by fatty acid profiles in soil samples, we conducted a PERMANOVA analysis with 999 permutations using the *adonis* function in the *vegan* package (Oksanen et al., 2025), and homogeneity of multivariate dispersions was examined via *PERMDISP* with the *betadisper* function (999 permutations). The factors tested included shrub species (*B. lutea* and *P. quadrangularis*), fire occurrence (control and burned), and time since fire (S1 and S2). Following this, we performed two-dimensional non-metric multidimensional scaling (NMDS) ordination plots based on Bray–Curtis dissimilarities to visualize the spatial distribution of the microbial communities based on the studied factors.

To explore differences in biomass of the main biomarkers, we conducted a three-way ANOVA, analyzing the effects of shrub species (*B. lutea* and *P. quadrangularis*), fire occurrence (control and burned) and time since fire (S1 and S2). When significant effects or interactions were detected ($p < 0.05$), multiple comparisons were performed using Tukey's HSD test.

Next, to examine the effects of fire, time since fire, and shrub species on microbial functionality, we again used a PERMANOVA analysis with 999 permutations, on enzymatic activity, basal respiration and microbial biomass variables. We then performed a three-way ANOVA on all functional variables, and then separately analyzed the effects for each shrub species. To understand the magnitude of the fire impact, we calculated the Cohen's *d* effect sizes comparing control and burned soils for all these variables in the final sampling (S2), followed by a two-way ANOVA to confirm the effects of shrub species and their interaction with fire occurrence.

Finally, it was explored whether the changes in microbial structure and composition were associated with fire-affected soil properties. First, we made a bivariate correlation analysis based on Spearman correlations, to test correlations between biomarkers and relevant soil parameters detected in the previous study (Coaguila et al. 2025) together with microbial functional variables including enzymatic activities, basal soil respiration and microbial biomass. Correlations were separated by species to depict differences by species in fire-affected soils. In addition, we performed a redundant analysis to see how statistically selected variables constrain the microbial community structure (represented by fatty acids profiles). The selection of variables was done after eliminating the multicollinearity ($vif > 10$ deleted).

Results

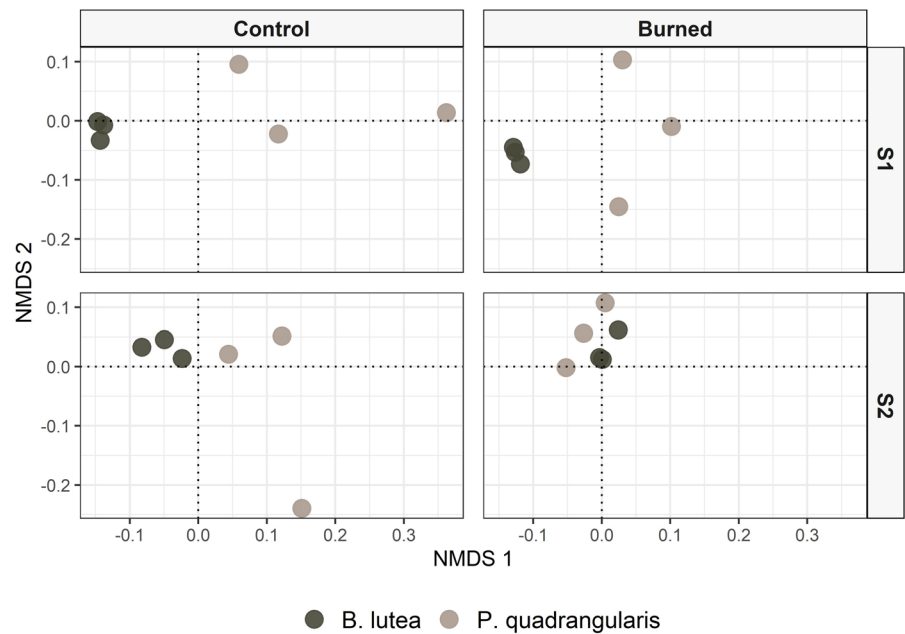
Microbial community response to fire in dry shrublands

PERMANOVA analysis revealed that microbial community composition, represented by fatty acid profiles, was significantly influenced by the shrub species being burned ($p < 0.001$) (Table 1). Neither fire occurrence nor time since fire showed significant main effects when considered independently. However, significant interactions between shrub species, either *B. lutea* or *P. quadrangularis*, and both fire occurrence and time since fire ($p < 0.001$) indicated that fire effects on microbial communities were species-specific and modulated by temporal dynamics post-fire.

Table 1 PERMANOVA results showing the effects of species (*B. lutea* and *P. quadrangularis*), fire occurrence (burned and controls), and time (S1 and S2), and interactions between them on the microbial community, represented by the fatty acids

	Df	SumOfSqs	R2	F	Pr(> F)
Specie	1	0.674	0.328	19.337	< 0.001***
Fire	1	0.081	0.039	2.312	n.s
Time	1	0.083	0.040	2.383	n.s
Specie:Fire	1	0.289	0.141	8.297	0.009**
Specie:Time	1	0.294	0.143	8.424	0.006**
Fire:Time	1	0.033	0.016	0.951	n.s
Specie:Fire:Time	1	0.043	0.021	1.234	n.s
Residual	16	0.558	0.271		
Total	23	2.055	1.000		

Significant codes: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; n.s., not significant

Fig. 3 Two-dimensional non-metric multidimensional scaling (NMDS) ordination plots based on Bray–Curtis dissimilarities for soil microbial community composition (based on fatty acid profiles), visualized by Specie (*B. lutea* and *P. quadrangularis*), Time (S1 and S2) and Fire (burned and control)

Differences in community composition were visualized in the NMDS ordination (Fig. 3), which showed clear separation of microbial assemblages associated with *B. lutea* and *P. quadrangularis* soils along X-axis, reflecting strong shrub species effects modulated by fire and temporal factors (stress 0.099). Tests for homogeneity of multivariate dispersion (PERMDISP) confirmed that within-group variability differed significantly with fire occurrence ($p = 0.027$; Table A1 in supporting materials), with lower dispersion in burned samples, suggesting an overall homogenization of microbial communities following fire.

Within *P. quadrangularis*, a visual tendency toward reduced dispersion (i.e., greater similarity among replicates in burned soils) in burned soils at the second sampling (S2, burned soils) was observed in the NMDS, but was not statistically supported by the PERMDISP.

The microbial biomarkers abundance showed similar significant differences between shrub species (*B. lutea* and *P. quadrangularis*), fire occurrence (control vs. burned), and time since fire (S1 and S2) (Fig. 4, Supporting materials Table A2). In soils beneath *B. lutea*, total, fungal, and bacterial biomass were

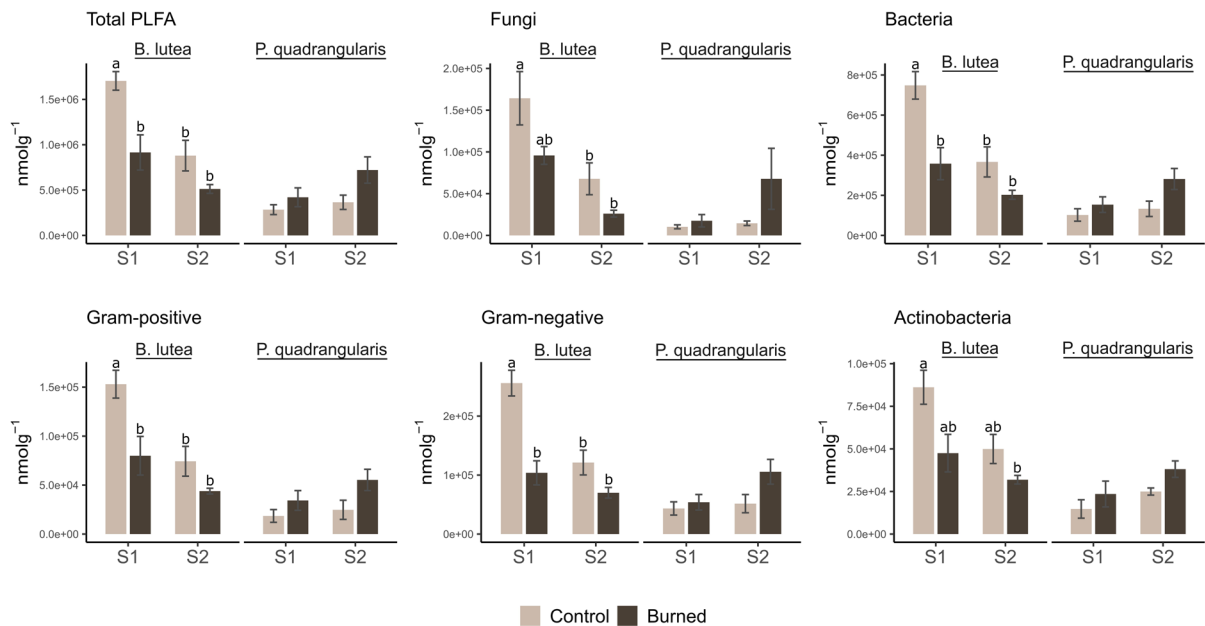


Fig. 4 Microbial biomarkers (PLFA) for each shrub species (*B. lutea* and *P. quadrangularis*) comparing burned and control soils across two sampling times (S1 and S2). Different letters

indicate significant differences (Tukey's test, $p < 0.05$) among the combinations of sampling time and fire occurrence within each species

higher in control soils and significantly reduced in burned soils. Biomass levels further decreased over time (S2), regardless of fire occurrence. In contrast, soils beneath *P. quadrangularis* showed consistently lower biomass values compared to *B. lutea*, with not statistically significant differences between burned and control treatments or sampling times. However, a non-significant increase in microbial biomass was observed in burned *P. quadrangularis* soils over time (S2) for all biomarkers.

Microbial functional response

Microbial functionality indicators, including enzymatic activities, basal soil respiration and microbial biomass, were significantly affected by the fire event. These effects were consistent regardless of the shrub species or the time elapsed since fire, as confirmed by PERMANOVA results (Table A3).

Mean values of enzymatic activities were significantly lower in burned soils compared to controls (Table A4). For nitrogen cycling, protease activity decreased in burned soils for both shrub species, with a pronounced decline in *P. quadrangularis* soils at the

later sampling (S2). Urease activity, indicative of nitrogen availability, also declined significantly in burned soils, with a significant interaction between fire and time observed in *B. lutea* soils ($p = 0.038$). Glucosidase activity, which reflects labile carbon decomposition, showed a marked reduction in burned soils for both species and sampling times. Phosphatase activity, involved in phosphorus cycling, was significantly reduced by fire in *B. lutea* soils ($p < 0.001$), while *P. quadrangularis* soils showed a smaller but still significant decrease. In contrast, dehydrogenase activity, representing overall microbial metabolic activity, increased significantly in burned soils, especially in *P. quadrangularis* soils ($p = 0.029$).

Basal soil respiration and microbial biomass also declined in burned soils of both species, with the reduction particularly marked in *B. lutea* soils (Fig. 5, Table A5).

As time since fire had no significant effect on overall microbial functionality (Table A3), treatment comparisons were made using data from the second sampling (S2). Most microbial indicators exhibited moderate to large negative effect sizes (Cohen's d) when comparing burned and control

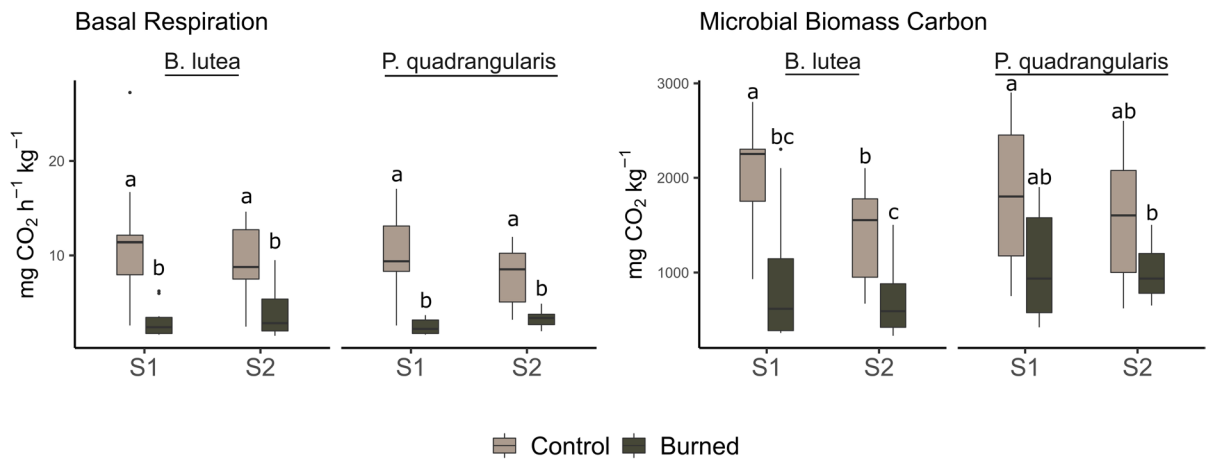


Fig. 5 Soil basal respiration and microbial biomass per shrub species comparing burned soils vs controls and for the two soil samplings (S1 and S2). Different letters indicate significant dif-

ferences (Tukey's test, $p < 0.05$) among the combinations of sampling time and fire occurrence within each species

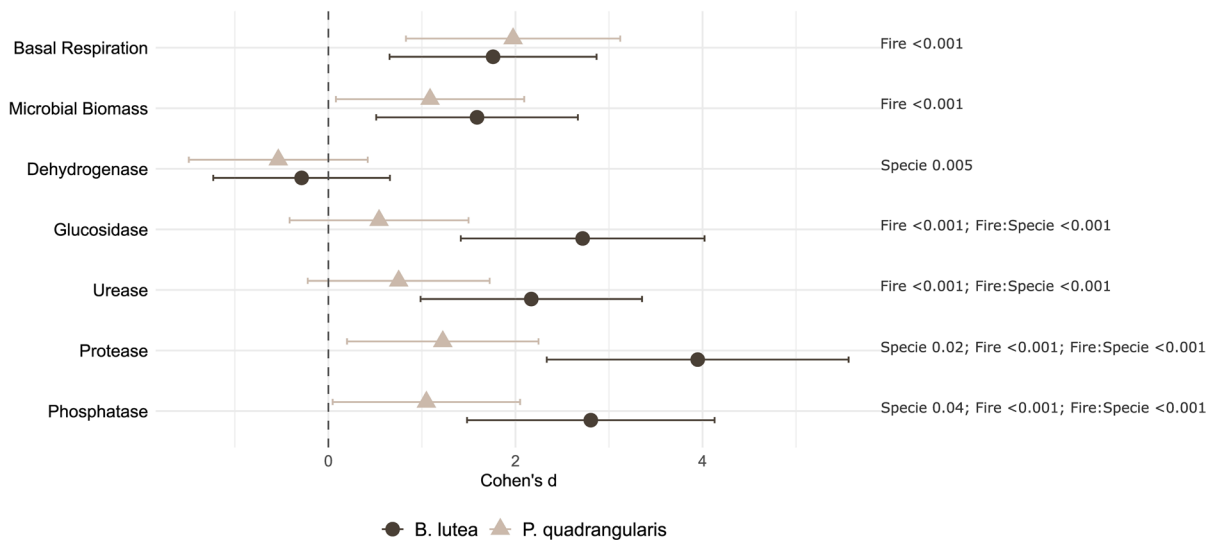


Fig. 6 Cohen's d effect sizes of burning on soil microbial functional indicators under *B. lutea* and *P. quadrangularis* (sampling time S2). Results of two-way ANOVA are included,

showing statistical effects for species (*B. lutea* and *P. quadrangularis*), fire occurrence (burned and controls), and their interactions

soils (Fig. 6), with larger effects in *B. lutea* soils (Cohen's $d > 0.8$). ANOVA models corroborated these patterns, showing significant effects of fire, with significant interactions between shrub species and fire for most variables ($p < 0.05$) (Fig. 4). In contrast, dehydrogenase activity was the only variable showing a positive, although small, response to the fire effect.

Soil variables associated with microbial communities changes

Bivariate correlations between microbial biomarkers and soil properties in burned soils revealed distinct patterns influenced by the burned shrub species (Table 2). In *B. lutea* soils, PLFA biomass (total and specific groups) was positively correlated with

key soil properties, including aggregate stability and water repellency, and negatively correlated with indicators of microbial functionality such as urease and dehydrogenase activity. In contrast, correlations in *P. quadrangularis* soils were generally weaker and showed an opposite trend, with negative correlations with aggregate stability (except for the fungi group) and clay content.

Redundancy analysis was used to explore how soil properties influence microbial community composition based on fatty acid profiles (Fig. 7). The analysis revealed distinct patterns associated with shrub species and fire occurrence. Microbial communities under *P. quadrangularis* showed tight clustering, indicating high similarity between control and burned soils, in contrast to the greater dispersion observed under *B. lutea*. In *P. quadrangularis* soils, microbial communities were negatively associated with increased aggregate stability (AS) and water repellency (WR), while higher dehydrogenase activity was notably characteristic of these samples. Conversely, in *B. lutea* soils, fire induced a clear separation between burned and control communities, with minimal overlap. Control soils in *B. lutea* were strongly associated with higher soil organic carbon (SOC) content and basal respiration (BR), while increases in bulk density (BD) and clay content showed strong negative correlations with microbial community composition, indicating fire-induced soil degradation.

Discussion

Wildfires in the high Andean dry shrublands of southern Peru caused persistent alterations in soil microbial community structure, biomass and activity beneath the dominant shrub species in the shrubland, *Berberis lutea* and *Parastrephia quadrangularis*. Three to four years after the fire, soil microbial communities and their associated functions had not fully recovered, indicating a medium-term legacy of fire disturbance. These results suggest that recovery trajectories in these dry Andean ecosystems are slow, likely constrained by low soil organic matter, weak soil structure (low aggregation and coarse texture), and arid climatic conditions that limit plant regrowth and thus microbial recolonization (Muñoz-Rojas et al. 2016; Xu et al. 2024; Coaguila et al. 2025). The soil microbial response to fire

widely varies across ecosystems. In fire-prone ecosystems such as chaparral, savannas or sagebrush steppe ecosystems, fire acts as a recurrent ecological force regulating vegetation and soil biodiversity (McLauchlan et al. 2020), as microbial communities often recover within a few years following vegetation regrowth (Pérez-Valera et al. 2020; Pulido-Chavez et al. 2021; Nichols et al. 2021). In contrast, in arid and semi-arid shrublands where fire is naturally infrequent, reductions in microbial biomass and enzymatic activities can persist over decades due to limited organic matter inputs and nutrient replenishment, and may intensify with increasing fire frequency (Butler et al. 2018; Pellegrini et al. 2018; Kooch et al. 2024). The medium-term legacies observed in our study indicate that the high-altitude Andean dry shrublands can be considered fire-sensitive ecosystems. Fire occurrence is rare in those ecosystems because of low fuel load availability and connectivity (Oliveras et al. 2014), so the persistence of microbial alterations three to four years after fire indicates the onset of a slow recovery trajectory, likely characterized by reduced decomposition rates, limited microbial growth, and shifts in successional composition. Comparable studies in other high-elevation or arid shrublands have shown that under similar conditions (i.e., low organic matter inputs, limited soil moisture, and strong interannual rainfall variability) fire effects on microbial communities can persist for decades (Nelson et al. 2014; Kooch et al. 2024).

An important finding of this study is that the effects of fire on soil microbial community composition, structure and biomass were plant species-specific, reflecting distinct responses beneath *Berberis lutea* and *Parastrephia quadrangularis* soils. These species-specific differences arise from two mechanisms: variations in fire intensity and heat transfer to the soil driven by fuel intrinsic properties such as its biomass and chemical composition, and extrinsic fuel traits including its arrangement; and also distinct pre-existing soil characteristics that modulate the magnitude of fire effects. First, differences in fuel traits likely determined fire intensity and the residence time of heat during combustion. Based on species attributes, *Berberis lutea* would be expected to sustain higher and more prolonged combustion than *Parastrephia quadrangularis*, due to its greater aboveground biomass, denser branches, and more

Table 2 Correlation coefficients (*r*) between the main PLFA biomarkers and physicochemical and biological soil properties separately by species in burned soils. Significant correlations are highlighted in bold

		Aggregate stability	Clay	Bulk density	Water repellency	SOC	Microbial biomass	Basal respiration	Glucosidase	Urease	Phosphatase	Dehydrogenase	Protease
<i>B. lutea</i>	Total	0.61	0.17	-0.21	0.69	-0.24	-0.25	-0.42	-0.34	-0.57	-0.26	-0.75	-0.41
	Fungi	0.87	0.49	0.08	0.61	-0.36	-0.41	-0.61	0.11	-0.56	-0.45	-0.89	-0.05
	Bacteria	0.59	0.2	-0.28	0.75	-0.22	-0.21	-0.44	-0.37	-0.56	-0.21	-0.72	-0.39
	Gram-positive	0.61	0.26	-0.32	0.82	-0.25	-0.1	-0.4	-0.39	-0.6	-0.21	-0.65	-0.37
	Gram-negative	0.52	0.16	-0.39	0.76	-0.11	-0.21	-0.44	-0.43	-0.45	-0.09	-0.7	-0.39
	Actinobacteria	0.47	0.06	-0.32	0.71	-0.21	-0.17	-0.35	-0.51	-0.57	-0.17	-0.64	-0.52
<i>P. quad-rangula-ris</i> sp.	Total	-0.52	-0.69	-0.25	-0.18	0.16	-0.01	0.15	0.1	0.37	0.12	0	0.15
	Fungi	-0.39	-0.58	0.15	-0.18	0.07	-0.11	0.26	-0.05	0.17	-0.06	-0.02	-0.11
	Bacteria	-0.58	-0.73	-0.28	-0.26	0.17	-0.07	0.18	0.13	0.4	0.18	0.07	0.21
	Gram-positive	-0.47	-0.57	-0.35	-0.39	-0.03	-0.22	-0.04	-0.04	0.33	0.13	-0.01	0.15
	Gram-negative	-0.6	-0.74	-0.23	-0.3	0.17	-0.12	0.21	0.11	0.39	0.19	0.1	0.2
	Actinobacteria	-0.58	-0.59	-0.41	-0.55	-0.09	-0.33	0.02	0.05	0.48	0.33	0.04	0.33

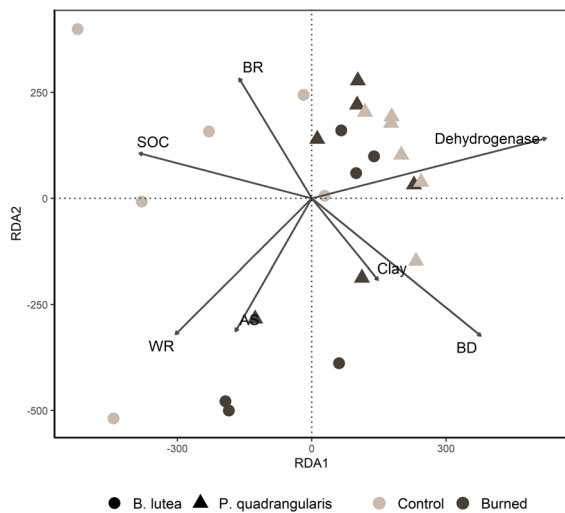


Fig. 7 Redundancy Analysis showing the relationships between soil microbial community composition (based on fatty acid profiles) and selected soil properties. Arrows represent the loadings of significant environmental variables (Dehydrogenase, SOC: soil organic carbon, BR: basal respiration, WR: water repellency, AS: aggregate stability, Clay, BD: bulk density), while colors represent soil condition (control and burned) and point shape the shrub species (*B. lutea* and *P. quadrangularis*)

fuel bed accumulation (DeBano et al. 1998; Jenkins et al. 2016; García-Carmona et al. 2025). Higher combustion intensity under *B. lutea* would have prolonged soil heat exposure, which could explain the stronger microbial biomass reductions observed beneath this species, through heat-induced mortality and substrate depletion (Pressler et al. 2019; Nelson et al. 2022). Secondly, pre-existing soil conditions would have also contributed to the species-specific responses to fire, reflecting the long-term influence of each shrub on its underlying soil. Soils beneath *P. quadrangularis* contained higher clay content, higher bulk density, and lower organic carbon content than those under *B. lutea* (Coaguila et al. 2025). These physical and chemical characteristics potentially buffered soil heating during combustion, mitigating microbial losses. In contrast, the sandier and carbon-rich soils beneath *B. lutea* were more susceptible to organic matter combustion and structural degradation (Mataix-Solera et al. 2009; Agbeshie et al. 2022), amplifying the fire impact on soil microorganisms. These distinct pre-soil conditions, shaped by the shrub species, therefore determined

contrasting starting points for microbial recovery trajectories following the wildfire.

The differing responses observed between shrub species may also reflect inherent differences in their associated soil microbial communities prior to the fire. Soils beneath *B. lutea* and *P. quadrangularis* likely hosted distinct microbial assemblages, shaped by vegetation-driven soil legacies. Such dissimilarities are common in drylands, which are considered hotspots of microbial community turnover due to strong spatial heterogeneity and nutrient limitation (Guerra et al. 2022). In addition, plants influence microbial communities both directly (through root exudates and litter inputs) and indirectly by altering soil structure and moisture (Hart et al. 2005; Dove et al. 2021), generating distinct microbial assemblages associated with each shrub species. After the fire, microbial community composition showed a strong fire effect but exhibited different temporal trajectories between the two shrub species. In *P. quadrangularis* soils, NMDS ordination suggested a visual tendency toward reduced dispersion over time, suggesting a potential convergence in community composition compared to *B. lutea* soils. Such homogenization after fire may reflect temporal reductions in oligotrophic taxa (e.g. gram-negative bacteria), which are commonly negatively affected in favor of copiotrophs and heat-resistant taxa (Fierer et al. 2007; Goberna et al. 2012; Prendergast-Miller et al. 2017). Fungal and bacterial groups responded similarly to fire in these dry shrublands, despite fungi being generally more sensitive to heat-effects than bacteria (Dooley and Treseder 2012; Ferrenberg et al. 2013; Pressler et al. 2019). This comparable response may be mediated by soil moisture, a major environmental driver of microbial activity and recovery (Paul and Frey 2024). Inter-annual precipitation variability, characteristics of drylands, were reflected in microbial biomass differentiation in non-burned soils, with higher microbial biomass during periods of greater rainfall (Coaguila et al. 2025). These effects were more pronounced in *B. lutea* soils, where higher plant biomass likely buffers microclimatic conditions and provides more favorable microbial habitats. However, after the fire, these soils may become more susceptible to erosion, a process observed in the area, which can further limit microbial recovery over time.

Three and four years post-fire, the direct impact of fire on microbial metabolic activity remained evident, regardless of the shrub species burned. This persistence aligns with earlier findings that reductions in microbial biomass and shifts in community structure can trigger cascading effects on microbially mediated ecosystem functions (Semenova-Nelsen et al. 2019; Nelson et al. 2022). Although post-fire increases in microbial respiration rates are frequently observed indicating short-term access to fire released nutrients (Choromanska and DeLuca 2002; Bárcenas-Moreno et al. 2011), respiration rates in our burned soils remained substantially lower, indicating a strong legacy of disturbance and a sign of degradation in these low-carbon ecosystems (Hudiburg et al. 2023). The marked decline in microbial carbon utilization suggests a sustained disruption to nutrient cycling in these drylands, where soil microbiota plays a key role in regulating biochemical cycles (Coleine et al. 2024).

Persistent enzymatic inhibition further supports the evidence of functional degradation. Our results showed β -glucosidase (C cycling), urease, protease (N cycling), and phosphatase (P cycling) activities all declined consistently in burned soils, in line with findings from other arid ecosystems where microbial growth and decomposition rates are restricted by moisture and substrate availability (Hedo de Santiago et al. 2016; Hinojosa et al. 2019). Negative fire impacts were stronger in *B. lutea* enzymatic activities, where stronger combustion likely temporarily will slow litter and organic matter decomposition (Butler et al. 2019). Such reductions are expected to delay ecosystem recovery, as microbial functioning is likely to be indispensable for plant recolonization and reestablishment of ecosystem stability in Andean dry shrublands (Philippot et al. 2013; Delgado-Baquerizo et al. 2016; Crowther et al. 2019).

Specific soil properties altered by fire and subsequent post-fire processes are key modulators in shaping microbial responses after disturbance. In these Andean shrublands, soil organic matter content, water repellency, clay fraction, and aggregate stability have been identified as indicators of soil vulnerability to burning (Coaguila et al. 2025). Our results are consistent, as these properties correlated with microbial responses and help explain the contrasting recovery trajectories observed between shrub species. In *B. lutea* soils, higher pre-fire organic carbon and greater

aggregate stability did not translate into faster microbial recovery, probably because the higher combustion intensity led to stronger reduction in microbial biomass and pronounced shifts in community structure. Nevertheless, the lower degree of structural degradation observed was positively correlated with microbial biomass groups, suggesting a pathway for recovery. In contrast, in *P. quadrangularis* soils, initially poorer in organic matter, experienced lower combustion intensity. Although these soils experienced strong losses in aggregate stability and showed evidence of clay particle loss through post-fire erosion, the milder heat impact prevented severe microbial biomass decline. This may explain why *P. quadrangularis* soils maintained microbial abundance despite their less favorable soil structure.

Water repellency also behaved differently between species. In *B. lutea* soils, higher water repellency was positively correlated with microbial groups biomass, whereas *P. quadrangularis* soils showed less extreme and more uniform water repellency and no apparent relationship with microbial abundance (Coaguila et al. 2025). Although severe hydrophobicity restricts infiltration and exacerbates erosion risks in coarse textured soils (Mataix-Solera et al. 2011), moderate and spatially heterogeneous water repellency can have the opposite effect. When repellency is patchy (different degrees of severity), preferential flow pathways develop toward the less hydrophobic zones, allowing water to infiltrate more deeply into the soil (De Rooij and De Vries 1996; Rye and Smettem 2017). This process enhances subsurface water storage and reduces soil evaporation, creating microsites with more persistent moisture that facilitate microbial regrowth in coarse-textured soils (Riveras-Muñoz et al. 2022), despite the challenges posed by organic matter combustion in these dry ecosystems.

In the high Andean dry shrublands, where wild-fires are infrequent but have long-lasting impacts on soils, our findings demonstrate that fire represents a significant ecological disturbance, reducing microbial biomass and activity. The magnitude of these effects depended on the shrub species, suggesting that vegetation community composition modulates fire resilience of these dry ecosystems. From a management perspective, these results highlight the importance of integrating soil biological indicators into restoration practices and fire prevention strategies. Identifying microsites with greater vulnerability, such as

those soil patches beneath *B. lutea* where combustion intensity and soil degradation were higher, could help prioritize restoration actions focused on adding organic amendments or promoting organic matter accumulation to enhance aggregate stability at a landscape level. Preventive measures should aim to limit burning in these shrub-dominated areas, as the loss of microbial functionality can delay vegetation recovery and enhance erosion risk. Protecting soil biodiversity is therefore essential to prevent irreversible degradation and to guide adaptive management in these fragile high-altitude drylands.

Conclusions

This study evidence that wildfires in high-altitude dry shrublands of the Peruvian Andes have long-lasting effects on soil microbial communities, with significant impacts on microbial biomass and metabolic activity three and four years post-fire. The microbial response was plant species-specific, with *Berberis lutea* soils showing greater reductions in microbial activity and biomass compared to *Parastrephia quadrangularis* soils, which showed higher recovery potential despite the loss in soil structure. These findings highlight a persistent suppression of microbial functionality in burned soils, ultimately affecting soil recovery and ecosystem stability.

Specific soil properties affected by fire, particularly soil aggregation and water repellency, were key in shaping microbial community structure and resilience. The contrasting recovery trajectories between shrub species emphasize the importance of plant-soil interactions in driving microbial recovery in these ecosystems. In these high-altitude drylands, the slow reestablishment of carbon pools and biological activity highlights the vulnerability of these ecosystems to fire disturbances. Understanding plant-microbe-soil interactions and integrating soil biological indicators into restoration and management strategies is imperative for mitigating the long-term impacts of wildfires on these fragile Andean landscapes.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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