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Fire enhances recent carbon inputs without mobilizing ancient soil carbon in Andean páramos

Jhonatan Julián Díaz-Timoté [1,2], Carlos A. Sierra [2,4], Andrés Tangarife-Escobar [2], Estefanía Muñoz[3], Stijn Hantson[1]

[1]School of Sciences and Engineering, Universidad del Rosario, Bogotá, Colombia
[2]Max Planck Institute for Biogeochemistry, Jena, Germany
[3]CREAF, Cerdanyola del Vallès, Barcelona, Spain
[4]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

Correspondence to: Jhonatan Julián Díaz-Timoté. Mail: jtimote@bgc-jena.mpg.de

Abstract.

Tropical Andean páramos store large amounts of soil organic carbon including long-term carbon reservoirs whose response to fire remains poorly understood. Understanding whether fire promotes the mobilization of old soil carbon or primarily affects recently fixed carbon is critical for predicting carbon–climate feedback in these ecosystems. We evaluated the effects of fire history on soil carbon dynamics in a Colombian páramo in across gradients of elevation, soil depth, and time since last fire. To do this, we measured total carbon concentrations, radiocarbon signatures ($\Delta^{14}C$) of bulk soil organic matter, and the radiocarbon signature of heterotrophically respired carbon dioxide ($\Delta^{14}CO_2$) from controlled soil incubations.

Bulk soil $\Delta^{14}C$ ranged from −474 to +65‰, with progressively older carbon pools in deeper soils and at higher elevations. Burned soils exhibited more modern radiocarbon signatures than unburned soils (−111 ± 96‰ vs. −158 ± 104‰, respectively) and higher carbon (11.1 ± 5.8% vs. 9.1 ± 3.8%) concentrations. In contrast, $\Delta^{14}CO_2$ ranged from 18.8 to 55.3 ‰ across all fire-history categories with no significant differences among burned and unburned sites, remaining consistently enriched in ^{14}C relative to bulk soil organic matter and indicating that microbial respiration was dominated by relatively young carbon sources despite the presence of older carbon pools.

Our results indicate that fires modify the age of soil organic matter primarily through the incorporation and cycling of young carbon rather than through the accelerated mineralization of old, stabilized soil carbon. Specifically, long-term post-fire

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vegetation recovery visibly narrows the isotopic disequilibrium between stored and respired carbon by modernizing the bulk soil pool. Similar radiocarbon values in deeper and more elevated soils suggest that long-term carbon reservoirs remain relatively resistant to individual fire events. However, increasing fire frequency and climate warming may alter the balance between carbon inputs and outputs, potentially affecting the long-term stability of carbon-rich tropical alpine soils.

1 Introduction

Soils represent the largest terrestrial carbon reservoir, storing more carbon than the atmosphere and vegetation combined, and thus play a central role in regulating atmospheric CO_2, nutrient cycling, and ecosystem productivity (Shi et al., 2020; Trumbore, 2000, 2009). Measurements of soil organic carbon (SOC) provide key information on soil carbon sequestration potential, soil fertility, and soil biogeochemical cycling (Franzluebbers et al., 2000; Wen-Qiang et al., 2016). SOC is a heterogeneous mixture of organic compounds characterized by cycling timescales ranging from months to millennia (Shi et al., 2020; Trumbore, 2000, 2009). The composition and stability of SOC strongly influence its susceptibility to decomposition and its response to environmental change. A large proportion of young carbon derived from recent plant inputs cycles rapidly through surface horizons, while only a small proportion goes to slow-cycling pools, where carbon may persist for centuries or millennia, when protected by low temperatures, mineral associations, or physical occlusion (Czimczik and Masiello, 2007; Shi et al., 2020).

Climate change may accelerate soil organic matter decomposition and increase the release of previously stabilized carbon, particularly in cold, carbon-rich ecosystems where decomposition is naturally constrained (Buytaert et al., 2011; Schuur et al., 2016). Disturbance regimes such as fire can further modify SOC turnover and storage by altering the amount, stability, and age of carbon available for microbial decomposition, thereby influencing the amount of CO_2 released from soils to the atmosphere (Schuur et al., 2009, 2016; Trumbore, 2000, 2009). Among these disturbances, the effects of fire on soils vary according to fire characteristics such as intensity (energy released during combustion), severity (degree of ecological and soil alteration), and time since burning (time elapsed after fire occurrence) (Certini, 2005). Fire alters belowground carbon dynamics through the combustion and transformation of organic matter, changes in soil structure and microclimate, and shifts in microbial communities and decomposition pathways (Certini, 2005; DeBano et al., 1998; González-Pérez et al., 2004; Neary et al., 1999). Fire can also reduce vegetation inputs to soils through biomass mortality while generating pyrogenic and more recalcitrant forms of carbon from incomplete combustion, potentially altering the stability and turnover of soil carbon pools (Certini, 2005; González-Pérez et al., 2004). As a result, fire can produce contrasting effects on SOC persistence and turnover across ecosystems and post-fire recovery stages (Certini, 2005; Cui et al., 2014; Gui et al., 2023; Köster et al., 2024).

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These fire-induced changes in soil carbon dynamics are particularly relevant in mountain ecosystems, where soils represent major carbon reservoirs and low temperatures constrain decomposition and promote the long-term persistence of organic matter (Hagedorn et al., 2019; Ward et al., 2014). Mountain grasslands and shrublands contain an estimated 60.5–82.8 Pg C globally, of which approximately 98.1% is stored within the upper 1 m of soil (Ward et al., 2014). Elevational gradients can further influence soil carbon dynamics through associated changes in temperature, moisture, vegetation, and other soil-forming factors, which regulate carbon inputs, decomposition, and the persistence of organic matter (Trumbore, 2009). Consequently, carbon stocks and the age of stored carbon may vary substantially with elevation, with colder conditions at higher elevations generally favoring slower carbon turnover and the persistence of older carbon. Because these environmental controls operate over decadal to millennial timescales, radiocarbon provides a particularly useful tool for assessing how soil carbon dynamics vary across environmental gradients (Trumbore, 2009; Shi et al., 2020; Tashi et al., 2016).

Páramos are unique high-elevation tropical grassland ecosystems of the northern Andes, occurring between approximately 3,000 and 5,000 m a.s.l. (Hofstede et al., 2003; Luteyn, 1999). These ecosystems are characterized by low temperatures, frequent cloud immersion, and high humidity (Buytaert et al., 2011). Their soils store exceptionally large amounts of organic matter, with carbon densities exceeding 500–1,500 Mg C ha^{-1} in the upper meter (Hofstede et al., 2003; Hribljan et al., 2017). In these ecosystems, most carbon is stored belowground as soil organic matter (Alvarez-Yela et al., 2017). Although paramo soils are known to be rich in carbon and nitrogen (Chuncho Morocho and Chuncho, 2019; Vargas-Ríos et al., 2021), quantitative information on how fire influences the turnover and age of these carbon pools remains limited. Recent spatial estimates indicate that Colombian páramo soils store approximately 423 Tg C in the upper 40 cm, representing a critical climate mitigation opportunity that is often overlooked in favor of forest ecosystems (Benavides et al., 2026).

Recent regional assessments show that fire occurrence and burned areas exhibit heterogeneous spatiotemporal patterns across the tropical Andes, with shifting fire frequencies and extents linked to climatic and socio-environmental factors (Buytaert et al., 2011; Obando-Cabrera et al., 2025; Díaz-Timoté et al., 2026) In these high-elevation landscapes, fire acts as both a natural and anthropogenic disturbance (Díaz-Timoté et al., 2026; Keating, 2007). While several studies have documented that fire alters soil properties, organic matter, carbon and nitrogen contents, and soil respiration, these effects are often concentrated in the upper soil layers, where heating and combustion are most intense, potentially limiting short-term impacts on carbon stored at greater depths (Camargo García et al., 2012; Carrión-Paladines et al., 2023; Poulenard et al., 2001; Ramsay and Oxley, 1996). However, the magnitude and depth of fire effects depend on fire severity, soil moisture, and the amount and characteristics of soil organic matter, and organic-rich soils can experience substantial carbon losses under severe or prolonged burning (Carrión-Paladines et al., 2023; Xu et al., 2022; Certini, 2005; Neary et al., 1999), the magnitude and persistence of fire effects on paramo soil carbon remain difficult to predict. Moreover, most studies have

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focused on changes in carbon stocks or concentrations rather than on the turnover and age of SOC and the sources of carbon fueling post-fire respiration.

It remains unclear whether post-fire CO_2 emissions in páramos primarily reflect the rapid cycling of young carbon inputs or the mobilization of older, previously stabilized SOC pools, and how these processes vary along elevational gradients. Radiocarbon (^{14}C) measurements provide a powerful tool to differentiate between carbon stocks with contrasting turnover times and identify the sources of carbon fueling heterotrophic respiration in non–steady-state soil systems (Shi et al., 2020; Sierra et al., 2012, 2014, 2017; Trumbore, 2000, 2009). Furthermore, incubation-based approach combining bulk soil and respired CO_2 radiocarbon measurements highlight the value of explicitly comparing these diagnostics to detect decoupling between soil carbon stocks and microbial carbon use (Tangarife-Escobar et al., 2024a; Trumbore, 2000).

In this context, the aim of this study was to evaluate how soil carbon contents vary with fire occurrence and elevation in páramo grasslands, and to assess whether fire alters the source of carbon respired. We combined soil laboratory incubations, bulk SOC measurements, and radiocarbon analyses of both respired CO_2 and bulk soil across burned and unburned sites spanning an elevational gradient (3,300 to 3,700 m a.s.l.). Specifically, we hypothesize that (i) soil carbon becomes progressively older with increasing elevation, as colder conditions at higher elevations slow down decomposition and promote longer carbon ages; consistent with global temperature–SOC age relationships (Schuur et al., 2016; Shi et al., 2020); (ii) fire increases the relative contribution of older, previously stored carbon to SOC and heterotrophic respiration by disrupting soil carbon cycling and reducing the relative importance of recent carbon inputs; and (iii) fire effects are strongest in soil upper layers.

2. Methodology

2.1 Study area

The study area is located in the department of Boyacá, Colombia, in the Tota–Bijagual–Mamapacha páramo complex (72° 46′ 48″ W, 5° 38′ 24″ N) (Figure 1). This site was selected based on its history of frequent fire occurrence and its classification among the ten páramo units with the largest burned area reported between 2000 and 2022 (Díaz-Timoté et al., 2026). Fire occurrence and burned-area histories were identified using the páramo satellite-derived burned-area database developed by Obando-Cabrera et al. (2025). Sites classified as unburned correspond to areas without detected fire occurrence since 1985, the beginning of the available satellite record. The study area also includes a large fire that occurred near the Siscunsí lagoon in February 2024, providing an opportunity to collect soil samples shortly after disturbance.

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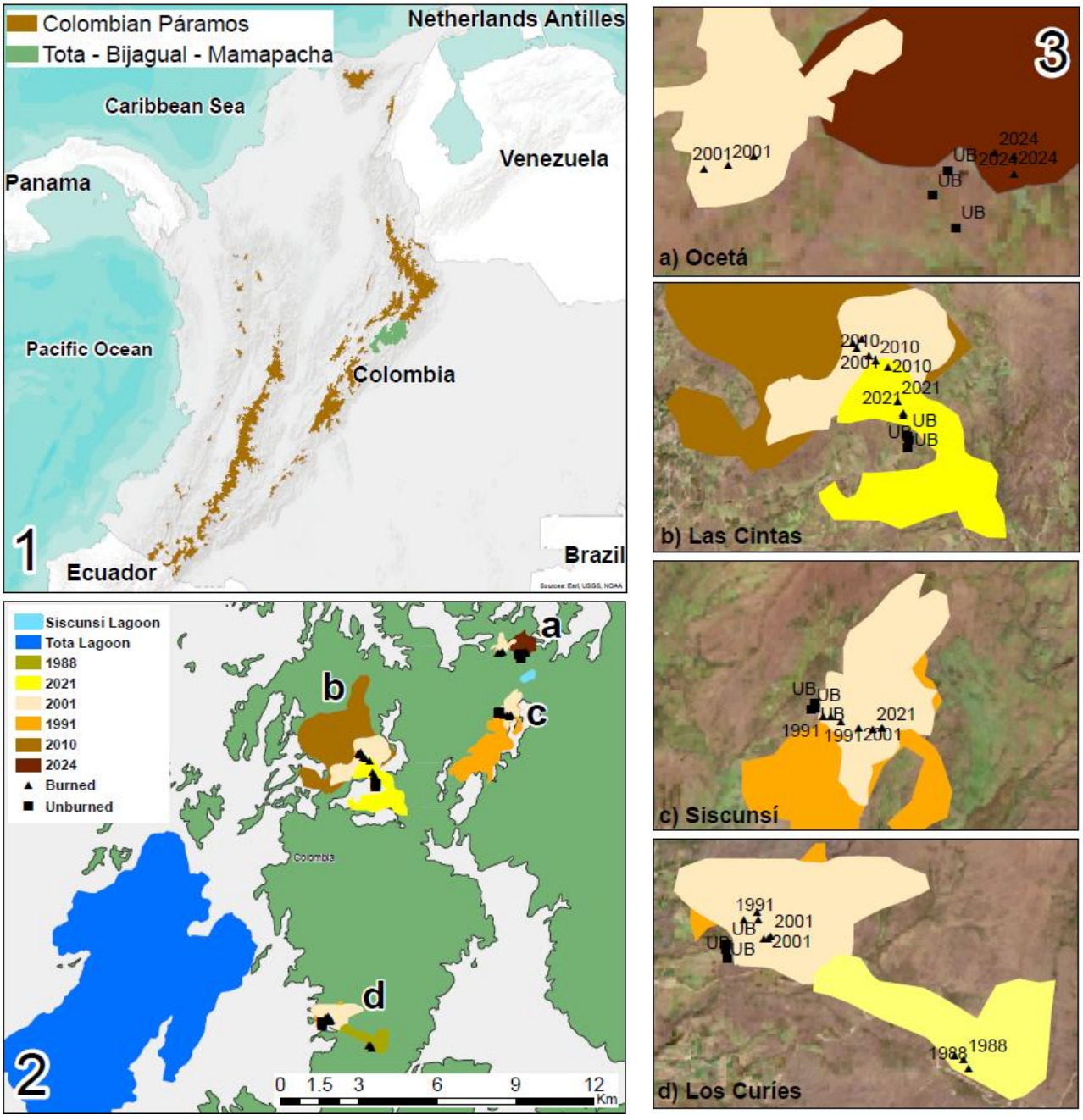


Figure 1. Location of the study area and soil sampling sites in the Tota–Bijagual–Mamapacha páramo complex, Boyacá, Colombia. Panel 1 shows the distribution of Colombian páramos and the location of the Tota–Bijagual–Mamapacha páramo complex (green; base map: Esri, Maxar, Earthstar Geographics, and the GIS User Community | Powered by Esri), which is enlarged in Panel 2. Panel 2 shows the location of the four sampling localities: (a) Ocetá, (b) Las Cintas, (c) Siscunsí, and (d) Los Curies, as well as the spatial distribution of areas affected by fires in different years. Panel 3 provides detailed views of each locality based on Landsat 8 satellite imagery acquired via USGS GloVis (data courtesy of the U.S. Geological Survey); squares indicate unburned (UB) sampling sites. All spatial datasets were processed, analyzed, and composed into the final figure layout by the authors.

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2.2 Sampling

We sampled a fire chrono-sequence in 2024, across three elevations (3,300, 3,500, and 3,700 m a.s.l.). Sampling was conducted in four areas: Ocetá, Siscunsí, Las Cintas, and Los Curíes (Figure 1). The sampling design included 20 × 20 m plots representing fire events in 1988, 1991, 2001, 2010, 2021, and 2024 and unburned conditions. Unburned sites were
140 defined as areas with no recorded fire since 1984 and were located within 50 or 100 m of the corresponding burned areas.

Three plots were established within each burn patch for bulk soil analysis, where the spatial extent of the burned area and terrain accessibility permitted. Within each plot, soil was sampled at three depths (10, 20, and 30 cm). At each depth, four soil subsamples were collected from fixed locations halfway between the plot center and the midpoint of each side and
145 combined into one composite sample of approximately 300 g per plot and depth. Each composite sample was homogenized and subsequently divided into subsamples for the determination of carbon contents and bulk soil radiocarbon ($\Delta^{14}C$).

Because unburned conditions provided a larger number of available composite samples than burned conditions, a random subsampling procedure was used to obtain a comparable representation of burned and unburned soils in the bulk soil
150 analyses. At each elevation, composite samples from unburned plots were randomly selected based on the number of samples available from the corresponding burned conditions, resulting in similar, although not necessarily identical, sample sizes between burned and unburned soils. A total of 152 samples were analyzed to determine carbon, and $\Delta^{14}C$. Table 1 summarizes the distribution of samples across elevations, sampling areas, fire-history categories, plots, and soil depths.

155 For the incubation experiment, fresh soil samples were collected exclusively from Ocetá (Figure 1). This sampling area provided a recent fire from 2024 together with nearby plots representing a previous fire (2001) and unburned conditions, allowing three contrasting fire histories to be compared within the same area. The use of freshly collected soil ensured preservation of the microbial activity required for the assessment of heterotrophic respiration. Three plots were sampled per fire-history category, yielding nine plots. Within each plot, four soil cores were collected from the upper 5 cm of the soil
160 profile and combined into one composite sample of approximately 500 g, resulting in nine composite samples.

Each composite sample was incubated in triplicate, resulting in 27 initial incubations. Some replicates did not yield usable radiocarbon measurements due to failures during AMS measurement. Consequently, a total of 25 successful $\Delta^{14}CO_2$ measurements were obtained, ranging from 2 to 3 measurements per plot. Replicate measurements from the same composite
165 soil sample were treated as technical replicates and averaged at the plot level prior to statistical analyses, with plot considered as the independent experimental unit.

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Table 1. Distribution of soil samples by altitude, locality, fire history (year of last fire or unburned condition), sampling plots, and soil depth. The samples marked with an asterisk (*) were used in the incubation experiment too. No burned (NB)

Altitude (m)	Locality	Year	Depth (cm)	Total samples
3300	Curies	NB	10, 20, 30	25
		1991	10, 20, 30	24
		2001	10, 20, 30	
3500	Las Cintas	NB	10, 20, 30	22
	Curies	1988	10, 20, 30	24
	Las cintas	2021	10, 20, 30	
3700	Siscunsi	NB*	10, 20, 30	27
	Las cintas	2010	10, 20, 30	30
	Siscunsi	2001*	10	
		2024*	10	
Total	**152**			

2.3 Laboratory analysis and radiocarbon measurements

All soil samples were processed following standardized protocols to ensure consistency among laboratory analyses and to prevent isotopic contamination (protocols available at https://github.com/MPIBGC-TEE/persam). Samples were oven-dried

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at 40 °C and subsequently sieved through a 2 mm mesh to remove roots and stones. All samples were then finely ground and homogenized prior to subsequent bulk soil analyses and incubation.

A subsample of the ground bulk soil was used to determine absolute dry mass and was subsequently analyzed for total carbon concentration using elemental analysis (Börnert et al., 2024). The resulting carbon concentrations were used to determine the appropriate amount of material required for subsequent radiocarbon analysis. Another subsample of the homogenized soil was then prepared for the determination of bulk soil Δ14C following the protocol described by Steinhof (2024). For the incubation experiment, the maximum water-holding capacity (WHCmax) was determined for a subsample of each dried and ground composite soil sample (Heublein, 2016). Soil moisture was subsequently adjusted to 60% WHCmax to establish standardized moisture with aerated conditions suitable for microbial respiration, avoiding water saturation and oxygen limitation. Soil subsamples (15 ± 0.5 g) were incubated at 10 °C, corresponding to mean soil temperatures reported for paramo ecosystems (Podwojewski and Poulenard, 2004; Cuesta et al., 2023).

During incubation, CO_2 concentrations in the headspace were monitored periodically until sufficient CO_2 had accumulated for radiocarbon analysis (~1 mg C). On average, this threshold was reached after three days of incubation. Once reached, CO_2 was extracted from each incubation jar and prepared for analysis (Steinhof et al., 2024). Both, bulk soil samples and incubation-derived CO_2 were analyzed for radiocarbon content using a MICADAS accelerator mass spectrometer (Ionplus, Switzerland) at the radiocarbon laboratory of the Max Planck Institute for Biogeochemistry in Jena, Germany. The resulting measurements represented the radiocarbon signatures of bulk SOC ($\Delta^{14}C$) and heterotrophically respired carbon ($\Delta^{14}CO_2$).

2.4 Data analysis

2.4.1 Statistical data analysis

Prior to statistical testing, data distributions were assessed using visual inspection through histograms and Q–Q plots, and formal normality tests (Shapiro–Wilk). When assumptions of normality and homoscedasticity were met, differences among fire-history categories at each depth were evaluated using one-way analysis of variance (ANOVA). When these assumptions were violated, the non-parametric Kruskal–Wallis test was applied. Statistical significance was assessed at $\alpha = 0.05$. Data distributions and group-level contrasts were visualized using boxplots.

Bulk-soil $\Delta^{14}C$ and the $\Delta^{14}C$ of CO_2 produced during the incubation experiment were analyzed separately because they provide complementary information on soil carbon dynamics. Bulk-soil $\Delta^{14}C$ represents the integrated radiocarbon signature of accumulated over a range of ages, whereas $\Delta^{14}CO_2$ reflects the radiocarbon signature of the carbon substrates mineralized during heterotrophic respiration. Therefore, $\Delta^{14}CO_2$ provides information on the time elapsed since that carbon was fixed from the atmosphere. Radiocarbon values were interpreted in relation to the atmospheric bomb-14C record (Hua et al.,

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2022). Positive Δ14C values indicate the incorporation of bomb-derived radiocarbon introduced into the atmosphere by thermonuclear weapons testing during the late 1950s and early 1960s, whereas negative values generally indicate a greater contribution of older, pre-bomb carbon. Values approaching contemporary atmospheric Δ14C levels at the time of sampling (2024) indicate a stronger contribution of recently assimilated carbon. Because paramo soils act as open systems with continuous carbon inputs and losses, identifying the exact position of a sample on the atmospheric bomb curve is challenging due to isotopic ambiguity (i.e., a single Δ14C value may correspond to multiple dates). Consequently, rather than applying exact age models, the interpretation of recent versus older carbon sources was constrained contextually using soil depth, if the uppermost layer (10 cm) is dominated by more recent, actively cycling carbon compared to deeper (Trumbore, 2009; Feyissa et al., 2023).

2.4.2 Effects of fire history, altitude, and soil depth on bulk soil $\Delta^{14}C$

To evaluate the combined effects of fire history, altitude, and soil depth on bulk soil $\Delta^{14}C$, a linear mixed-effects model (LMM) was fitted. Fire history was represented by the time elapsed since the last fire event relative to the sampling year (2024), where burned sites corresponded to the known fire years (1988, 1991, 2001, 2010, 2021, and 2024). Unburned sites, which had no recorded fire events since at least 1985, were assigned a baseline time-since-fire value representing undisturbed conditions (≥39 years). The model accounted for the hierarchical structure of the dataset by including plot identity as a random intercept. The model is expressed as follows:

$$\Delta^{14}C_{ij} = \beta_0 + \beta_1(\text{FireHistory})_{ij} + \beta_2(\text{Altitude})_{ij} + \beta_3(\text{Depth})_{ij} + b_j + \varepsilon_{ij}$$

where $\Delta^{14}C_{ij}$ represents the bulk soil radiocarbon value for measurement i in plot j; β_0 is the fixed intercept; β_1, β_2, and β_3 are the fixed-effect slope coefficients associated with fire history, altitude, and soil depth, respectively; b_j is the random intercept for plot j ($b_j \sim \mathcal{N}(0, \sigma_b^2)$); and ε_{ij} is the residual error term ($\varepsilon_{ij} \sim \mathcal{N}(0, \sigma^2)$). Model assumptions of residual normality and homoscedasticity were verified using quantile–quantile plots and residual-versus-fitted plots. The statistical significance of fixed effects was evaluated using t-tests derived from the fitted model.

2.4.4 Comparison between respired CO_2 and bulk soil carbon

To assess the relationship between the radiocarbon signature of carbon mineralized during microbial respiration and that of bulk soil organic carbon, $\Delta^{14}CO_2$ values were compared directly with the corresponding bulk soil $\Delta^{14}C$ values. Values were plotted against a 1:1 line, representing equal radiocarbon signatures in respired CO_2 and bulk soil carbon; deviations from this line were interpreted as radiocarbon disequilibrium between the bulk carbon pool and the substrate for microbial activity

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(Bolin and Rodhe, 1973). Because the relationship between $\Delta^{14}C$ and carbon age is not strictly linear for post-bomb carbon, these differences were interpreted in the context of the atmospheric bomb-^{14}C record following Trumbore (2000).

All statistical analyses and visualizations were performed using R (version 4.5.2). Linear mixed-effects models were fitted using the *lme4* package, maps and spatial layouts were generated using ArcGIS Pro (version 3.7.2, Esri Inc.), and figures were produced using *ggplot2*.

3.Results

3.1 Bulk soil carbon across fire history and depth

Bulk soil carbon content decreased markedly with increasing soil depth across all elevations (3300, 3500, and 3700 m a.s.l.) and fire-history conditions (Figure 2). Differences in soil carbon between burned and unburned sites were most pronounced in the surface horizon (10 cm), where carbon content was significantly higher in burned soils than in unburned baseline soils ($p = 0.043$). At 30 cm depth, a significant difference between fire conditions was also detected ($p = 0.010$), primarily driven by higher values in burned plots at lower to mid-elevations (3300 and 3500 m a.s.l.). In contrast, no significant differences in soil carbon were observed between burned and unburned soils at intermediate depths (20 cm across all elevations) or at the highest elevation (3700 m a.s.l.) at 30 cm depth ($p > 0.05$).

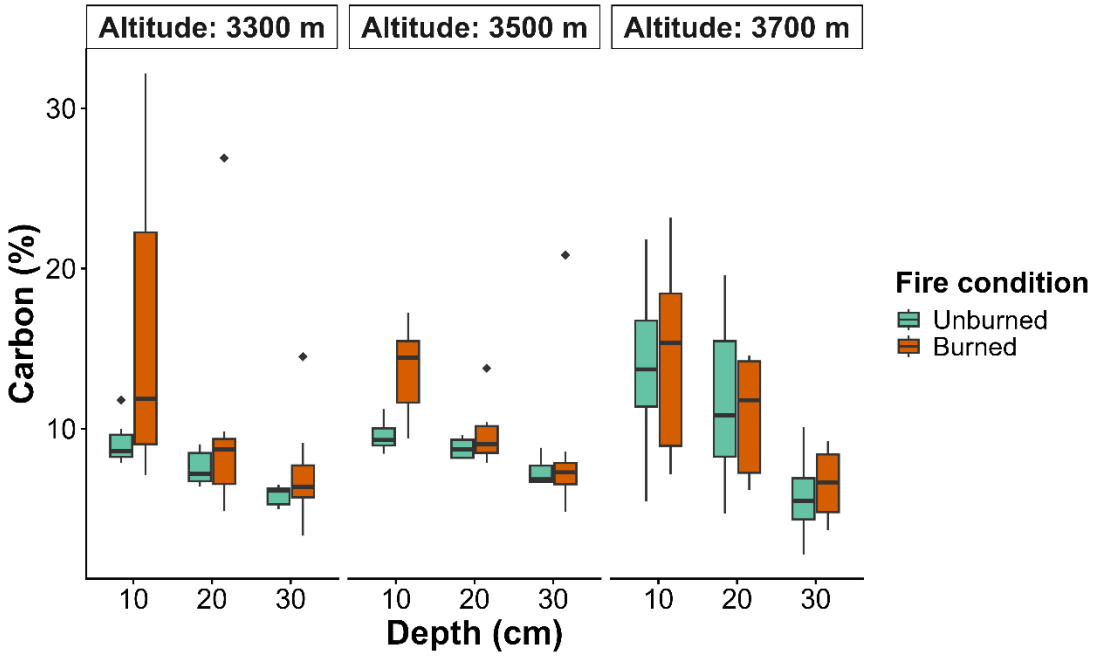


Figure 2 Bulk soil C across three elevations (panels), soil depths (horizontal axis), and fire conditions (color boxes).

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3.2 Radiocarbon in bulk soil

Across the entire dataset, bulk soil $\Delta^{14}C$ values ranged from -473.80 ‰ to $+64.90$ ‰ (mean: -133.94 ± 102.51 ‰). Despite this broad range, values were predominantly negative across elevations, soil depths, and fire histories (Figure 3). At 10 cm depth, group values remained centered below 0 ‰ at all elevations, although individual positive $\Delta^{14}C$ values occurred at 3,300 m, reflecting the presence of bomb-derived radiocarbon in some surface samples without implying a specific single deposition date. No comparable positive values were observed at 3,500 or 3,700 m. The spread of $\Delta^{14}C$ values also varied among elevation–depth combinations, with particularly wide interquartile distributions observed in the surface soils (10 cm) at 3,300 m, and in the deepest soils (30 cm) at 3,700 m, which reached the most depleted signatures (down to -473.80 ‰).

Bulk soil $\Delta^{14}C$ decreased significantly with increasing soil depth. The linear mixed-effects model indicated a decrease of 8.87 ‰ in $\Delta^{14}C$ for each centimeter of depth increment ($\beta = -8.87 \pm 0.65$, $t = -13.74$, $p < 0.001$), consistent with progressively lower radiocarbon signatures in deeper soil layers. This pattern was evident across the three elevations, although the magnitude and variability of $\Delta^{14}C$ differed among specific elevation–depth combinations; for instance, residual variability expanded dramatically in the deepest horizons at 3,700 m. Altitude also had a significant negative effect on bulk soil $\Delta^{14}C$ ($\beta = -0.200 \pm 0.032$ ‰ m^{-1}, $t = -6.16$, $p < 0.001$). Thus, after accounting for soil depth and fire history, $\Delta^{14}C$ decreased by approximately 20 ‰ for every 100 m increase in elevation. However, this overall modelled trend did not imply that every individual observation at lower elevations had a higher $\Delta^{14}C$ value than observations at higher elevations; for example, the 3,300 m sites included both strongly negative values and the only positive values observed in the dataset.

Finally, fire-history was positively associated with bulk soil $\Delta^{14}C$ ($\beta = 1.16 \pm 0.38$ ‰ yr^{-1}, $t = 3.03$, $p < 0.01$), indicating that more recent recorded fire years were associated with higher $\Delta^{14}C$ values after accounting for altitude and depth. Descriptively, as visualized in the overall group contrasts (Figure 3), unburned baseline soils generally showed more negative $\Delta^{14}C$ values than soils recovering from more recent fire histories.

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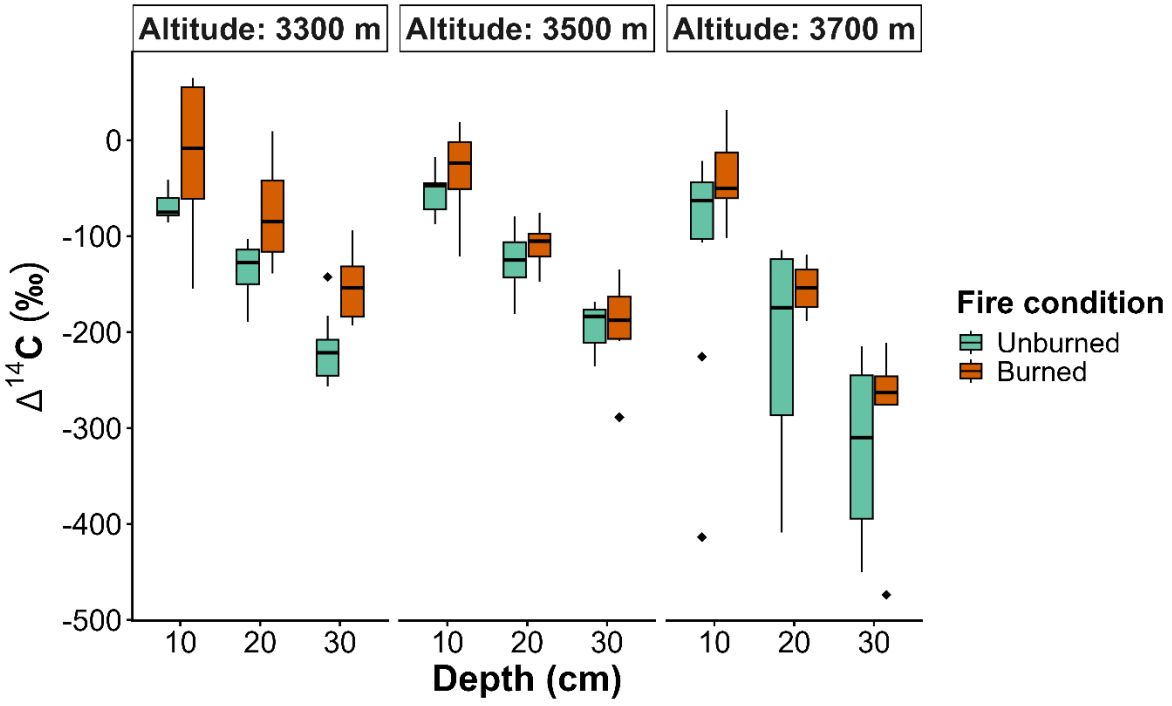


Figure 3. Bulk soil $\Delta^{14}C$ across elevations (panels), soil depths (horizontal axis), and fire conditions (color boxes).

3.3 Radiocarbon signature of heterotrophic respiration

Across all fire-history categories, $\Delta^{14}CO_2$ values from incubated soils were positive (ranging from +3.9 to +75.7 ‰) and within the post-bomb range, indicating a substantial contribution of recently fixed, bomb-derived carbon to heterotrophic respiration (Figure 4). Values showed substantial overlap among unburned, previously burned (2001), and recently burned (2024) soils. Descriptively, mean $\Delta^{14}CO_2$ values tended to be higher in previously burned (47.69 ± 14.74 ‰) and recently burned soils (44.46 ± 21.64 ‰) compared to unburned baseline soils (41.53 ± 7.78 ‰), although these mean differences among fire-history categories were not statistically significant (ANOVA, $p = 0.82$). Recently burned soils also exhibited the widest descriptive spread of $\Delta^{14}CO_2$ values (standard deviation: 21.64 ‰), followed by previously burned (14.74 ‰) and unburned soils (7.78 ‰); however, this apparent difference in variability did not represent a statistically significant shift in dispersion among groups.

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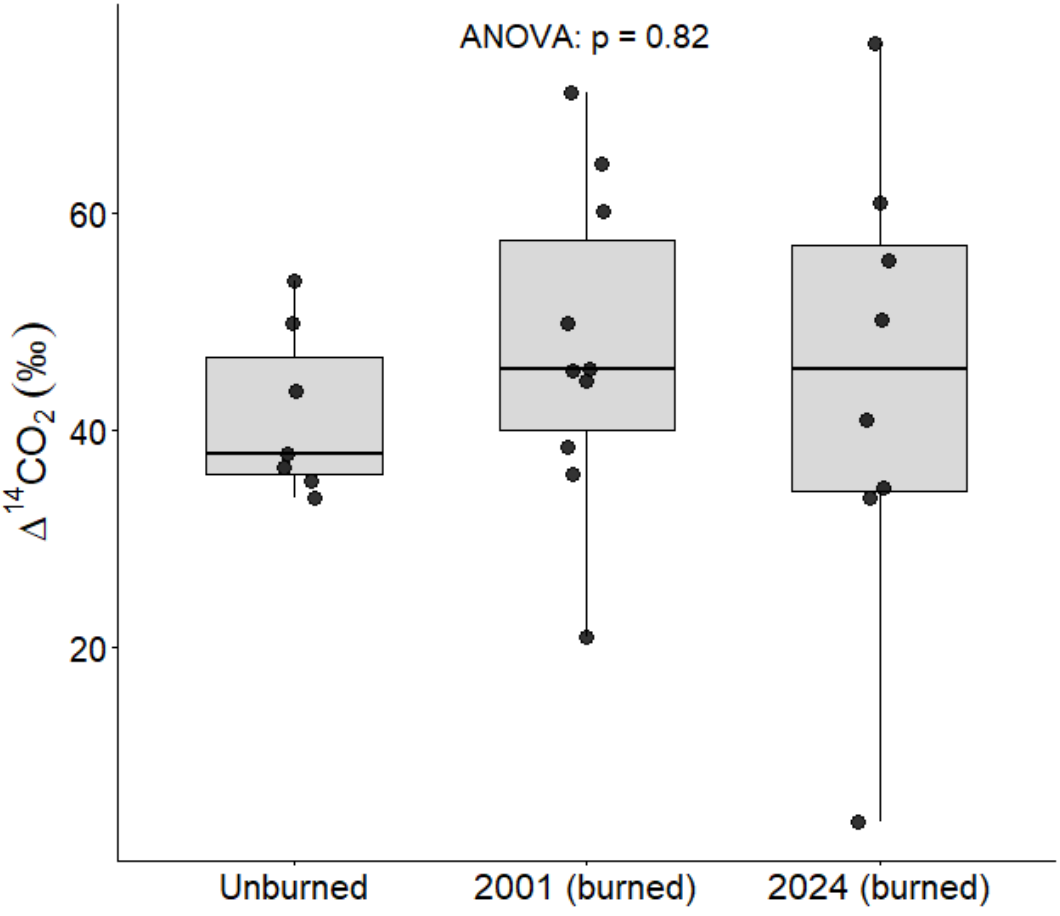


Figure 4. Boxplots of $\Delta^{14}CO_2$ values from heterotrophic soil respiration across fire-history categories (unburned baseline, previously burned in 2001, and recently burned in 2024). Soil incubations were conducted using samples collected in 2024. Neither global nor pairwise differences among fire-history groups were statistically significant (ANOVA, $p = 0.82; Tukey's HSD, p > 0.05).

3.4 Comparison between radiocarbon in respired CO_2 and bulk soil

At the plot level, the radiocarbon signature of heterotrophically respired CO_2 was consistently higher than the corresponding bulk soil $\Delta^{14}C$ signature (Figure 5). Plot-level mean $\Delta^{14}CO_2$ values were used for this comparison to account for replicate incubations originating from the same composite soil sample. All observations fell above the 1:1 line, indicating that respired CO_2 was enriched in ^{14}C relative to bulk soil organic carbon. Notably, some burned plots, particularly those affected by the 2001 fire events, were located closer to the 1:1 line than the unburned plots, although this proximity was not uniform across all burned sites. Overall, the radiocarbon disequilibrium between bulk soil and respired CO_2 indicates that microbial respiration draws disproportionately on a more ^{14}C-enriched component of the soil carbon pool.

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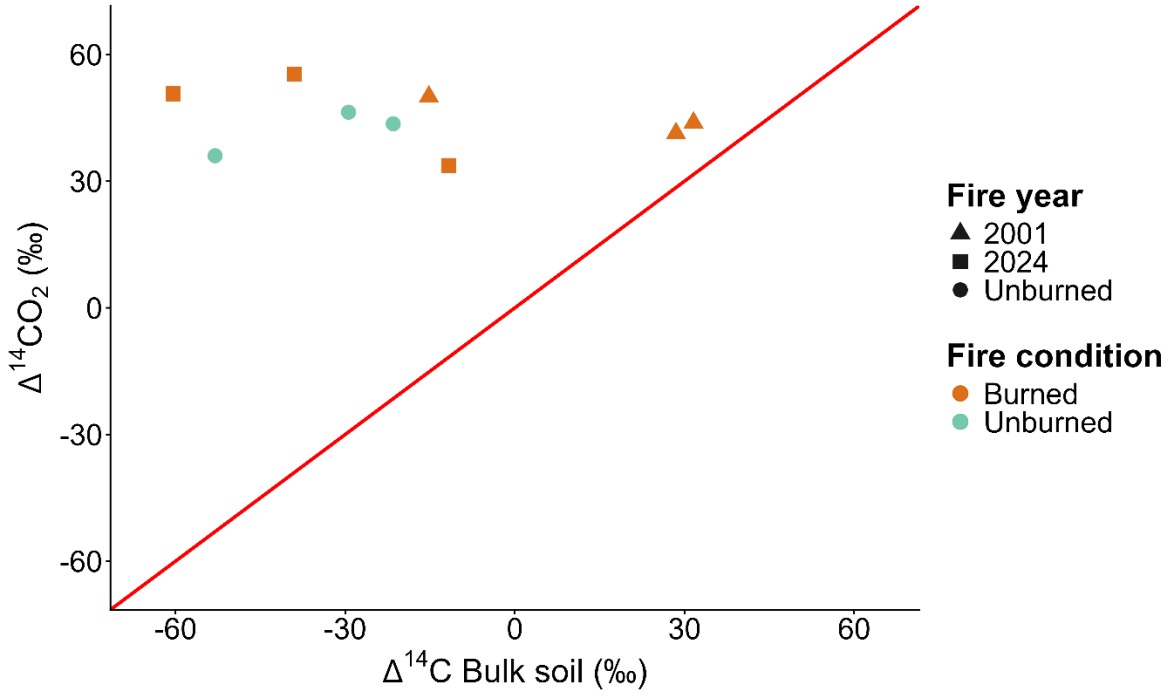


Figure 5. Relationship between the radiocarbon signature of heterotrophically respired CO_2 ($\Delta^{14}CO_2$) and bulk SOC($\Delta^{14}C$) in burned and unburned sites. The red line represents the 1:1 relationship, where respired CO_2 and bulk soil carbon have equal $\Delta^{14}C$ values. Points above the line indicate higher $\Delta^{14}C$ in respired CO_2 relative to the corresponding bulk soil carbon.

4. Discussion

4.1 Fire effects on soil carbon stocks in páramo soils

The clearest pattern observed across the study sites was the strong vertical stratification of soil carbon, with higher concentrations in surface soils and progressively lower values with depth (Figure 2). This pattern is consistent with the concentration of litter and root-derived organic inputs near the soil surface, together with decreasing organic matter inputs and limited downward transport into deeper soil horizons (Xu et al., 2022; Trumbore, 2000, 2009). Burned soils showed higher total organic carbon concentrations than unburned soils, particularly in the upper 10 cm (Figure 2). Although fire is often regarded primarily as a driver of degradation in páramo ecosystems, it has also been part of their long-term ecological and socioecological history through both natural and anthropogenic processes, and its effects on soil carbon cycling may therefore vary depending on fire characteristics, environmental conditions, and post-fire recovery stage (Díaz-Timoté et al., 2026; Keating, 2007). While chronic disturbances such as overgrazing and intensive agriculture drastically reduce soil organic carbon reserves in páramo landscapes (Benavides et al., 2026), our results suggest that fire, by itself, introduces pulses of recent carbon without necessarily triggering a massive destabilization of ancient deposits. Similar responses have been reported following low-severity fire in Andean páramo ecosystems, where changes in soil organic matter and soil

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organic carbon were concentrated in surface soils (Carrión-Paladines et al., 2023). Although fire can result in carbon losses through combustion, these losses may be limited in páramo soils when high soil moisture and cool environmental conditions restrict heat penetration and the combustion of belowground organic matter (Carrión-Paladines et al., 2023; Vargas Ríos, 2000). Under these conditions, subsequent inputs of organic material may partly compensate for initial carbon losses (Agbeshie et al., 2022; Camargo García et al., 2012; Poulenard et al., 2001).

Several non-mutually exclusive mechanisms may contribute to the higher carbon concentrations observed in burned surface soils. Post-fire regeneration of grasses and rosette plants can provide new belowground organic inputs (Carrión-Paladines et al., 2023; Neary et al., 1999; Suárez R. and Medina, 2001), while root mortality and turnover following disturbance can also contribute organic material to the soil. In addition, incomplete combustion may leave dead above- and belowground plant material in situ, which can subsequently be incorporated into surface soil organic matter (Carrión-Paladines et al., 2023; Neary et al., 1999). Fire can also generate pyrogenic carbon, including charred organic material, which may contribute to the increased concentrations and persistence of carbon in burned soils (Certini, 2005; González-Pérez et al., 2004).

In Colombian páramo grasslands, root biomass decreases markedly with depth, with a substantial proportion of belowground biomass concentrated in the upper soil layers (Hofstede and Rossenaar, 1995). This shallow distribution of root-derived inputs, together with the incorporation of fire-killed plant material, may therefore contribute to the stronger differences in carbon observed at 10 cm between burned and unburned soils (Figure 2). The incorporation and subsequent microbial processing of this organic material could contribute to parallel changes in soil carbon concentrations during post-fire recovery (Agbeshie et al., 2022; Czimczik et al., 2006; Beltrán Pineda and Lizarazo-Forero, 2014; Gui et al., 2023; Neary et al., 1999).

4.2 Bulk soil radiocarbon across elevation, depth, and fire history

Bulk soil $\Delta^{14}C$ declined significantly with increasing soil depth and elevation (Figure 4; and linear mixed-effects model), indicating a progressively greater contribution of older carbon in deeper horizons and at higher elevations. The negative relationship with depth is consistent with the concentration of more recent plant-derived carbon near the soil surface and the longer persistence of carbon in deeper horizons. Similarly, the decline in $\Delta^{14}C$ with elevation supports our hypothesis that colder conditions at higher elevations constrain decomposition and favor longer carbon ages (Schuur et al., 2016; Shi et al., 2020). Our finding of older carbon at higher altitudes complements recent regional patterns showing how cold climates restrict decomposition rates and shape carbon density in the Colombian Andes (Benavides et al., 2026). Together, these results suggest that the persistence of carbon stored in high-elevation soils is closely linked to environmental controls on decomposition and may therefore be sensitive to climate warming. This sensitivity is particularly relevant in the tropical

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Andes, where climate projections indicate elevation-dependent changes in temperature, including enhanced warming of maximum temperatures at higher elevations (Toledo et al., 2022). Such warming could accelerate microbial decomposition and increase the mobilization of previously stored soil carbon (Schuur et al., 2016; Shi et al., 2020).

Fire history also significantly influenced bulk soil $\Delta^{14}C$ (Figure 4), with more recent fire years associated with higher, generally less negative, $\Delta^{14}C$ values after accounting for altitude and soil depth. Importantly, this pattern should not be interpreted as evidence of post-bomb carbon throughout burned soils. Positive $\Delta^{14}C$ values occurred only in some samples at 3,300 m, whereas burned soils at 3,500 and 3,700 m remained below zero. Rather, the overall shift toward higher $\Delta^{14}C$ values suggest a greater relative contribution of more recently fixed carbon to the bulk soil pool following fire. Recently assimilated plant biomass reflected the atmospheric radiocarbon conditions under which the carbon was fixed, and its incorporation into soil organic matter can shift bulk-soil $\Delta^{14}C$ toward more modern values, although the magnitude of this shift depends on its mixing with older soil carbon (Schuur et al., 2016; Tangarife-Escobar et al., 2024a).

Several non-mutually exclusive mechanisms may explain this pattern. Because combustion is incomplete, a portion of the above- and belowground biomass killed by fire may remain in situ rather than being fully oxidized to CO_2, thereby transferring carbon assimilated during the years preceding the fire into the soil organic matter pool. In addition, subsequent vegetation recovery, root growth, root mortality, and turnover may provide further inputs of recently fixed carbon. This interpretation is consistent with the higher carbon concentrations observed in burned surface soils (Figure 3). These processes provide a plausible explanation for the association between more recent fire histories and higher bulk-soil $\Delta^{14}C$ values, including effects detectable below the surface horizon (Carrión-Paladines et al., 2023).

4.3 Sources of post-fire soil respiration: evidence from $\Delta^{14}CO_2$

The radiocarbon signature of heterotrophic respiration ($\Delta^{14}CO_2$) consistently indicated a substantial contribution of post-bomb carbon across all fire-history categories (Figure 5). Respired CO_2 was more ^{14}C-enriched than the corresponding bulk soil carbon pool, indicating that microbial respiration drew disproportionately on a different and more recently cycling component of soil carbon (Hua et al., 2022; Trumbore, 2000). Differences among unburned soils and soils burned in 2001 and 2024 were not statistically significant, although burned soils tended to exhibit higher $\Delta^{14}CO_2$ values. Within the bomb-^{14}C framework, however, higher positive $\Delta^{14}CO_2$ values should not be interpreted directly as younger carbon, because they may reflect carbon fixed during earlier decades when atmospheric $\Delta^{14}C$ was elevated (Hua et al., 2022). Importantly, the post-bomb signature of respired CO_2 suggests that substantially older soil carbon did not become a dominant source of microbial respiration following fire, although the available data do not allow this possibility to be excluded entirely. Rather, respiration across all fire histories was supported by carbon carrying a relatively recent atmospheric radiocarbon signature. This interpretation is consistent with the availability of plant-derived substrates associated with vegetation recovery, root

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production and turnover, and the decomposition of fire-killed plant tissues. Previous radiocarbon studies have similarly shown that carbon contributing to soil respiration can be substantially younger than the mean age of bulk soil organic matter because decomposition is weighed toward faster-cycling components of the soil carbon pool (Tangarife-Escobar et al., 2024b; Trumbore, 2000). Similar responses following fire have been reported in other ecosystems, where effects on soil respiration depend on fire severity and ecosystem characteristics and do not necessarily involve increased mineralization of old soil carbon pools (Gui et al., 2023; Xu et al., 2022; Zhou et al., 2023).

The absence of a clear old-carbon signal in heterotrophic respiration may also be related to the physical characteristics of páramo soils. Their high moisture content can limit heat penetration into deeper soil horizons during fire, reducing direct thermal alteration of older carbon stored below the surface (Carrión-Paladines et al., 2023). Together with the predominance of post-bomb carbon in respired CO_2, this suggests that fire in this system primarily affects relatively recent and surface-associated carbon dynamics rather than causing widespread mobilization of long-stabilized soil carbon.

4.4 Decoupling between bulk soil and respired carbon radiocarbon signatures

The radiocarbon disequilibrium between bulk SOC and heterotrophically respired CO_2 indicates that the radiocarbon signature of stored soil carbon does not directly represent the carbon that is actively mineralized by microorganisms. Across all study plots, respired CO_2 was consistently enriched in ^{14}C relative to the bulk soil, demonstrating that microbial communities preferentially mineralize more recent, accessible carbon sources. Bulk soil $\Delta^{14}C$ integrates organic matter with a wide range of ages and degrees of stability whereas respiration is heavily weighted toward these young, easily decomposable carbon substrates. Consequently, soils containing predominantly older bulk carbon can simultaneously support respiration derived from substantially more recent carbon sources (Tangarife-Escobar et al., 2024b; Trumbore, 2000).

Fire, and the subsequent post-fire vegetation recovery, alter the underlying mechanisms driving this disequilibrium. In recently burned plots (2024), fire causes extensive mortality of aboveground biomass and shallow roots without completely combusting them. This generates a sudden pulse of fresh, modern necromass. Microbial communities rapidly exploit this highly accessible, newly dead material, maintaining a highly modern respiratory signature despite the bulk soil remaining dominated by the historically accumulated ancient carbon pool. Conversely, over more than two decades of post-fire recovery (as seen in the 2001 plots), the isotopic disequilibrium is visibly reduced, and these plots plot closer to the 1:1 line (Figure 5). This convergence occurs because the continuous input of ^{14}C-enriched root material and litter from regenerating vegetation becomes integrated into the bulk soil pool, shifting its overall signature toward more modern values. In unburned sites, however, modern carbon inputs from continuous vegetation growth represent a proportionally smaller fraction of the ancient carbon pool, maintaining a highly negative bulk signature and a larger isotopic disequilibrium.

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Taken together, these results demonstrate that fire does not significantly alter the biological mineralization of ancient carbon in these páramo soils. Regardless of fire history, microbial communities consistently respire carbon that is newer than the bulk soil average (ANOVA, $p = 0.82$), indicating a strict preference for modern, recently fixed carbon sources. Fire does not force microbes to shift their preference toward old, recalcitrant carbon, nor does it trigger a biological destabilization of ancient carbon reserves. Instead, the immediate post-fire stage provides fresh necromass for decomposition, while long-term post-fire recovery gradually modernizes the bulk soil pool through new carbon inputs. This dynamic narrows the isotopic gap between total stored carbon and the actively mineralized fraction, confirming that the ancient carbon pool remains functionally decoupled from heterotrophic respiration.

4.5 Implications and limitations for carbon–fire dynamics in páramo soils

Our results suggest that individual fire events do not necessarily lead to an immediate, dominant mobilization of older soil carbon in páramo ecosystems, even though these massive, long-term carbon stocks are often considered vulnerable to disturbance (Camargo García et al., 2012; Schuur et al., 2016). The post-bomb radiocarbon signature of heterotrophically respired CO_2 indicates that relatively recent carbon made a substantial contribution to soil respiration following fire. However, because $\Delta^{14}CO_2$ represents an integrated signal from substrates with potentially different ages, these results do not exclude some contribution of older carbon to respiration; rather, they indicate that older carbon did not dominate the measured radiocarbon signal. This distinction is important when evaluating carbon–fire feedback, as changes in the radiocarbon composition of bulk soil do not necessarily translate into proportional changes in the carbon being actively mineralized (Czimczik et al., 2006). At longer timescales, repeated fires could nevertheless alter vegetation structure, root dynamics, microbial communities, and the balance between carbon inputs and losses, potentially modifying the composition and persistence of soil organic matter (Agbeshie et al., 2022; Cheng et al., 2025). Increased inputs of recently fixed carbon following disturbance could also partially obscure longer-term changes in older, more persistent components of the soil carbon pool (Shi et al., 2020). The inclusion of páramo soils in climate mitigation mechanisms requires a profound understanding of their resilience to disturbances and clear management baselines (Benavides et al., 2026). Our isotopic findings provide the necessary mechanistic evidence to address this gap, demonstrating that under typical fire regimes, historically deep carbon sinks remain functionally decoupled and stable.

Several limitations should be considered when interpreting these findings. First, the incubation experiment was restricted to the Ocetá sampling area and included three contrasting fire-history categories (unburned, 2001, and 2024), limiting the extent to which respiration responses can be generalized across the full elevational and spatial range represented by the bulk-soil dataset. Second, incubations were conducted under standardized temperature and moisture conditions selected to

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represent typical páramo soil conditions. This experimental design facilitated comparison among fire histories by minimizing environmental variability, but it does not capture temporal fluctuations in temperature and soil moisture or other field conditions that may influence heterotrophic respiration in situ. Third, radiocarbon measurements integrate carbon substrates with different ages and cannot, without additional modelling, be translated into a unique carbon age or transit time. Finally, the chrono-sequence approach relies on the most recent recorded fire and on unburned sites defined by the absence of recorded fire since 1985; consequently, earlier or undocumented fire events may contribute to the observed variability. These limitations highlight the need for longer-term and spatially replicated studies combining radiocarbon measurements within situ respiration, repeated-fire histories, and additional constraints on carbon age distributions to better assess how fire affects long-term carbon persistence in páramo soils.

5. Conclusions

Our results support the hypothesis that soil carbon becomes progressively older with increasing elevation, consistent with greater carbon persistence under the colder conditions of high-elevation páramo soils. Strong declines in $\Delta^{14}C$ with depth and elevation revealed the persistence of older carbon pools in deeper soils and at higher elevations, highlighting the importance of environmental controls on long-term carbon storage and persistence.

In contrast, our hypothesis that fire would increase the contribution of older, previously stored carbon to heterotrophic respiration was not supported. Although fire history was associated with shifts in bulk-soil radiocarbon signatures, respired CO_2 retained a predominantly post-bomb signature across fire histories, providing no evidence that older carbon became a dominant source for microbial respiration after fire. Instead, the contrasting radiocarbon signatures of bulk soil and respired CO_2 indicate that fire can modify the composition of stored soil carbon without producing an equivalent shift in the carbon actively mineralized by microorganisms. These findings highlight the importance of distinguishing between changes in stored soil carbon and changes in the carbon contributing to respiration when assessing the vulnerability of páramo carbon reservoirs to fire and climate change.

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6. Appendices

Results: Bulk soil nitrogen concentrations across fire history and depth

Overall, total nitrogen contents decreased with increasing soil depth across elevations and fire-history conditions (Figure A1). Differences between burned and unburned soils were generally more pronounced in the upper 10 cm than in deeper soil layers. At 10 cm depth, nitrogen contents were significantly higher in burned soils than in unburned soils ($p=0.019$). At greater depths, differences between fire-history conditions were generally smaller and not statistically significant ($p>0.05$).

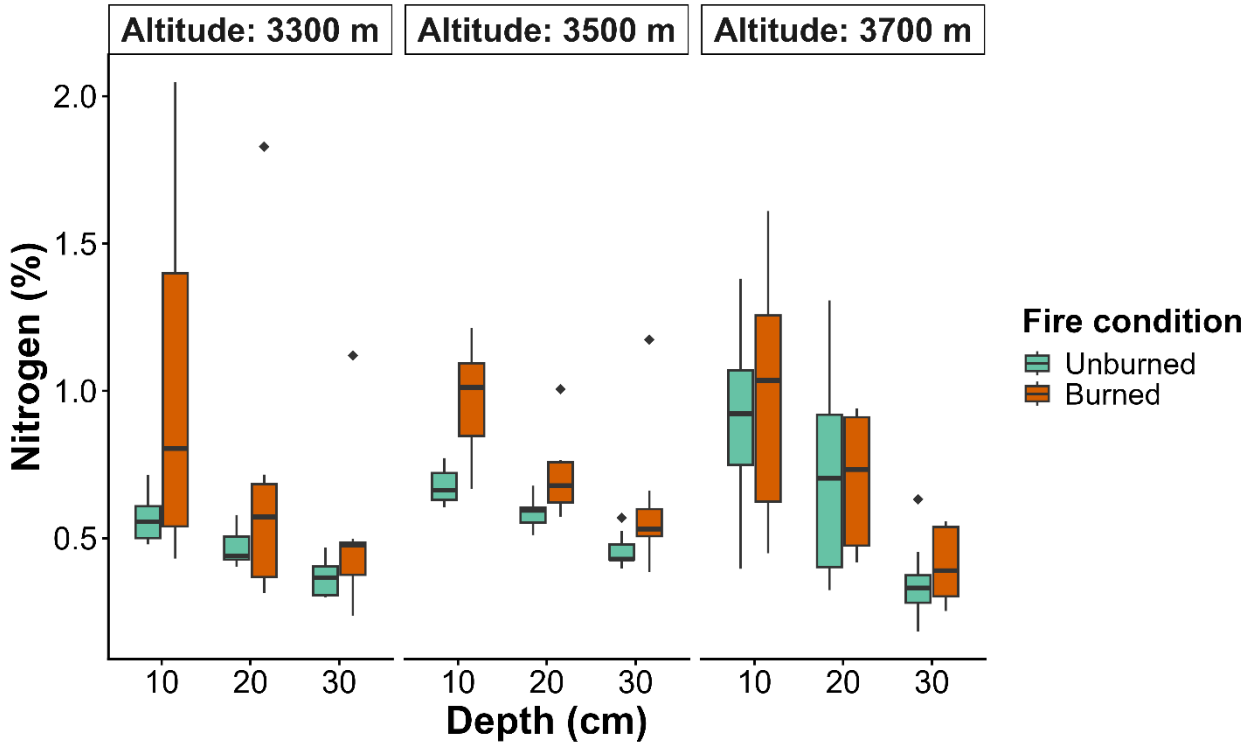


Figure A1. Bulk soil N across three elevations (panels), soil depths (horizontal axis), and fire conditions (color boxes).

Discussion: Fire effects on soil nitrogen stocks and carbon-nitrogen coupling in páramo soils

The vertical stratification of soil nitrogen mirrored that of carbon, showing higher concentrations in surface soils and progressively lower values with depth (Figure A1). Burned soils showed higher total nitrogen concentrations than unburned soils, particularly in the upper 10 cm. While high-severity fires in certain ecosystems can result in substantial nutrient volatilization and nitrogen losses (Alexis et al., 2007; Neary et al., 1999), low-severity fires in organic-rich and humid alpine environments often exhibit contrasting patterns. In these systems, subsequent inputs of organic material, root mortality, and

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post-fire vegetation recovery can compensate for or even outweigh initial changes, leading to elevated nutrient concentrations in the surface horizons (Franzluebbers et al., 2000; Tashi et al., 2016).

The accompanying increase in nitrogen observed alongside carbon in burned surface soils reflects the incorporation of plant-derived organic material rather than an independent mechanism controlling the radiocarbon signal. Because nitrogen and carbon inputs are tightly coupled through organic matter accumulation, microbial immobilization, and plant tissue composition in alpine and high-elevation grasslands (Chen et al., 2016; Tashi et al., 2016), the higher nitrogen concentrations in recently affected soils support the interpretation of fresh substrate additions rather than a deep thermal alteration or decoupling of the soil profile.

Data availability

The dataset containing the soil radiocarbon measurements, soil carbon concentrations, and incubation fluxes supporting this study is publicly available in the Zenodo: Díaz-Timoté, J. J. (2026). Fire enhances recent carbon contributions without mobilizing old carbon in páramo ecosystems [Dataset]. Zenodo. https://zenodo.org/records/23702517

Code availability

The R scripts and statistical code used for the linear mixed-effects models (LMMs) and data visualization are available in the Zenodo: Díaz-Timoté, J. J. (2026). Fire enhances recent carbon contributions without mobilizing old carbon in páramo ecosystems [Dataset]. Zenodo. https://zenodo.org/records/23702517

Author contributions

JJDT and CAS designed the study. JJDT performed field sampling, sample preparation, and laboratory analyses. AT-E and EM contributed to radiocarbon and incubation methodologies and data processing. SH supervised the spatial analysis and fire-history framework. JJDT wrote the manuscript with contributions and editorial feedback from all co-authors.

Competing interests

At least one of the (co-)authors is a member of the editorial board of Biogeosciences.

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