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# Early floristic and structural post-fire recovery of páramo vegetation: implications for ecological restoration

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# Abstract

**Background:** Páramos are high-elevation Neotropical ecosystems that harbor unique biodiversity and provide essential ecosystem services. Fire is an important disturbance in páramos, and its frequency is expected to increase under climate warming. However, post-fire vegetation recovery and its effects on species diversity and composition remain poorly understood, particularly in the Northern Andes of Colombia. Here, we assess the extent of vegetation recovery two years after fire by evaluating changes in vegetation cover, plant species diversity, species and growth-form composition relative to unburned reference vegetation.

**Results:** After two years, vegetation cover recovered by 90%, while beta diversity showed 75% and 79% recovery based on the Jaccard and Bray–Curtis indices, respectively. Gamma diversity recovered by 89%. In contrast, alpha diversity increased above reference values, with plot-level species richness and Shannon diversity exceeding reference values by 47% and 24%, respectively. Species and growth-form composition also showed substantial convergence toward reference vegetation, reaching 53% and 54%, respectively, of the compositional space occupied by reference plots. Recovery was mainly driven by the rapid recovery of grasses, including tussock and cushion forms, herbs, and resprouting woody species.

**Conclusions:** Our results demonstrate rapid early recovery of páramo vegetation during the first two years after fire, with alpha diversity increasing above reference values in a pattern consistent with the founder-controlled phase of post-fire succession. The structurally diverse recovery trajectory suggests that active restoration may not be necessary following isolated fires under similar conditions. However, longer-term monitoring is needed to determine whether this early recovery leads to convergence with pre-fire conditions and how increasing fire frequency and climate warming may alter long-term recovery trajectories.


# BACKGROUND

Páramos are high-elevation ecosystems of the tropical Andes and Central America, occurring from Costa Rica and Panama to Venezuela, Colombia, Ecuador, and Peru, generally between the upper limit of montane forests and the permanent snowline between 2,800 and 4,800 m a.s.l. (Pedraza-Peñalosa et al. 2004; Morales-Rivas et al. 2007; Hofstede et al. 2014). Their environmental conditions, including low temperatures, high humidity, strong winds, intense solar radiation, and marked daily thermal oscillations, have promoted the evolution of highly specialized plant communities with exceptional levels of diversity and endemism (Hofstede et al. 2014). Because of their geographic isolation and ecological singularity, páramos have been described as “sky islands”, where lowland areas act as biogeographic barriers that restrict dispersal and promote floristic differentiation among páramo complexes (Flantua et al. 2019; Vargas-Ríos and León 2021).

Páramos provide multiple ecosystems services, including erosion control, carbon sequestration, microclimate and air-quality regulation, pollination, biological control, cultural values, tourism, and aesthetic benefits (Bernal et al. 2006; Vargas-Ríos and León 2021). Among these services, one of their

most critical contributions is water provision and regulation, because páramo soils and vegetation act as natural hydrological buffers that capture, store, and gradually release water, maintaining streamflow and supplying freshwater to downstream populations (Vargas-Ríos and León 2021; Vásquez and Buitrago 2011). In addition to these services, páramos are among the most diverse high-mountain ecosystems in the world, with biodiversity patterns shaped by complex historical processes of migration, isolation, speciation, and range shifts associated with glacial and interglacial cycles in the Northern Andes (Hooghiemstra et al. 2006; Hooghiemstra and Flantua 2019; Flantua et al. 2019). This makes them the species-richest and fastest evolving biodiversity hotspot of alpine ecosystems worldwide (Madriñán et al. 2013; Testolin et al. 2021).

Floristic syntheses of vascular plants in páramo ecosystems have reported approximately 127 families, 540 genera, and more than 3,500 species (Sklenář et al. 2005). This vegetation is organized into distinctive structural and functional growth forms that reflect adaptations to harsh high-mountain conditions (Ramsay and Oxley 1997). Among the most representative growth forms are giant rosettes of the genus *Espeletia* and *Espeletiopsis*, tussock grasses, acaulescent rosettes, cushion plants, sclerophyllous shrubs, herbs, and graminoid communities (Hedberg 1964; Ramsay and Oxley 1997). These growth forms play complementary ecological roles in páramo functioning. Giant rosettes contribute to water capture, hydrological regulation, and microclimatic buffering, whereas tussock grasses and other monocotyledons contribute to soil protection, erosion control, carbon accumulation, nutrient cycling, and habitat provision.

Páramos are highly fragile due to their geographic isolation, alpine climate, slow ecological dynamics, high levels of endemism, and the narrow environmental tolerances of many of their species (Luteyn 1999; Hofstede et al. 2014). These characteristics make them particularly sensitive to disturbances such as land-use change, fire, grazing, and climate warming, which can alter vegetation structure, reduce biodiversity, and compromise key ecosystem functions and services (Vargas-Ríos and Pedraza 2003; Vargas-Ríos 2013). Fire is one of the most recurrent and ecologically significant disturbances in páramo ecosystems (Horn and Kappelle 2009; Obando-Cabrera et al. 2025) and is expected to become more frequent due to climate warming (Horn and Kappelle 2009; Armenteras et al. 2020; Obando-Cabrera et al. 2025). Although many fires are associated with human activities, fire has occurred naturally in tropical high mountains for thousands of years and is therefore not exclusively an anthropogenic phenomenon (Vargas-Ríos 1996, 1997). Páramos are highly susceptible to fire because the accumulation of necromass, particularly in tussock grasses and dead leaves retained by rosettes, together with low moisture content during dry periods, slow decomposition rates, and low herbivory levels (Vargas-Ríos and Pedraza 2003; Vargas-Ríos 2013).

The ecological effects of fire in páramos depend on its frequency, intensity, seasonality, spatial extent, and type, as well as on the pre-fire composition and structure of the vegetation (Keeley 1981; Whelan 1995). Consequently, post-fire recovery is not a uniform process, but a trajectory shaped by differential responses among species and growth forms. Severe fires can consume a large proportion of aboveground phytomass, reduce vegetation cover, expose soils, alter nutrient availability, and facilitate

the establishment of opportunistic or invasive species (Hofstede et al. 1995; Ramsay and Oxley 1996). Tussock and grassland structures may recover within three to five years (Ramsay 1992), but rosette-dominated communities and vegetation structures similar to pre-disturbance conditions may require longer periods to recover depending on local conditions and disturbance history (Horn 1990; Janzen 1973; Ramsay and Oxley 1996; Vargas-Ríos and Pedraza 2003). Even more, páramos exhibit substantial differences in vegetation structure and composition across latitude (Ramsay and Oxley 1997). While páramos in Ecuador are grass dominated with species that originated in temperate regions (of the Poaceae family), páramos in Colombia are dominated by giant rosette plants, shrub formations and Chuscales (i.e. bamboo of the genera Chuscea). Thus, changes in the relative abundance, cover, and dominance of key growth forms, such as tussock grasses, monocotyledons, and giant rosettes, may serve as early indicators of ecosystem response and recovery after fire but also depend on the type of páramo vegetation (Zomer and Ramsay 2018).

The effects of fire on páramo floristic composition remain poorly understood, particularly regarding long-term trajectories of species turnover and community convergence after disturbance. Although several studies have investigated post-fire responses in Andean páramos, most have focused on Ecuadorian páramos or have evaluated specific components of vegetation recovery, such as plant survival, growth-form dynamics, biomass responses, or functional traits (Ramsay and Oxley 1996; Zomer and Ramsay 2021; Ocampo-Zuleta and Parrado-Rosselli 2023; Benítez et al. 2026). This knowledge gap is partly related to the logistical challenges associated with long-term monitoring in remote high-elevation ecosystems, resulting in limited empirical evidence on how fire influences floristic composition, species dominance, and recovery pathways across different páramo regions. In particular, Colombian páramos remain underrepresented in post-fire studies that simultaneously evaluate species-level and growth-form responses, and compositional convergence with reference vegetation.

The Santurbán páramo complex is located in the Eastern Cordillera in northeastern Colombia. It comprises a mosaic of páramo vegetation, wetlands, lagoons, grasslands, shrublands, and high-Andean forest remnants, and is recognized for its importance in biodiversity conservation and water regulation. The angiosperm diversity of the Santurbán páramo includes more than one hundred genera distributed across several dozen families, with Asteraceae, Ericaceae, Orchidaceae, Poaceae, and Hypericaceae among the most representative groups (Aguilar Garavito and Ramírez Hernández 2021). On January 22, 2024, a fire occurred in the Santurbán páramo, affecting approximately 312 ha of páramo vegetation (CDMB 2024). Here, we evaluate the early post-fire recovery of páramo vegetation two years after the wildfire by quantifying the extent to which vegetation structure, species diversity and composition recover within two years, whether natural regeneration approaches reference conditions, and whether the observed recovery suggests a need for active restoration. By integrating species- and growth-form responses, this study provides insights into the resilience and early successional dynamics of Colombian páramo vegetation following fire.

# METHODS

# Study area

This study was conducted at the *Picacho* peak in the Santurbán páramo complex, municipality of Tona, Santander, northeastern Colombia (7.1122972, -72.975744), at 3,454 m a.s.l. The Santurbán páramo covers approximately 1,055 km² and ranges from 2,800 to 4,300 m a.s.l. It has a cold climate, with temperatures between 0°C and 15°C, two annual periods of precipitation, and annual rainfall ranging from 500 to 2,000 mm (Morales-Rivas et al. 2007; CDMB 2010). During a pronounced dry season in January 2024, a wildfire affected approximately 312 ha, including a reserve of the Metropolitan Aqueduct of Bucaramanga that supports an important population of *Espeletia standleyana* A.C. Sm. within a highly transformed landscape. The present study has been carried out within this reserve (Fig. 1).

# Sampling design

Sampling of vascular plants, bryophytes, and lichens was conducted in 30 plots of 5 × 5 m, covering a total sampled area of 0.075 ha. We used 5 × 5 m plots because 25 m² is a commonly used sampling area for open páramo vegetation, allowing the characterization of local plant diversity and dominant growth-form structure in these ecosystems (Ramsay and Oxley 1997; Rangel-Ch. and Velásquez 1997). Plots were established following a stratified random design that considered the area affected by fire, hereafter referred to as the recovery area, and nearby unburned vegetation, hereafter referred to as the reference area. Accordingly, 19 plots were established in the recovery area and 11 in the reference area, encompassing both concave and convex microtopographic positions associated with temporary surface water flow. Each plot was divided into four 2.5 × 2.5 m quadrants to facilitate species-specific cover estimation. The first quadrant was placed in the northernmost corner of the plot, and the remaining quadrants were numbered clockwise. In each quadrant, we recorded the total vegetation cover including vascular, non-vascular plant, and lichen species. Species cover was used as an approximation of abundance because individual counts are difficult to obtain in grass-dominated páramo vegetation (Ferro-Díaz 2015). Since cover was estimated on a scale from 1% to 100% in each quadrant, the total cover of each species per plot was calculated as the average cover across the four quadrants. Species richness was calculated as the number of different species recorded in each plot (Moreno 2001). For taxonomic identification, plant or lichen specimens that could not be identified in the field were collected outside the plots in order to avoid affecting subsequent monitoring. Specimens were identified at the Herbarium of the Universidad Industrial de Santander (UIS) in Bucaramanga using specialized literature for lichens (Moncada and Lücking 2011), non-vascular plants (Churchill and Linares 1995), ferns (Moran and Riba 1995; Moran 2022), and vascular plants (Luteyn 1999; Pedraza-Peñalosa et al. 2004; Sklenář et al. 2005; Marín and Parra 2015; Bernal et al. 2016; Betancur et al. 2018), virtual herbarium resources (Index Fungorum Partnership n.d.; Instituto de Ciencias Naturales, Universidad Nacional de Colombia n.d.; JSTOR n.d.; Missouri Botanical Garden n.d.), comparison with reference specimens from the UIS Herbarium, and consultation with taxonomic specialists (see Acknowledgments section). Additionally, cover and richness were calculated at the growth-habit level using a modification of the classification

proposed by Ramsay and Oxley (1997) (Fig. 2). Vegetation was surveyed twice: one year after the fire in January 2025, and again in February 2026.

# Data analysis

All analyses were conducted at the plot level, considering two vegetation conditions: recovery and reference plots. For each plot, year, and species, cover values were averaged across the four quadrants and used to construct species-by-plot matrices. Vegetation cover was analyzed at three complementary levels: total plot cover, growth-form cover, and species cover. Plant growth forms were standardized into seven categories: caulescent rosettes, acaulescent rosettes, tussocks, cushions, shrubs/trees, herbs, and lichens (Fig. 2). Shrubs and trees were grouped because both represent woody growth forms within the sampled vegetation. Temporal changes in vegetation cover between 2025 and 2026 were evaluated separately for each condition using paired Wilcoxon signed-rank tests, as the same plots were re-measured over time. When multiple comparisons were performed, p-values were adjusted using the Benjamini–Hochberg procedure (Benjamini and Hochberg 1995). Diversity was evaluated using alpha, beta, and gamma diversity to characterize complementary dimensions of community recovery. Alpha diversity was calculated at the plot level as species richness, defined as the number of species recorded per plot. Shannon diversity was also calculated at the plot level using species cover as the abundance measure. Gamma diversity was calculated as the total number of species recorded within each condition and year, representing the cumulative species richness of recovery and reference vegetation. Beta diversity was interpreted as the mean compositional dissimilarity of each plot relative to all other plots within the same condition and year. For each condition × year group, pairwise dissimilarity matrices were calculated among plots. Then, for each plot, beta diversity was estimated as its mean dissimilarity to the remaining plots in the same group, excluding self-comparisons. Incidence-based beta diversity was assessed using Jaccard dissimilarity calculated from presence–absence matrices, whereas abundance-based beta diversity was assessed using Bray–Curtis dissimilarity calculated from species cover matrices. Temporal changes in alpha and beta diversity between 2025 and 2026 were evaluated separately for recovery and reference plots using paired Wilcoxon signed-rank tests. Floristic composition was evaluated using Principal Coordinates Analysis (PCoA) based on Bray–Curtis dissimilarity. Ordinations were performed separately for species composition and growth-form composition. The species-level PCoA was based on species-by-plot cover matrices, whereas the growth-form PCoA was based on plot-level cover matrices aggregated by growth form. PCoA was used to represent compositional variation along orthogonal axes, and dashed ellipses represent 95% confidence regions for each condition by year group. All statistical analyses were performed in R (R Core Team 2026). Diversity and compositional analyses, including Jaccard and Bray–Curtis dissimilarities and Principal Coordinates Analysis, were conducted using the vegan package (Oksanen et al. 2026). Paired Wilcoxon signed-rank tests and p-value adjustments were performed using rstatix package (Kassambara 2026). Data cleaning and matrix construction were performed using dplyr and tidyr, and figures were produced using ggplot2 (Wickham 2016; Wickham et al. 2019).

# RESULTS

We recorded 89 species across the 0.075 ha sampling area, comprising 71 angiosperms (50 eudicots and 21 monocots), eight bryophytes, four ferns, and three lichens (SI Table 1). These species belong to 37 families and 67 genera. Asteraceae, Poaceae, and Rosaceae are the most species-rich families, with 13, 12, and six species, respectively. *Geranium* and *Hypericum* exhibit the highest richness, with four species each, followed by *Gaultheria*, *Lachemilla*, and *Sphagnum*, with three species each. Eight genera contain two species, whereas the remaining 54 are represented by a single species. Among growth forms, herbs are the most species-rich (31 species), followed by shrubs (25) and tussocks (17), whereas acaulescent herbs, cushion herbs, and caulescent rosettes are each represented by a single species.

While overall vegetation cover in reference plots remained relatively stable between 2025 and 2026, recovery plots show a significant recovery of vegetation cover and biodiversity. Mean cover per plot nearly doubled, increasing from 48% to 94%, approaching the values observed in reference plots (104%). Species richness and Shannon diversity also increased markedly, in average from 16 to 25 species per plot and from 1.6 to 2.3, respectively, surpassing values of unburned reference plots. The total number of species increased from 47 to 67 species. Jaccard dissimilarity decreased slightly, suggesting a decrease in beta diversity among recovery plots over time. Bray-Curtis dissimilarity, however, remained stable, indicating persistent spatial variation in species-specific cover. These results suggest rapid recovery of vegetation cover and plot-level (alpha) diversity. Nevertheless, beta diversity indices (Jaccard, Bray-Curtis) and gamma diversity (overall species number) indicate yet incomplete convergence with reference vegetation.

Table 1
Summary of plant cover and diversity indices in recovery and reference plots between 2025 and 2026.

| **Mean cover per plot (%)** | **Recovery 2025** | **Rel. recovery 2025** | **Recovery 2026** | **Rel. recovery 2026** | **Reference (2025 + 2026)** |
|---|---|---|---|---|---|
| | **48.03 ± 14.77** | **46.2%** | **93.55 ± 19.85** | **89.9%** | **104.03 ± 30.3** |
| Species richness | 15.84 ± 4.74 | 92.9% | 25.11 ± 6.94 | 147.3% | 17.05 ± 5.23 |
| Shannon diversity | 1.58 ± 0.35 | 83.7% | 2.34 ± 0.5 | 123.5% | 1.89 ± 0.4 |
| Jaccard | 0.65 ± 0.15 | 84.6% | 0.58 ± 0.17 | 75% | 0.77 ± 0.12 |
| Bray-Curtis | 0.6 ± 0.21 | 77.5% | 0.61 ± 0.18 | 79% | 0.77 ± 0.18 |
| Total species number | 47 | 62.7% | 67 | 89.3% | 75 |

Values for cover, species richness, and Shannon diversity represent mean ± standard deviation at the plot level. Jaccard and Bray–Curtis values represent mean pairwise dissimilarity among plots within each

group. Jaccard was calculated using presence–absence data, whereas Bray–Curtis was calculated using species cover.

By further inspecting plot-level diversity indices, we find significant differences between years for recovery vegetation, but not for reference vegetation (Fig. 3). The only exception is the Jaccard index, which indicates no significant changes in beta diversity between early years of recovery. Interestingly, we find weak but significant differences of abundance-based diversity indices (Shannon and Bray-Curtis) for reference vegetation between years indicating differences (i.e. temporal variability) in species cover, but not occurrence. This suggests that vegetation cover is not static in undisturbed páramo ecosystems (Fig. 3).

Considering growth-forms, we did not find significant temporal changes in cover for reference plots, but for recovery plots we did identify significant increases in mean cover for caulescent rosettes, tussocks, cushions, shrubs/trees, and herbs (Fig. 4). The strongest increase we observed for tussocks, which became the dominant structural component of the recovering vegetation in 2026. Herbs and shrubs/trees also showed clear increases, indicating that early vegetation recovery involved both herbaceous and woody growth forms. Cushions and caulescent rosettes increased significantly but remained less dominant in terms of absolute cover, whereas acaulescent rosettes and lichens did not show significant temporal changes.

At the species level, most dominant species showed no significant cover change in reference vegetation, whereas several species increased significantly in recovering vegetation, particularly *Danthonia secundiflora* J. Presl, *Espeletia standleyana* A.C. Sm., *Parablechnum loxense* (Kunth) Gasper & Salino, and *Sphagnum compactum* DC. (S.I. Figure 1). These species-level responses were consistent with the observed increases in tussocks, caulescent rosettes, cushions, and herbs, indicating that early post-fire recovery was driven by a subset of dominant species rather than by uniform increases across all taxa.

Principal Coordinates Analysis (PCoA) shows the recovery of species and growth-form composition within two years as compared to the reference vegetation (Fig. 5). From 2025 to 2026, growth-form and species composition in recovery plots evolve occupying more ordination space (Fig. 5). In growth-forms this expansion is mainly driven by increases in cover by tussocks, caulescent rosettes, shrubs/trees, and herbs and revealed by the first two Principal Coordinate Axes explaining 33% of variance (Fig. 5a). The area of the confidence ellipses occupied by recovery plots increased from 20% in 2025 to 54% in 2026 as compared to the ordination space covered by the reference plots. At the species-level, the first three PCoA axis reveal not only an expansion of ordination space but also a directional shift of species composition from 2025 to 2026, mainly along PCoA axes 3 (Fig. 5c). This shift is associated with increased cover of dominant species during recovery such as *Danthonia secundiflora, Cortaderia spp.*, *Agrostis perennans, Lachemilla spp.*, and *Espeletia standleyana*. In 2026 recovery plots occupy 24% of ordination space as compared to reference vegetation considering PCoA axis 1 and 2 (Fig. 5b) and 53% considering PCoA axis 1 and 3 (Fig. 5c) indicating a rapid recovery of species composition as compared

to reference vegetation. Interestingly, this ordination also reveals compositional differences of reference plots between years (Fig. 5c), suggesting significant interannual variation in species-specific cover.

# DISCUSSION

Between 1985 and 2022 across Colombia, Venezuela, Ecuador, and Peru, approximately 6370 km² of páramo vegetation burned, representing about 15% of the total páramo area; the majority of fires probably of anthropogenic origin (Obando-Cabrera et al. 2025). Ongoing climate change may increase future fire risk by intensifying droughts, extreme weather events, and fire-conducive conditions that promote fuel accumulation followed by moisture deficits (Horn and Kappelle 2009; Armenteras et al. 2020; Obando-Cabrera et al. 2025). Understanding early post-fire vegetation recovery is essential to assess whether páramo communities can maintain their structure, diversity, and ecological functions under potentially more frequent or severe disturbance regimes.

Previous studies have examined fire effects on páramo vegetation, but most empirical evidence comes from Ecuadorian páramos or has focused on biomass, grazing–fire interactions, functional traits, or selected species (Hofstede et al. 1995; Verweij and Budde 1992; Ocampo-Zuleta and Parrado-Rosselli 2023). This geographic bias is important because páramo vegetation is not structurally or floristically homogeneous across the Tropical Andes. Ecuadorian páramos have often been described as grass-dominated systems, with growth-form composition largely structured by tussock grasses, although shrub, rosette, bamboo, cushion, and desert páramo formations also occur (Ramsay and Oxley 1997). In the Ecuadorian páramos, mean plot-level richness ranges between approximately 20 and 30 species per 5 × 5 m plot (Sklenář and Ramsay 2001). In contrast, Colombian páramos, particularly those of the Eastern Cordillera, commonly occur as heterogeneous vegetation mosaics that include giant rosettes, shrubs, tussock grasslands, cushions, wetlands, and high-Andean forest remnants (Rangel-Ch. and Velásquez 1997; Rangel-Ch. et al. 2024). At the broader Andean scale, observed plot-level richness in páramo vegetation has been reported to vary from 1 to 52 species per 25 m², highlighting the strong spatial heterogeneity of local plant diversity across the páramo biome (Peyre et al. 2019).

Contemporary páramos are rarely pristine ecosystems and often bear legacies of human land use and fire (Peyre et al. 2021; Obando-Cabrera et al. 2025). In the Santurbán páramo, given its proximity to the metropolitan area of Bucaramanga, land uses such as mining, agriculture (e.g., onion and potato cultivation), and extensive cattle grazing are widespread, with agricultural and grazing areas accounting for approximately 20% of the páramo area (Romero Martínez 2021). Our study site is a protected reserve of the Metropolitan Aqueduct of Bucaramanga since the early 1990s and supports an estimated 86,000 adult individuals of *Espeletia standleyana*, reaching up to 2 m in height (Uzcátegui-León et al. 2026). Nevertheless, in the past extensive cattle grazing and possibly burning has occurred, and therefore the reference vegetation should not be considered pristine. Despite this history, both plot-level and total species richness are within the range reported for relatively undisturbed páramo vegetation, with up to 25 species recorded in 25-m² plots in the Santurbán massif (Galván-Carvajal et al. 2023). We therefore

consider the reference plots an appropriate benchmark for evaluating the post-fire recovery trajectory, while recognizing that they may retain legacies of past disturbance.

Post-fire trajectories reported for Ecuadorian páramos have been described as a sequence of growth-form changes, beginning with an early recruitment phase characterized by high growth-form diversity, followed by a phase of dense tussock dominance with reduced light availability and altered soil temperatures, and later by increasing canopy stratification and the return of growth-form diversity (Zomer and Ramsay 2021). Similarly, post-fire survival in Ecuadorian grass páramos is strongly associated with the protection of buds and meristems by plant tissues or belowground structures, favoring species with resprouting capacity (Ramsay and Oxley 1996). Our results are consistent with this successional trajectory. Alpha diversity increased from the first to the second year after fire and surpassed reference-plot values, suggesting sufficient niche space and resources available for the establishment of newly arriving and resprouting species, consistent with the founder-controlled phase described by Zomer and Ramsay (2021). At the same time, the decline in Jaccard beta diversity from the first to second year indicates increasing similarity in species occurrence among recovery plots, suggesting an early phase of species sorting and increasing competition. However, the parallel increase in Bray–Curtis dissimilarity indicates substantial heterogeneity in species-specific cover among burned plots, suggesting that species sorting acts at an early stage and that the recovering plant community has not yet reached the relative abundance structure of the reference vegetation.

Growth-form specific responses further indicate that the observed successional trajectory is structurally more diverse than those described for Ecuadorian páramos. Although tussocks showed a strong increase in cover and became a major structural component of recovering plots, recovery also involved early increases in caulescent rosettes, cushions, shrubs and trees, and herbs, with dominant species including *Danthonia secundiflora*, *Espeletia standleyana*, *Parablechnum loxense*, and *Sphagnum compactum*. Our results therefore indicate that Santurbán páramo vegetation follows a successional trajectory broadly consistent with that described for Ecuadorian páramos, with rapid early recovery, a transient increase in alpha diversity, and initial species sorting within two years after fire. However, this recovery seems to occur through a more structurally diverse trajectory of growth forms, highlighting the importance of regional vegetation context when interpreting post-fire successional dynamics in páramos.

Although recovery plots reached high values of vegetation cover and alpha diversity after two years, this should not be interpreted as complete ecological recovery. Mean plot-level richness in recovery plots reached 25.11 ± 6.94 species per 25 m², a value that falls within the higher range reported for undisturbed páramo vegetation at comparable spatial scales across the Andean páramo (Sklenář and Ramsay 2001; Peyre et al. 2019; Galván-Carvajal et al. 2023; Rangel-Ch. et al. 2024). This rapid increase in local richness, together with the increase in Shannon diversity, probably reflects an early successional phase in which surviving species, resprouting individuals, colonizing herbs, and newly arriving species favored by increased post-fire resource availability coexist. Similar increases in local diversity after disturbance have been reported in several plant communities, where intermediate levels of disturbance

can temporarily reduce dominance and increase establishment opportunities (Connell 1978; Huston 1979). In páramo ecosystems, this pattern is consistent with the idea that early recovery may involve rapid recruitment and reorganization of growth forms before vegetation returns to a more stable and compositionally structured state (Ramsay and Oxley 1996; Zomer and Ramsay 2021). Thus, the high alpha diversity observed in recovery plots may reflect an early stage of community reassembly consistent with the intermediate disturbance hypothesis (Connell 1978), rather than full floristic recovery, as diversity may decline as composition converges toward reference vegetation.

Interestingly, we recorded 14 taxa exclusively in recovery plots, which contributed to this early increase in diversity. Although most of these taxa occur naturally within high-elevation Andean vegetation, several have broader distributions extending into subpáramo or Andean forests (e.g. *Symplocos theiformis, Ugni myricoides*). Their occurrence in recovering plots may therefore reflect early colonization from the surrounding species pool. This finding is relevant in the context of ongoing climate-driven elevational upward shifts of páramo plant species (Sklenář et al. 2021) and increasing occurrence of species with broader and warmer thermal niches in high-elevation Andean plant communities (Cuesta et al. 2023). Thus, post-fire recruitment may provide establishment opportunities for species whose distributions are currently expanding upslope under climate warming.

To our knowledge, this study provides one of the first integrated, plot-based assessments of post-fire recovery of floristic diversity and community composition in a Colombian páramo. Unlike previous studies that have focused primarily on fire temperature, biomass, functional traits, or growth-form responses (Ramsay and Oxley 1996; Hofstede et al. 1995; Verweij and Budde 1992; Zomer and Ramsay 2021; Ocampo-Zuleta and Parrado-Rosselli 2023), we combined vegetation cover, alpha, beta, and gamma diversity, dominant species responses, and multivariate analyses of species and growth-form composition. From a restoration perspective, these results suggest that passive recovery may be sufficient following isolated fire events where soil structure, remnant vegetation, and nearby propagule sources remain available, although this conclusion may not apply under repeated or high-frequency fire regimes.

# CONCLUSION

As climate change progresses, fire frequency in páramos is expected to increase, raising concerns about how repeated burning may alter the floristic and growth-form diversity and composition of these strategic ecosystems in the Colombian Andes. Our results indicate a rapid early recovery of páramo vegetation, consistent with the founder-controlled phase of post-fire succession, and reveal a structurally diverse recovery trajectory involving multiple species and growth forms. This resilience suggests that active restoration may not be necessary following isolated fires under similar conditions. However, whether this resilience persists under more frequent fires remains unknown, emphasizing the need for long-term monitoring and experimental studies that examine the combined effects of increasing fire frequency and climate-driven species upward shifts.

# Declarations


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### Authors' contributions

BR conceived the study. AOL, DS collected data and identified species. JAR and BR analyzed data and synthesized the first draft. All authors contributed to writing and editing.


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### Data availability

Data and code available upon reasonable request.

### Ethics approval and consent to participate

Not applicable.

### Consent for publication

Not applicable.

### Competing interests

The authors declare no competing interests.

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# Figures

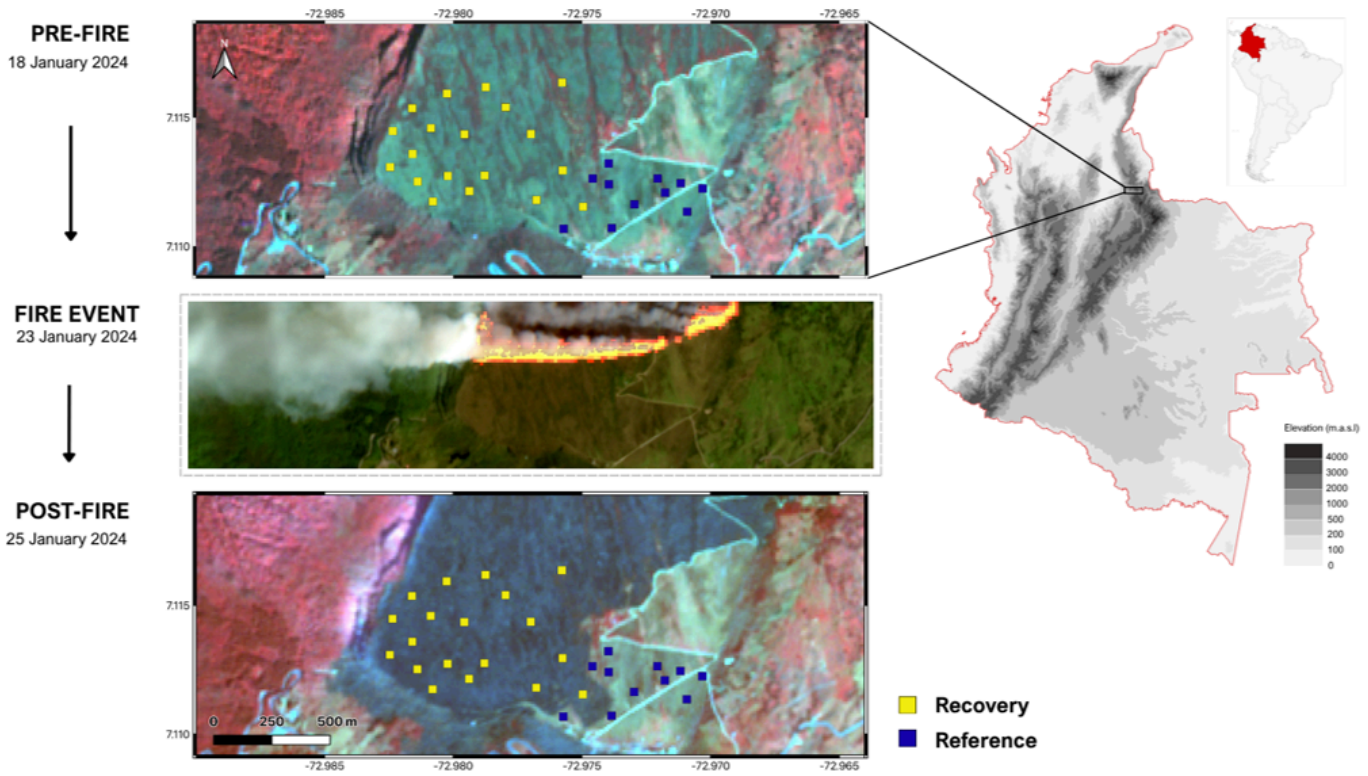
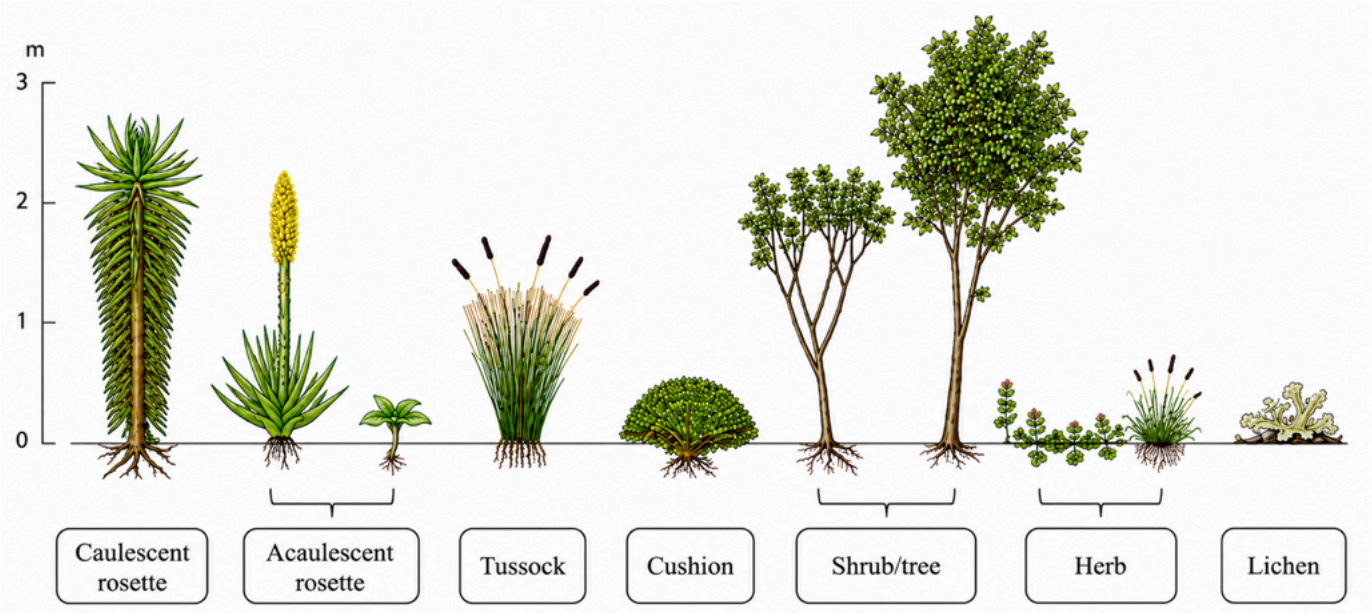


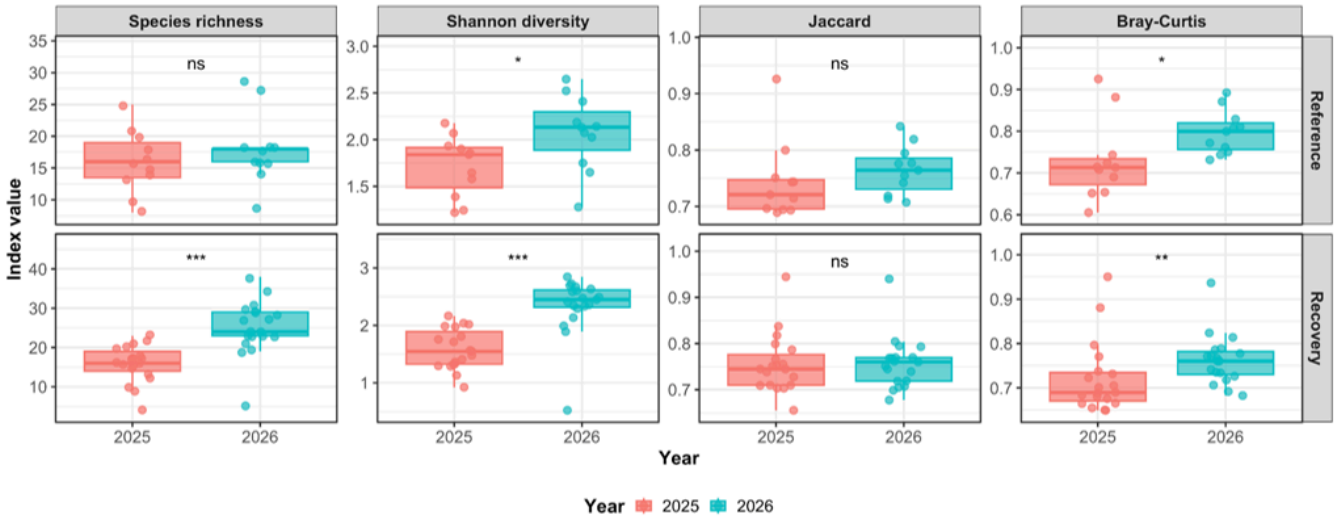

**Figure 1**

Location of the study area shown as false color infrared imagery obtained from Sentinel-2 imagery before (upper panel) and after the fire event (lower panel). The mid panel shows the study area during the fire event using the wildfire visualization provided by Copernicus. Sentinel-2 imagery was obtained from Copernicus Browser: *https://browser.dataspace.copernicus.eu*.



## Figure 2

Growth forms considered in this study according to the classification proposed by Ramsay and Oxley (1997).




## Figure 3

Temporal changes in diversity indices between 2025 and 2026 for recovery and reference vegetation. * indicate significance levels between years, whereas “ns” indicates not significantly evaluated using paired Wilcoxon signed-rank tests.

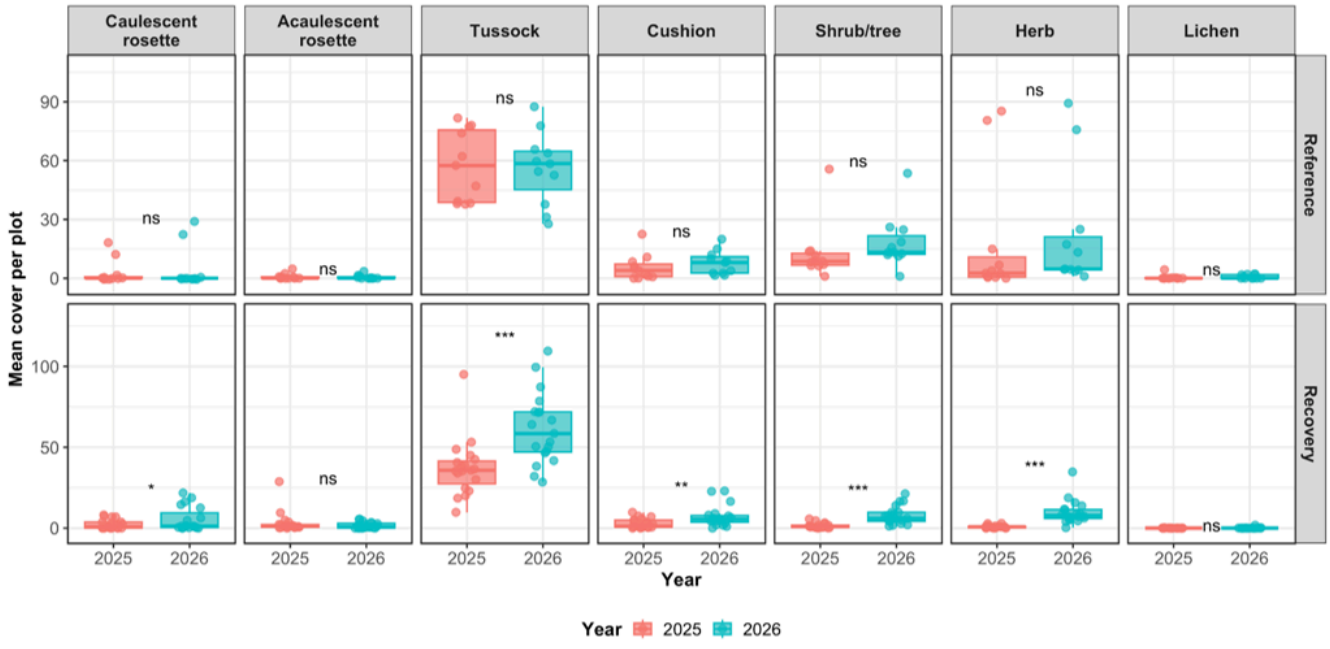


**Figure 4**

Temporal changes in mean plant cover by growth form between 2025 and 2026. * indicate significance levels between years, whereas “ns” indicates not significantly evaluated using paired Wilcoxon signed-rank tests.

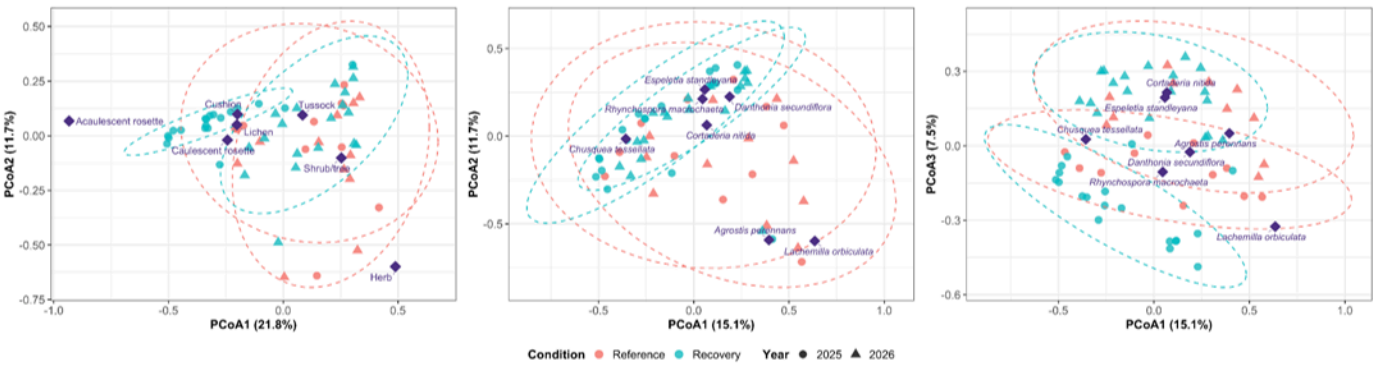



**Figure 5**

Biplots of Principal Coordinates Analysis (PCoA) of growth-form (left) and species composition (middle and right). Purple diamonds represent weighted-average scores of growth forms and dominant species.

## Supplementary Files

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