Effects of fire on functional traits and diversity of *Puya* in the Colombian páramo

Juan Jose Pinzon Bustos

Universidad del Rosario
Facultad de ciencias naturales
Bogotá, Colombia
2024

Effects of fire on functional traits and diversity of *Puya* in the Colombian páramo

Juan Jose Pinzon Bustos

Tesis presentada como requisito para obtener el título de:
Biólogo

Director
ADRIANA SANCHEZ

Co-director
STIJN HANTSON

Facultad de ciencias naturales
Biología
Universidad del Rosario
Bogotá, Colombia
2024

Effects of fire on functional traits and diversity of *Puya* in the Colombian páramo

Juan José Pinzón[1], Stijn Hantson[2], Adriana Sanchez[1]

[1] Programa de Biología, Facultad de Ciencias Naturales, Universidad del Rosario, Bogotá, Colombia
[2] Programa de Ciencias del Sistema Tierra, Facultad de Ciencias Naturales, Universidad del Rosario, Bogotá, Colombia

Abstract

Fire is the major natural disturbance agent that has transformed the global landscape, consuming surface biomass and altering the physicochemical properties of the soil. However, anthropogenic intervention has increased the frequency of this disturbance, affecting various ecosystems, including the páramo, a high-altitude Andean Mountain ecosystem. In this ecosystem, there are indications that fire facilitates species establishment in the understudied genus *Puya*. To further investigate their response to fire, transects were established in areas impacted by fires in 1988 and 2002, as well as in undisturbed areas (no fire prior to 1985). The study aimed to understand how fire interacted with species diversity and abundance, as well as with aboveground and belowground plant functional traits, and mycorrhizal colonization. Our results revealed that in the undisturbed transects, there was higher plant diversity (four species), and that fire disturbance led to a decrease in species richness. In the 2002 fire-affected transects, only *Puya goudotiana* was present. Interestingly, this species did not undergo changes in functional traits when comparing individuals growing in undisturbed conditions with those affected by fire. *Puya nitida* was present in the 1988 and the no fire transects and exhibited significantly higher root branching and lower root diameter under undisturbed conditions. Mycorrhizal colonization did not show significant differences between species or time since fire disturbance. Considering the ecological importance of *Puya* in the páramo ecosystem, and the large impact fire has on abundance and diversity, more research on the genus is needed to better understand how these plants respond to disturbance events and colonization in affected areas.

Keywords

Disturbance, Leaf traits, Mycorrhizal colonization, Plant height, *Puya*, Root traits

1 INTRODUCTION

Fire, as an ecological process, has shaped the planet, posing a constant challenge to survival (Cochrane & Ryan, 2009), affecting the structure and function of ecosystems (Pausas & Schwilk, 2012). Fire also influences their global distribution and composition (Bond et al., 2005; Bond & Keeley, 2005), consuming a large part of terrestrial biomass (Archibald & Hempson, 2016). However, this process has increased in frequency due to climate change (Burton et al., 2023), as well as human activity (Neary, 2009), reaching a point where it is difficult to distinguish a natural fire regime from an anthropogenic one (Bowman et al., 2011). Fire can vary in intensity and frequency, impacting community assembly. However, the effect of low-intensity fire on community assembly is negligible, and the latter is mainly influenced by competition (Verdú & Pausas, 2007).

Fires can cause changes in soil chemical composition (Ondik et al., 2022). Some studies have emphasized the importance of carbon and nitrogen in soil water retention (Strydom et al., 2019), highlighting the need to understand how fire dynamics affect nutrient acquisition in different ecosystems. For instance, after a low-intensity fire, there may be an increase in carbon (C) and nitrogen (N), but after a higher-intensity fire, there is not a further increase in mineral content (Krishnaraj et al., 2016). However, available phosphorus (P) will increase (Agbeshie et al., 2022). If fires are constant, soil N decreases and the C:N ratio increases (Liechty & Hooper, 2016). Moderate fires have no impact on soil and heterotrophic respiration compared to low and high intensity (Gui et al., 2023). In larch forests, high intensity fire increased the time needed to recover soil organic and mineral content (Liu & Pan, 2019).

Fire regime intensity effects are not unique to the soil. Vegetation communities in the Mediterranean basin have also shown increases in grassland cover recovery after a fire (Fernández-Guisuraga et al., 2023). The suppression of fires can significantly alter forest composition, leading to heighten risks of intense fires, drought, or pest infestations (Odland et al., 2021). Plant communities also face challenges related to their location, with communities in areas of heavy seasonal rainfall being most affected by fires (Miller et al., 2019). It has been found that the community response to fire is usually determined by the strongest species. If the strongest competitor is adapted to fire, the community will not present composition changes after a fire; otherwise, species composition will vary (Magnani et al., 2023).

There are functional plant traits that confer adaptive value to fire and vary depending on frequency and intensity (Keeley et al., 2011). Functional traits are measurable, heritable, morphological, physiological, or phenological characteristics that serve as proxies for understanding an individual's performance in a specific environment and community and are valuable for comprehending ecosystem dynamics (Perez et al., 2020; Violle et al., 2007). Short-term studies, following a fire, show a lower mean for leaf dry matter content (LDMC) and a higher specific leaf area (SLA) at the community level (Abedi et al., 2022). Yet, when communities are dominated by *Pinus palustrius* and *Aristida stricta*, there is a decrease in SLA and a non-significant increase in LDMC in areas with repeated burns (Mitchell et al., 2021). In general, fire favors species with low nitrogen requirements (Moretti & Legg, 2009). In fire-prone areas, there is an increase in plant leaf length, a trait that is linked to higher fire intensity (Schwilk & Caprio, 2011). Other responses such as increased flammability (Pausas et al., 2012) or changes in seeds (Gómez-González et al., 2011) are caused by the constant disturbance of fire.

Mycorrhizae are root-symbiotic fungi that improve the nutrient and water uptake of host plants, by increasing the volume of soil covered (Dighton, 2009). There are four main types of mycorrhizae, arbuscular (AMF), orchid, ectomycorrhizae (EMC) and ericoid, that associate with ca. 86% of flowering plants (Brundrett, 2009). Some studies have shown that EMC mycorrhizal colonization is reduced after a fire (Buscardo et al., 2012; Longo et al., 2011). Controlled studies have also shown that fire reduces the quantity of propagules of *Glomus spp.* (AMF) on the soil surface (Pattinson et al., 1999), but successive fires have no effect on AMF diversity (Mirzaei et al., 2023).

One of the ecosystems that has been historically affected by fires is the páramo, a tropical ecosystem found between 3000 and 5000 m.a.s.l., distributed from Venezuela to northern Peru (Sayre et al., 2020). The páramo is typically divided into subpáramo, páramo, and superpáramo, based on altitude (Cleef, 1981) and dominated by different forms of vegetation (Christmann & Oliveras, 2020). Despite its high richness, with around 3500 plant species (Sklenář et al., 2011), and high endemicity, the páramo faces challenges such as climate change and land use changes related to livestock and agriculture, which significantly impact plant species diversity (Vásquez et al., 2015). This ecosystem, dominated by grasslands and shrubs, is periodically burned, mostly due to human activities (Horn & Kappelle, 2009). Therefore, fire alongside grazing and other human activities, can affect the conservation status of this ecosystem (Hofstede et al., 2002), with post-fire succession resulting in changes in plant abundance by growth type (Zomer & Ramsay, 2021).

The genus *Puya*, belonging to the Bromeliaceae family, is endemic to the Andes (Liu et al., 2022), with 221 species described (Luther, 2014). Fourteen of these species are found at altitudes above 3000 m in Colombia (Raz & Agudelo-Zamora, s. f.), where *Puya* is crucial in the diet of the Andean bear (*Tremarctos ornatus*) (Suarez, 1988), and is also an important food source for hummingbirds and other pollinators. *Puya* is known to enhance water availability for the avifauna, by diluting the nectar (Hornung-Leoni et al., 2013). Despite its importance, little is known about the morphological characteristics or habitats of this genus (Jabaily & Sytsma, 2010). *Puya* is monocarpic (Mora et al., 2005) and some species exhibit resistance to fire through specialized rosettes that protect the meristem from high temperature and radiation (Miller & Silander, 1991). This would make them ideal as indicators of recent fires, due to their increased post-fire survival (García-Meneses & Ramsay, 2014). For example, species like *P. hamata*, show low mortality and significant recruitment after a fire (García-Meneses, 2012; Rivadeneira et al., 2020), while species like *P. chiliensis* is not affected by fire (Ramírez et al., 2017). Therefore, it is essential to explore if this positive response to fire is present in all species, and if functional trait values change with fire disturbance.

This study aims to evaluate how species diversity and abundance changes under fires. Additionally, we studied how functional traits respond to fire disturbance over a temporal scale at three points in time (No fire prior to 1985, 1988 and 2002) for the genus *Puya* in the páramo ecosystem. We specifically tested three hypotheses: (1) Given that some *Puya* species have been shown to resist fire, we hypothesize that recent fires (2002) have no effect on diversity and abundance compared to areas with no recent fire. (2) We also expect a decrease in SLA and higher LDMC in *Puya* after a fire, as shown in other studies. (3) Regarding mycorrhizal colonization, we expect to find colonization, given that in *Puya trianae* (a species widely distributed in the Colombian páramo) vesicles and arbuscules have been reported (Guerrero Forero, 1996). Nonetheless, we expect less colonization in the fire affected zones.

2 MATERIALS AND METHODS

2.1 Study site and soil analysis

The Matarredonda Natural Reserve (Fig. 1), located in the municipality of Choachí, at an elevation of 3300 m.a.s.l., was selected for this study. The average temperature is 8.8 °C, with a daily maximum of 29.6 °C and a minimum of 2.6 °C (Leon-Garcia & Lasso, 2019). The precipitation ranges from 1000 to 1500 mm annually (Cruz & Lasso, 2021). This reserve is part of the Cruz Verde páramo, one of the 36 páramo complexes in the country.

We delineated and analyzed the areas impacted by fires within the Matarredonda Natural Reserve. The mapping of burnt areas relied on Landsat satellite imagery, delivering optical data with a spatial resolution of 30 meters. This mapping spanned from 1985 to 2022, starting with the first complete year of available satellite imagery. The classification of burnt areas involved the creation of annual mosaics, incorporating the lowest normalized burnt ratio values for each pixel. These mosaics integrated optical bands and several spectral indices (NDVI, NBR, dNBR, and MIRBI), alongside considerations for temporal change derived from the variance between the current year's and previous years' values. Burnt area probability mapping employed a random forest classifier, utilizing these spectral and temporal parameters as input. An expert satellite image interpreter curated the training data for the classifier. To mitigate uncertainty associated with small burn patches, only burn scars exceeding 0.3 hectares were considered. However, the effectiveness of burnt area detection faced limitations or complete absence during the years 1993-1998 due to cloud cover and limited image availability.

Areas affected by fires in 1988 and 2002 were selected, as well as areas that have not been impacted by fire, at least prior to 1985, although with the caveat of the uncertainty in burnt area detection during part of the 90’s. We corroborated the fire with the owners of the reserve for all the 2000’s fires. Two transects of 100 x 40 m each were established in these areas. In each transect, soil samples were collected to a 10 cm depth at three randomly chosen points and mixed into one sample per site. For the soil analysis we obtained pH, electric conductivity (CE), total Nitrogen (N Total) and other variables found in Table S1. The texture of soil samples was determined as silt loam, with an organic matter average of 20%.

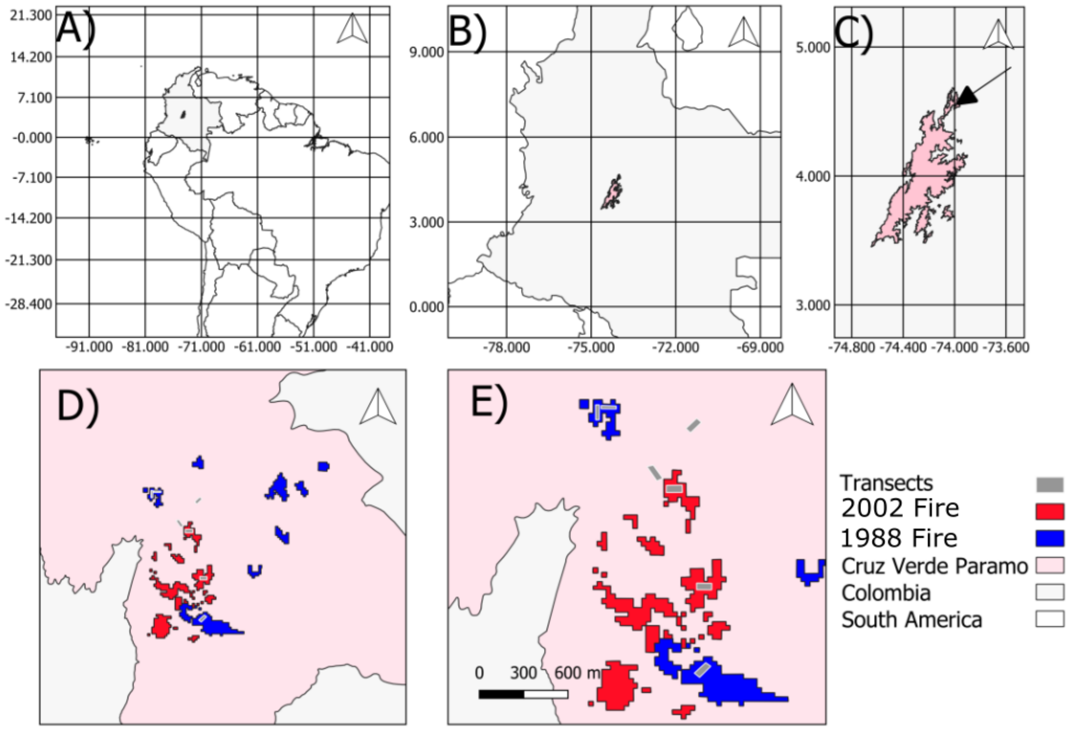

Figure 1. Study site with fires occurring in 1988 and 2002, and no fires prior to 1985. A) Location of Colombia on the map. B) Location of the Cruz Verde páramo within Colombia. C) Cruz Verde páramo with an indication (arrow) of the study area in the northern part of Cruz Verde páramo. D) Study area with regions unaffected by fire (pink) and affected by fire in 1988 (blue) and 2002 (red). E) Transects were placed inside and outside the areas impacted by fire.

2.2 Biodiversity indices

In each transect, the species present were identified using field guides (Cruz et al., 2016; Betancur et al., 2018) and herbarium samples. The number of individuals per species was also recorded. Four species of *Puya* have been described for Matarredonda: *Puya goudotiana*, *P. nitida*, *P. santosii*, *P. trianae* (Cruz et al., 2016). Others are also found in the Cruz Verde páramo area such as *P. bicolor* (Pico, 2020), *P. loca* (Madriñán, 2015), and *P. cryptantha* (Betancur, 2015; Gouda et al., 2023). Using the data on abundance and richness, we calculated the following indices (Moreno, 2001): Margalef for richness; McIntosh's D for dominance; first-order Jacknife (Jack 1) to estimate the hypothetical number of species in the zone. These indices only include *Puya* diversity, giving us an estimated diversity of the genus.

2.3 Functional traits

In this study, we measured 13 functional traits that reflect plant ecological strategies (conservative vs. acquisitive) and response to disturbance (Table S2). In addition to aboveground traits, we decided to include seven root traits that are related to mycorrhizal associations, as well as to resource acquisition and mobilization. Functional traits were measured using standard protocols (Pérez-Harguindeguy et al., 2016). Among the aboveground traits' data, we recorded height (H, cm) from the base of the rosette to the apex of the leaves. The rosette diameter (RD, cm) was measured with diameter tape by measuring the distance between the tips of the farthest leaves. Leaf traits were obtained by collecting three leaves, as healthy as possible, from the intermediate zone of the rosette. At the time of collection, leaf thickness data (Lt, mm) were obtained by measuring the thickness with calipers at three parts of the leaf (near the base, middle of the leaf, and near the tip). Other data collected included leaf weight (W, g), and area (LA, cm^2). Photographs of the leaves (Fig. S1A) were analyzed using ImageJ software (Rasband, 1997) to calculate LA. The leaves were then dried in an oven for 96 h at a temperature of 60 °C, and subsequently weighed to obtain leaf dry matter content (LDMC, mg g^{-1}); specific leaf area (SLA, cm^2 g^{-1}) was calculated as leaf area divided by leaf dry weight.

Root traits were obtained from roots collected at the base of the rosettes for each individual. Any soil residues were removed from the roots, and they were scanned using an Epson Scanner at 1200 DPI. The obtained images were analyzed using RhizoVision Explorer (Seethepalli & York, 2020) with the following thresholding parameters: 180-200 for the thresholding level, 3 for filtering non-root objects, and 2 for enabling edge smoothing. For the analyses we used samples that contained at least 77% fine roots (1 mm in diameter). Subsequently, the roots were dried for 36 h at a temperature of 60 °C and weighed. We also calculated specific root length (SRL, cm g^{-1}), specific root area (SRA, cm^2 g^{-1}), root tissue density (RTD, g cm^{-3}), and root branching index (Bi, root tips cm^{-1}). Branching frequency (BF, mm), average diameter (AD, mm) and surface area (SA, mm^2) were obtained directly from the software.

These traits were selected because they provide insights into whether there is a response to fires, and indicate if the ecological strategy is acquisitive or conservative (Table S2). Among these traits, increases in SLA and SRL could suggest a more acquisitive strategy (Shao et al., 2019), while an increase in LDMC indicates a conservative strategy in response to fires. Plant height (H) has been related to tolerance or resistance to fire disturbance and traits such as Lt

(Maracahipes et al., 2018) and LDMC (Toledo-Aceves et al., 2019) can indicate resistance to physical damage. SRL increases in non-resprouting plants affected by fire, showing more slender ramifications (Paula & Pausas, 2011).

2.4 Mycorrhizal colonization

We used a standardized staining process (Koske & Gemma, 1989) for roots, but modified it to achieve a clearer staining. We cut the roots into approximately 2 mm sections per individual, and these were stored in 80% ethanol. The ethanol was removed from each tube before the staining process, and enough KOH was added to immerse the roots. The tubes were then placed on a hot plate at 90 °C for 20 min, stirring at the 10-min mark. We then removed the KOH solution, and the roots were rinsed three times with distilled water.

Next, 3% H_2O_2 was added to the roots, repeating the 20-min heating while stirring at the 10-min mark. After this, the roots were washed twice with distilled water, and then 1% HCl was applied to the roots for 5 min. After removing the HCl, we applied a staining mixture, consisting of a solution of vinegar with 5% India ink by volume for 20 min, repeating the heating process. The solution was removed, and the roots were cleaned three times with distilled water. Finally, we stored the roots in a destain solution (50% glycerol, 45% distilled water, 5% HCl). Subsequently, colonization was determined by inspecting the root sections on a grid slide with 42 intersections, assessing the presence of structures such as vesicles (Fig. S1B) or arbuscules at each intersection.

We used a two-way ANOVA to understand the differences in colonization between fires and species. A Wilcoxon test was performed to find differences between *P. nitida* in the 1988 fire and the no fire area, and a Kruskal-Wallis test, to establish differences in *P. goudotiana* in the three moments. *Puya cf. bicolor* was excluded from this analysis, as all the root material was damaged by the staining process (even when decreasing the KOH and HCl concentrations).

2.5 Data Analysis

For the data analysis, we used R version 4.3.0 (R Core Team, 2023). Principal component analysis (PCA) was conducted using FactoMineR v 2.9 (Husson et al., 2023) and factoextra v 1.0.7 (Kassambara & Mundt, 2020).

Initially, we obtained the mean of the three trait measurements per individual. Normal distribution and homoscedasticity were assessed using the Shapiro-Wilk test and Levene's test using the car package v 3.2.1 (Fox et al., 2023). Given that *P. goudotiana* was present in the three fires (No fire, 1988, 2002), trait analysis was performed with an ANOVA, if traits followed a normal distribution and exhibited equal homoscedasticity. If either of these conditions was not met, the Kruskal test was performed. For *P. nitida,* comparisons were made at two fires (No fire, 1988). In this case, a Mann-Whitney U or T test was conducted. The ggplot2 package v 3.4.4 (Wickham et al., 2023) was utilized for making figures.

To understand trait changes between sites, a classical multidimensional scaling on the traits was performed, and an ordination using the vegan package 2.6-4 (Oksanen et al., 2022) to include soil variables in the functional trait analyses; these were graphed using ggordiplots (Quensen et al., 2023) to the minimum significant level for the soil variables.

3 RESULTS

3.1 Diversity of *Puya* spp.

We collected four species of *Puya* in Matarredonda: *P. goudotiana*, *P. santosii*, *P. nitida*, *P. cf. bicolor*. Fire history has an impact on the abundance of the four species in the area, where regions affected by recent fires experienced lower species richness. The fire in 2002 had the most notorious impact on species richness, with only *P. goudotiana* present. This was followed by the 1988 fire, which had two species: *P. goudotiana* and *P. nitida* (Fig. 2). *Puya goudotiana* was the only species found in all sites, with a total of 306 individuals and the highest abundance in the recent fire (2002 fire: 116, 1988 fire: 99, no fire: 91). *Puya nitida* had 713 individuals (no fire: 665, 1988 fire: 48); *P. cf. bicolor* had 6 individuals and *P. santosii* had 45 in the no-fire area.

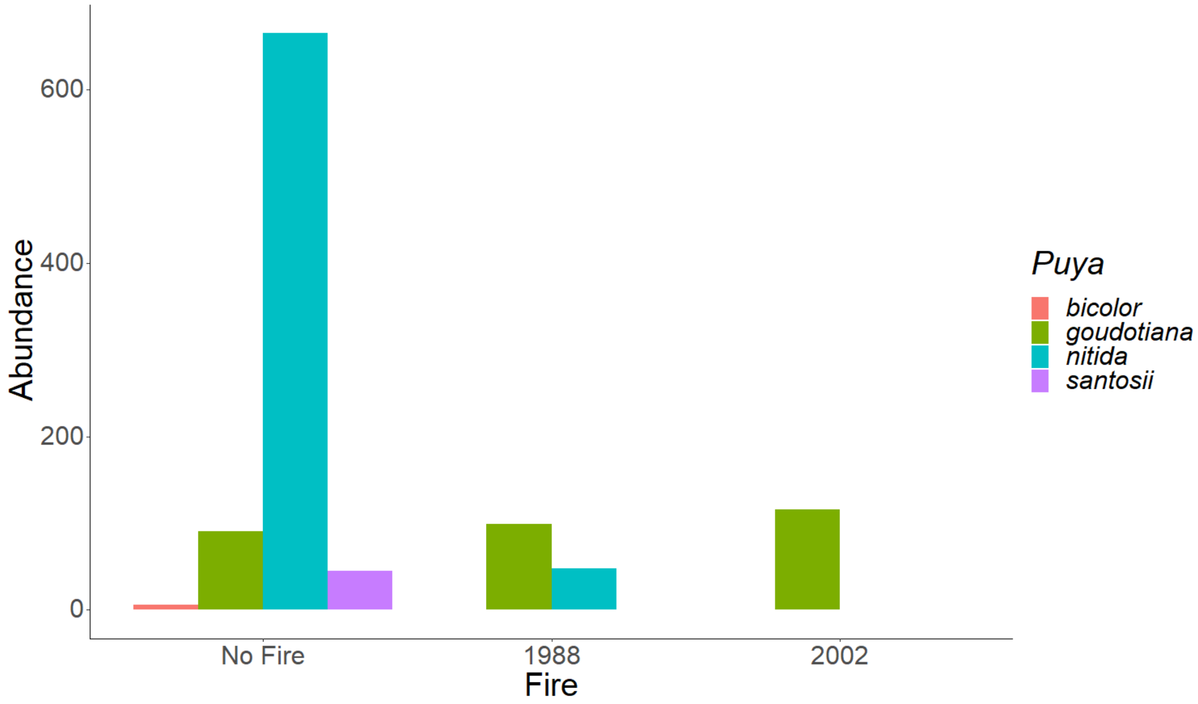

Figure 2. Abundance per species in the established transects in páramo de Cruz Verde (No fire, 1988, 2002).

The impact of fires on diversity was compared in the fires affected (1988 and 2002) and no fire transects (Table 1). The Jacknife index estimated six species in the area (Jack 1: 5.7), which is higher than the actual diversity reported. When combining the fire zones, the Margalef index estimated a long-term effect, reducing richness (Margalef Fire: 0.179; No Fire: 0.448) after a fire event. The dominance of *P. goudotiana* increased in the area impacted by fires (McIntosh D Fire: 0.575, No Fire: 0.345).

Table 1. Margalef richness index, McIntosh (D) for sites affected by fire and without fire. First order Jacknife estimation (Jack 1)

	Index		
Site	*Margalef*	*McIntosh D*	*Jack 1*
Fire	0.179	0.575	5.7
No fire	0.448	0.345	

3.2 Functional traits

Puya cf. bicolor, *P. nitida*, and *P. santosii* were grouped based on traits such as SLA and SRA (Fig. 3), while *P. goudotiana* differed from them, especially in terms of LA, Lt, LDMC, H, RD. However, the relationships with root traits are not as clear. In dimension 1, foliar traits dominate, and in dimension 2, root traits predominate. Although both dimensions explain 47.1% of the variation, it can be determined that conservative traits primarily explain the grouping of *P. goudotiana* individuals, while the other three species are mediated by acquisitive traits (i.e., SLA).

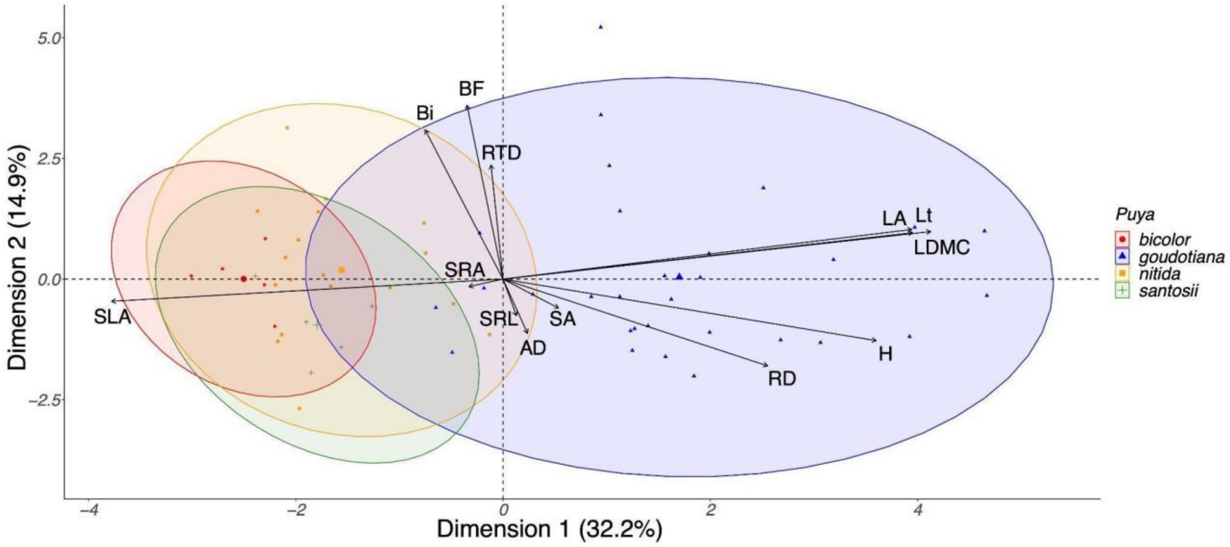

Figure 3. PCA of individuals collected per species in páramo de Cruz Verde, with traits. Red*:* *Puya cf. bicolor*, green*: santosii*, orange*: P. nitida*, blue*: P. goudotiana*. Functional traits measured include: Average diameter (AD, mm), Branching frequency (BF, mm), Branching index (Bi, root tips mm^{-1}), Leaf area (LA, cm^{2}), Leaf dry matter content (LDMC, mg g^{-1}), Leaf thickness (Lt, mm), Plant height (H, cm), Root tissue density (RTD, g cm^{-3}), Rosette diameter (RD, cm), Specific leaf area (SLA, cm^{2} g^{-1}), Specific root area (SRA, mm^{2} g^{-1}), Specific root length (SRL, mm g^{-1}), Surface area (SA, mm^{2}).

When analyzing the aboveground and root traits separately**,** a greater percentage of the variation is explained by aboveground traits, 76.7% (Fig. 4B), than by root traits (49.1% ; Fig. 4A). In the aboveground traits, the SLA relationship remains as the dominant trait grouping *P. santosii*, *P. nitida*, and *P. cf. bicolor*, while *P. goudotiana* shows wide phenotypic variation, and many traits associated with its variability. However, when evaluating root traits, there is no clear separation in these species.

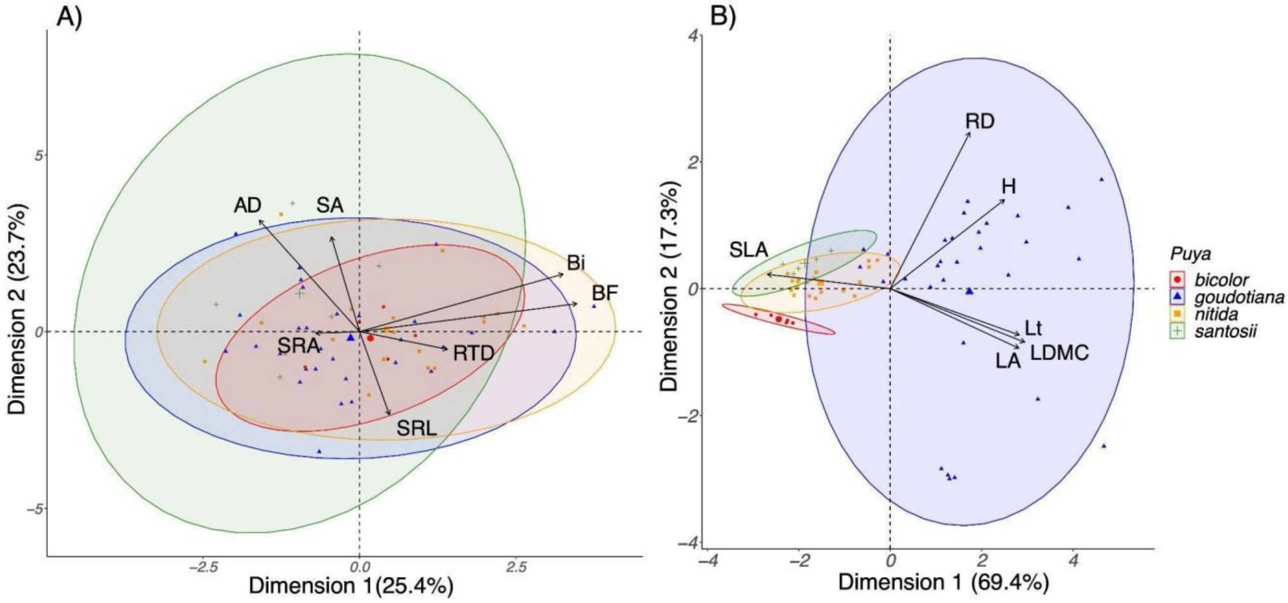

Figure 4. PCA of A) Radicular traits: Average diameter (AD, mm), Branching frequency (BF, per mm); Branching index (Bi, root tips mm^{-1}), Root tissue density (RTD, g cm^{-3}), Specific root area (SRA, mm^{2} g^{-1}), Specific root length (SRL, mm g^{-1}), Surface area (SA, mm^{2}); and B) Aboveground traits: Leaf area (LA, cm^{2}), Leaf dry matter content (LDMC, mg g^{-1}), Leaf thickness (Lt, mm), Plant height (H, cm), Rosette diameter (RD, cm), Specific leaf area (SLA, cm^{2} g^{-1}) by species. Red*: Puya cf. bicolor*, green*: P. santosii*, orange*: P. nitida*, blue*: P. goudotiana*.

Given that *P. goudotiana* was the only species present in the three fires, over a 35-year period, we compared the measurements of six aboveground traits (Fig. 5) and seven belowground traits (Fig. S2). The results indicate that fire events do not have a significant effect on *P. goudotiana*'s traits ($p > 0.05$). However, an increase in the mean of aboveground traits is observed for the 2002 fire event (except for SLA). For root traits, the mean tended to increase in the 1988 fire event compared to the 2002 and no fire, except for RTD, where the 2002 fire event was higher (Fig. S2).

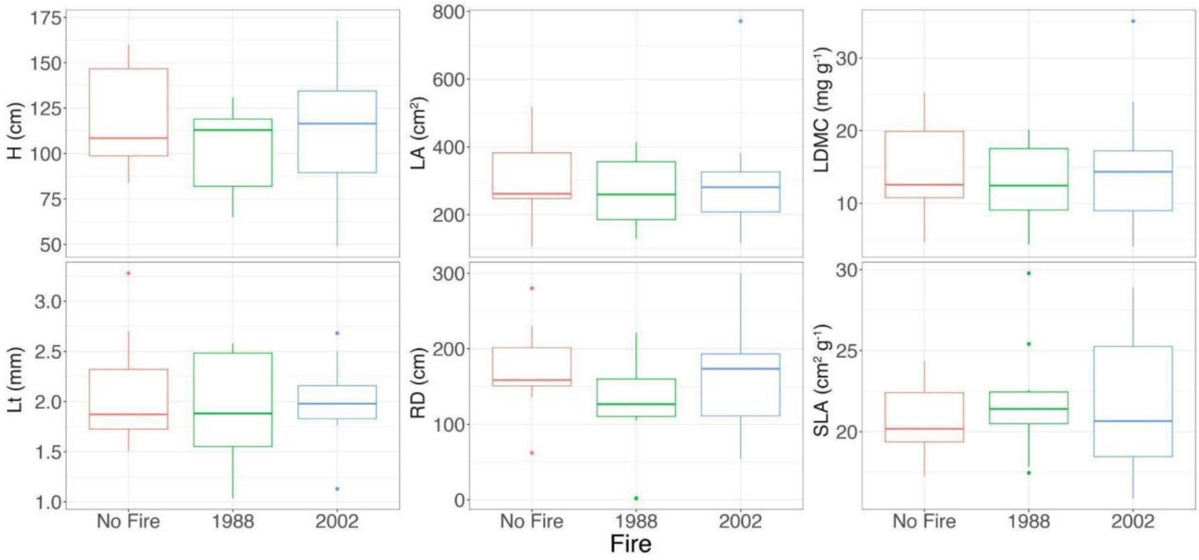

Figure 5. *Puya goudotiana* aboveground traits in three sites: No fire, 1988 fire, 2002 fire. From left to right, H: Plant height (cm), LA: Leaf area (cm^2), LDMC: Leaf dry matter content ($mg\ g^{-1}$), Lt: Leaf thickness (mm), RD: Rosette diameter (cm), SLA: Specific leaf area ($cm^2\ g^{-1}$).

3.3 Soil analysis and functional traits

All the collected soils (Table S1) were classified as silt loams and had an acidic pH (No fire: 4.3, 1998: 4.58, 2002: 4.35). Almost one fifth of the composition was organic matter (No fire: 19.1%, 1988: 21.6%, 2002: 21.2%). The no fire zone had the lowest percentage of N, 0.925%, compared to the 1988 fire, with 1.04% and 2002 with 1.02%. The no fire transects had the most calcium (34.7 mg kg^{-1}), potassium (170 mg kg^{-1}) and interchangeable acidity (1030 mg kg^{-1}). Meanwhile, the 2002 fire had the highest amount of sulfur (S; 8.67 mg kg^{-1}) and the least potassium (99.5 mg kg^{-1}). The soil characteristics did not have a significant effect on aboveground traits and the combination with radicular traits (Fig. S3) or on only radicular traits (Fig. S4), as root traits were not related to any soil variable.

No intraspecific differences were observed for *P. nitida* between sites for aboveground traits and most root traits (Fig. S5). However, the 1988 fire showed a significant decrease in branching frequency (Fig. 6A) ($p = 0.007$) and increase in average diameter (Fig. 6B) ($p = 0.007$), compared to the no fire zone.

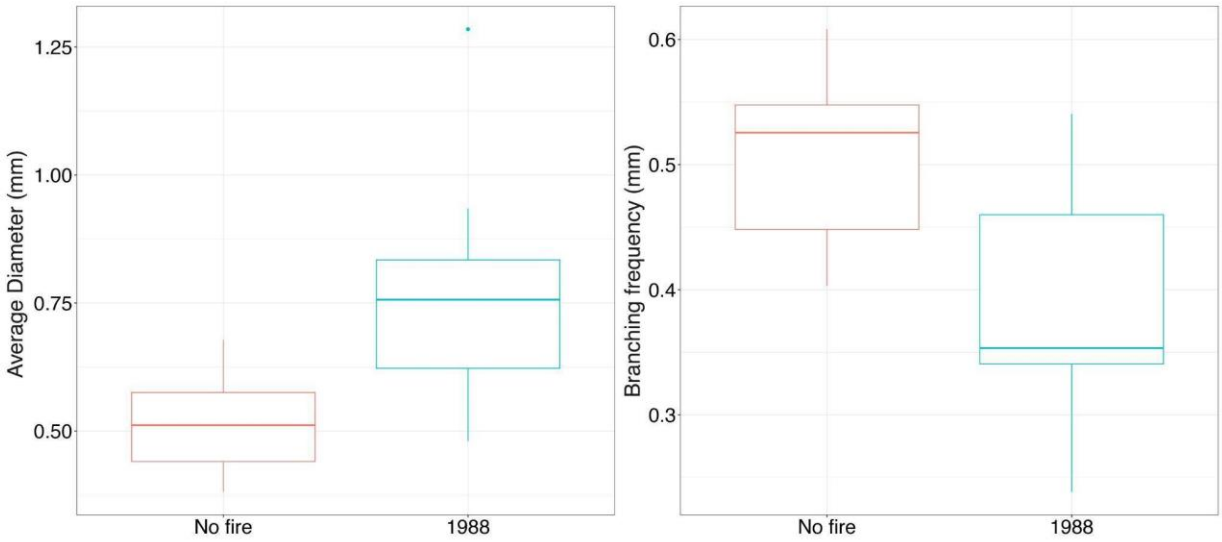

Figure 6. Significantly different root traits for *P. nitida* (p = 0.05) from left to right: A) Average diameter (mm) (p = 0.007), and B) branching frequency (per mm) (p = 0.007), in two fires categories (red: No fire, blue: 1988).

3.4 Mycorrhizal colonization

Three species (*P. goudotiana*, *P. nitida*, *P. santosii*) were colonized by arbuscular mycorrhizae, based on the presence of vesicles; *P. cf. bicolor* was excluded as root damage occurred in the staining process. Colonization is not high at the genus level (less than 16%), except for *P. nitida* which was colonized at 24.32% in the no fire zone (Table 2). This species shows the highest percentage of mycorrhizae, and its colonization was affected by the 1988 fire, decreasing to 14.32%. *Puya goudotiana* had its highest colonization in the 2002 fire. However, no significant differences were found between species (p = 0.608) or fire events (p = 0.238). There were also no significant differences between *P. goudotiana* (p = 0.995) and *P. nitida* (p = 0.092) in response to fire.

Table 2. Presence of mycorrhizal colonization in *Puya* roots. Percentage of colonization was obtained by dividing the colonized intersection by the total (colonized and non-colonized roots) per species and fire. NF = No fire. Dashes (-) indicate species not collected in a given fire site.

	Colonized			**Non-Colonized**			**Percent colonization (%)**		
Fire	*goudotiana*	*nitida*	*santosii*	*goudotiana*	*nitida*	*santosii*	*goudotiana*	*nitida*	*santosii*
NF	14	63	5	98	196	37	12.5	24.32	11.9
1988	19	6	-	165	54	-	10.3	10	-
2002	17	-	-	91	-	-	15.7	-	-

4 DISCUSSION

This study examined the impact of fire on diversity and abundance of *Puya*, as well as above- and belowground functional traits. We found results contrary to our three hypotheses. We had hypothesized that there would be no effect of fire on *Puya* diversity and abundance. However, only one of four species, *P. goudotiana,* was present in all sites (no fire and 1988 and 2002 fire sites) (Fig. 2). On our second hypothesis, we expected to find significant differences in SLA and LDMC after a fire. Yet, *P. goudotiana* showed no significant differences in any functional traits (Fig. 5) while *P. nitida* exhibited significant differences in root average diameter and branching frequency, but not in LDMC and SLA as hypothesized (Fig. 6). We expected to find less colonization in fire affected zones in our third hypothesis. However, mycorrhizal colonization did not significantly change between fires, except for *P. nitida* that showed a non-significant decrease of 14% in colonization from NF to the 1988 fire (Table 2).

In this study, we collected four of the seven species of the genus *Puya* reported in the Cruz Verde páramo (Betancur, 2015; Cruz et al., 2016; Pico, 2020). Fire impacted the richness of these sites (Fig. 2) but affected species differently. We found *P. goudotiana* in all sampled areas. This may indicate that the species is tolerant to fire or has the capacity to rapidly establish after disturbance, while others like *P. cf. bicolor* and *P. santosii* could be more sensitive to fire in the long term. Species such as *P. nitida* may be able to colonize areas that have not been impacted by fires over the long run, such as the 1988 fire (Fig. 2). Thus, our results show a decrease in diversity in fire affected zones, suggesting that high fire recurrence may homogenize the páramo landscape (Renvoize et al., 2000), favoring the establishment of few species such as *P. goudotiana*. However, fire suppression may also be problematic in ecosystems where fire has been historically recurrent. The buildup of dead biomass acting as fuel increases the severity of the fires (Bond & Keane, 2017) and suppression can cause changes in community composition, leading to an increase of both pathogen epidemics and insect outbreaks (Hawkins, 2004). Although fire has an impact on páramo diversity, due to an increase in tussock grass abundance, as time passes the tussock thins out, allowing the colonization of other species (Zomer & Ramsay, 2021), possibly allowing the establishment of *P. nitida*.

Although the mechanisms for species establishment and resistance to fire are not yet fully understood, they can be related to the intensity of the events. In coniferous forests, severe fires consume the organic layer and seed bank, while those of lower intensity only consume the organic layer, allowing the dominant species on the seedbank to regenerate (Heinselman, 1973). In other ecosystems, such as shrublands and grasslands with long fire history, fire has no effect on seedbank richness or abundance, but high severity fire reduces both (Shi et al., 2022). Accordingly, fire in the Brazilian Cerrado had no effect on the overall seedbank density, yet monocot seed density values did not reach pre-fire values (de Andrade & Miranda, 2014). In the páramo ecosystem, high disturbance by fire and grazing tends to increase the species abundance of *Paspalum hirtum* and *Elocharis acicularis* (Premauer, 2004). In this study, we know the fire recurrence in the study area, but we do not know the intensity of those events. However, we can hypothesize that the seedbanks of species such as *P. goudotiana* are not affected by these events (even if the intensity was high). Interestingly, some studies have reported that the seed moisture content of *P. santosii* and *P. nitida* is less than 15% (Calderón-Hernández & Pérez-Martínez, 2018). Seeds with this moisture content, in fire-prone ecosystems, have been found to sustain a temperature increase of 38 °C (Tangney et al., 2019). Therefore, this would imply that these seeds would perish under fire events where the soil temperature is more than 40 °C. *Puya goudotiana* could thus have a higher temperature tolerance to persist and establish in more recent burned zones.

Functionally, *P. goudotiana* shows no change over the evaluated timescale. According to our hypothesis, we expected changes in traits, such as a reduction in SLA or an increase in LDMC and LT, in areas with recent fire. In flood-prone areas, the foliar traits of trees remain stable post-fire (de Almeida Souza et al., 2019), where a high presence of water keeps traits acting similarly. In páramos, precipitation is abundant, between 1000-1500 mm annually in Matarredonda (Cruz & Lasso, 2021). This could therefore explain the trait stability for this species. The presence of *P. goudotiana* in all fires, along with higher LDMC (compared to the other species; Fig. 4), which is a trait favoring flammability (Bond & Bond, 1995; Santacruz-García et al., 2019), could be an indication of the "*Kill thy Neighbor*" hypothesis. In this hypothesis flammable traits are favored if there is a fitness benefit with wildfires (Varner et al., 2022). As previously mentioned, *P. goudotiana* seedbank might be resistant to high intensity fires, and their higher LDMC and LA may increase the litter depth. Litter depth has been shown as the factor increasing flame temperature in fire-prone Mediterranean ecosystems (Ganteaume et al., 2011). This temperature increase could exclude other *Puya* species. However, studies on litter depth, temperature and seedbanks are needed to corroborate these hypotheses.

Puya nitida was the only other species present in the 1988 fire zone (Fig. 2), and there are changes in some root functional traits (Fig. 6; Fig. S5). Individuals in areas without fire had a higher branching frequency and a smaller average diameter compared to those with previous disturbances. Larger diameter and lower branching frequency indicate an adaptation to lower resource absorption but greater resistance to climatic events, which are typical of a more conservative response (Hogan et al., 2020) in affected areas. In areas without the effect of the fire (prior to 1985), they adopt a more acquisitive strategy. However, aboveground traits do not support this pattern. This difference between above- and belowground traits may be due to different evolutionary pressures (Bergmann et al., 2017; Caruso et al., 2019), chemical soil characteristics that shape root traits (Hogan et al., 2020), and/or changes caused by the mycorrhizal colonization (Brundrett, 2002; Hetrick, 1991; Perez-Lamarque et al., 2022). Our results suggest that both sets of traits (above- and belowground) are functionally independent or uncoupled. This has been found in other studies comparing stem and leaf traits (e.g., Baraloto et al., 2010) and leaf vs. stem and root traits (e.g., Fortunel et al., 2012), resulting in weaker functional coordination (de la Riva et al., 2016). Therefore, our results do not support the all plant coordination hypothesis (e.g., Carvalho et al., 2020; Messier et al., 2017).

Mycorrhizal colonization tended to decrease from the no fire area to the 1988 fire. However, colonization was not significantly affected by long-term fires, where perhaps the fire-fungus relationship is not present, or it is not evident on a large timescale. Previous studies have shown that colonization is reduced only in the first four months after fire (Barker et al., 2013) and full recovery is achieved if there is no subsequent disturbance (Dove & Hart, 2017). There is also the possibility that fire does not have an effect on root colonization of arbuscular fungi in páramo. In tallgrass prairies (Eom et al., 1999), Australian sclerophyllous shrublands (Bellgard et al., 1994) and North American sand-hill herbs (Anderson & Menges, 1997), fire does not seem to impact mycorrhizal colonization. In the Chaco region in Argentina, diversity and richness of arbuscular fungi spores decreased, but the spore density was the same post-fire (Longo et al., 2014). Hence, *Puya* mycorrhizal colonization, not being affected by fire, follows the trend of other ecosystems that present this disturbance. However, the diversity of fungi that colonizes *Puya* is yet to be established. We assume that they are mainly arbuscular mycorrhizae

(AM) given the structures identified (Fig. S1), and that they are the dominant type across the elevation gradient (Leon et al., 2023; Rendon-Espinosa et al., In review)

Solving the puzzle of the effect of fire on mycorrhizae and *Puya* species could provide insight into the genus *Puya's* ability to colonize areas affected by wildfires. Given the important ecological role of *Puya* in the páramo ecosystem, it is necessary to continue with studies to understand how species respond to fire and the interactions with mycorrhizae. This study can be used as a starting point for the study of functional traits in relation to fires affecting the Colombian páramos.

AUTHOR CONTRIBUTIONS

Juan Jose Pinzon: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (lead); visualization (equal); writing – original draft (lead); writing – review and editing (supporting). Stijn Hantson: Conceptualization (equal); methodology (equal); writing – review and editing (supporting). Adriana Sanchez: Conceptualization (equal); formal analysis (supporting); methodology (equal); supervision (lead); validation (lead); visualization (equal); writing – original draft (supporting); writing – review and editing (lead).

ACKNOWLEDGMENT

We would like to thank the University of Rosario for providing the funding and facilities for conducting this study. We would also like to acknowledge V. Vargas, Y. Hoyos, C. Marquez, J.J. Ceballos, J. Diaz, M. Torres, C. Peralta for helping with field data collection and data processing. We are grateful to the Sabogal family, owners of the Matarredonda Natural Reserve, for letting us work and collect samples in their páramo.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare

DATA AVAILABILITY STATEMENT

All the collected data in this study, figures, images and R script, are available in https://github.com/Antarticc/Puya_CV_2024

REFERENCES

Abedi, M., Omidipour, R., Hosseini, S. V., Bahalkeh, K., & Gross, N. (2022). Fire disturbance effects on plant taxonomic and functional β-diversity mediated by topographic exposure. *Ecology and Evolution*, *12*(1), e8552. https://doi.org/10.1002/ece3.8552

Agbeshie, A.A., Abugre, S., Atta-Darkwa, T. *et al.* A review of the effects of forest fire on soil properties. *J. For. Res.* **33**, 1419–1441 (2022). https://doi.org/10.1007/s11676-022-01475-4

Anderson, R. C., & Menges, E. S. (1997). Effects of fire on sandhill herbs: nutrients, mycorrhizae, and biomass allocation. *American Journal of Botany*, *84*(7), 938-948. https://doi.org/10.2307/2446284

Archibald, S., & Hempson, G. P. (2016). Competing consumers: contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1703), 20150309. https://doi.org/10.1098/rstb.2015.0309

Baraloto, C., Timothy Paine, C.E., Poorter, L., Beauchene, J., Bonal, D., Domenach, A.-M., Hérault, B., Patiño, S., Roggy, J.-C. and Chave, J. (2010), Decoupled leaf and stem economics in rain forest trees. Ecology Letters, 13: 1338-1347. https://doi.org/10.1111/j.1461-0248.2010.01517.x

Barker, J. S., Simard, S. W., Jones, M. D., & Durall, D. M. (2013). Ectomycorrhizal fungal community assembly on regenerating Douglas-fir after wildfire and clearcut harvesting. *Oecologia*, *172*(4), 1179-1189. https://doi.org/10.1007/s00442-012-2562-y

Bellgard, S. E., Whelan, R. J., & Muston, R. M. (1994). The impact of wildfire on vesicular-arbuscular mycorrhizal fungi and their potential to influence the re-establishment of post-fire plant communities. *Mycorrhiza*, *4*(4), 139-146. https://doi.org/10.1007/BF00203532

Bergmann, J., Ryo, M., Prati, D., Hempel, S., & Rillig, M. C. (2017). Root traits are more than analogues of leaf traits: the case for diaspore mass. *New Phytologist*, *216*(4), 1130-1139. https://doi.org/10.1111/nph.14748

Betancur, J. (2015). *Puya.Catálogo de plantas y líquenes de Colombia* (R. Bernal, S. R. Gradstein, & M. Celis, Eds.). Instituto de Ciencias Naturales, Universidad Nacional de Colombia.

Betancur, J., Gonzalez, M. F., Hernandez Aldana, E., Castro, C., Gomez Suescun, F., Hernandez Rodriguez, D. E., Jaimes R, M. S., & Galindo, R. (2018). *Los colores del páramo de Chingaza. Guía de plantas*. Editorial UN.

Bond, W., & Bond, M. (1995). Kill Thy Neighbour: An Individualistic Argument for the Evolution of Flammability. *Oikos*, *73*. https://doi.org/10.2307/3545728

Bond, W. J., & Keane, R. E. (2017). Fires, Ecological Effects of☆. En *Reference Module in Life Sciences*. Elsevier. https://doi.org/10.1016/B978-0-12-809633-8.02098-7

Bond, W., & Keeley, J. E. (2005). Fire as a global «herbivore»: the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, *20*(7), 387-394. https://doi.org/10.1016/j.tree.2005.04.025

Bond, W., Woodward, F. I., & Midgley, G. F. (2005). The global distribution of ecosystems in a world without fire. *New Phytologist*, *165*(2), 525-538. https://doi.org/10.1111/j.1469-8137.2004.01252.x

Bowman, D. M. J. S., Balch, J., Artaxo, P., Bond, W. J., Cochrane, M. A., D'Antonio, C. M., DeFries, R., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., Kull, C. A., Mack, M., Moritz, M. A., Pyne, S., Roos, C. I., Scott, A. C., Sodhi, N. S., & Swetnam, T. W. (2011). The human dimension of fire regimes on Earth. *Journal of Biogeography*, *38*(12), 2223-2236. https://doi.org/10.1111/j.1365-2699.2011.02595.x

Brundrett, M. C. (2002). Coevolution of roots and mycorrhizas of land plants. *New*

Phytologist, *154*(2), 275-304. https://doi.org/10.1046/j.1469-8137.2002.00397.x

Brundrett, M. C. (2009). Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. *Plant and Soil*, *320*(1), 37-77. https://doi.org/10.1007/s11104-008-9877-9

Burton, C., Kelley, D., & Thiery, W. (2023). *Global burned area increasingly explained by climate change*.

Buscardo, E., Rodríguez-Echeverría, S., Barrico, L., García, M. Á., Freitas, H., Martín, M. P., De Angelis, P., & Muller, L. A. H. (2012). Is the potential for the formation of common mycorrhizal networks influenced by fire frequency? *Soil Biology and Biochemistry*, *46*, 136-144. https://doi.org/10.1016/j.soilbio.2011.12.007

Calderón-Hernández, M., & Pérez-Martínez, L. (2018). Seed desiccation tolerance and germination of four Puya (Bromeliaceae) high-andean tropical species from Colombia. *Caldasia*, *40*, 177-187. https://doi.org/10.15446/caldasia.v40n1.67740

Caruso, Christina & Maherali, Hafiz & Martin, Ryan. (2019). A Meta-analysis of Natural Selection on Plant Functional Traits. International Journal of Plant Sciences. 181. 10.1086/706199.

Carvalho B, Bastias CC, Escudero A, Valladares F, Benavides R. Intraspecific perspective of phenotypic coordination of functional traits in Scots pine. PLoS One. 2020 Feb 13;15(2):e0228539. doi: 10.1371/journal.pone.0228539. PMID: 32053614; PMCID: PMC7018023.

Christmann, T., & Oliveras, I. (2020). Nature of Alpine Ecosystems in Tropical Mountains of South America. En M. I. Goldstein & D. A. DellaSala (Eds.), *Encyclopedia of the World's Biomes* (pp. 282-291). Elsevier. https://doi.org/10.1016/B978-0-12-409548-9.12481-9

Cleef, A. M. (1981). The vegetation of the páramos of the Colombian Cordillera Oriental. *Diss. Bot.*, *61*, 1-320.

Cochrane, M. A., & Ryan, K. C. (2009). Fire and fire ecology: Concepts and principles. En M. A. Cochrane (Ed.), *Tropical Fire Ecology: Climate Change, Land Use, and Ecosystem Dynamics* (pp. 25-62). Springer. https://doi.org/10.1007/978-3-540-77381-8_2

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., Steege, H. ter, Morgan, H. D., Heijden, M. G. A. van der, Pausas, J. G., & Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, *51*(4), 335-380. https://doi.org/10.1071/bt02124

Costa, C., Dwyer, L., Hamilton, R., Hamel, C., Nantais, L., & Smith, D. (2000). A Sampling Method for Measurement of Large Root Systems with Scanner-Based Image Analysis. *Agron J*, *92*, 621-627. https://doi.org/10.2134/agronj2000.924621x

Cruz, M., Avila, F., & Lasso, E. (2016). *Parque Ecológico Matarredonda - Laguna El Verjón - Choachí, COLOMBIA FLORA del PÁRAMO de MATARREDONDA*. https://fieldguides.fieldmuseum.org/es/gu%C3%ADas/gu%C3%ADa/829

Cruz, M., & Lasso, E. (2021). Insights into the functional ecology of páramo plants in Colombia. *Biotropica*, *53*(5), 1415-1431. https://doi.org/10.1111/btp.12992

de Almeida Souza, A. H., Batalha, M. A., Casagrande, J. C., Rivaben, R. C., Assunção, V. A., Pott, A., & Alves Damasceno-Junior, G. (2019). Fire can weaken or trigger functional responses of trees to flooding in wetland forest patches. *Journal of Vegetation Science*, *30*(3), 521-532. https://doi.org/10.1111/jvs.12719

de Andrade, L. A. Z., & Miranda, H. S. (2014). The dynamics of the soil seed bank after a fire event in a woody savanna in central Brazil. *Plant Ecology*, *215*(10), 1199-1209.

https://doi.org/10.1007/s11258-014-0378-z

de la Riva, E.G., Tosto, A., Pérez-Ramos, I.M., Navarro-Fernández, C.M., Olmo, M., Anten, N.P.R., Marañón, T. and Villar, R. (2016), A plant economics spectrum in Mediterranean forests along environmental gradients: is there coordination among leaf, stem and root traits?. J Veg Sci, 27: 187-199. https://doi.org/10.1111/jvs.12341

Dighton, J. (2009). Mycorrhizae. En M. Schaechter (Ed.), *Encyclopedia of Microbiology (Third Edition)* (pp. 153-162). Academic Press. https://doi.org/10.1016/B978-012373944-5.00327-8

Dove, N. C., & Hart, S. C. (2017). Fire Reduces Fungal Species Richness and In Situ Mycorrhizal Colonization: A Meta-Analysis. *Fire Ecology*, *13*(2), Article 2. https://doi.org/10.4996/fireecology.130237746

Eom, A.-H., Hartnett, D. C., Wilson, G. W. T., & Figge, D. a. H. (1999). The Effect of Fire, Mowing and Fertilizer Amendment on Arbuscular Mycorrhizas in Tallgrass Prairie. *The American Midland Naturalist*, *142*(1), 55-70. https://doi.org/10.1674/0003-0031(1999)142[0055:TEOFMA]2.0.CO;2

Fernández-Guisuraga, J. M., Fernandes, P. M., Tárrega, R., Beltrán-Marcos, D., & Calvo, L. (2023). Vegetation recovery drivers at short-term after fire are plant community-dependent in mediterranean burned landscapes. *Forest Ecology and Management*, *539*, 121034. https://doi.org/10.1016/j.foreco.2023.121034

Fortunel, C., Fine, P.V.A. and Baraloto, C. (2012), Leaf, stem and root tissue strategies across 758 Neotropical tree species. Funct Ecol, 26: 1153-1161. https://doi.org/10.1111/j.1365-2435.2012.02020.x

Fox, J., Weisberg, S., Price, B., Adler, D., Bates, D., Baud-Bovy, G., Bolker, B., Ellison, S., Firth, D., Friendly, M., Gorjanc, G., Graves, S., Heiberger, R., Krivitsky, P., Laboissiere, R., Maechler, M., Monette, G., Murdoch, D., Nilsson, H., … R-Core.

(2023). *car: Companion to Applied Regression* (3.1-2). https://cran.r-project.org/web/packages/car/index.html

Ganteaume, A., Marielle, J., Corinne, L.-M., Thomas, C., & Laurent, B. (2011). Effects of vegetation type and fire regime on flammability of undisturbed litter in Southeastern France. *Forest Ecology and Management*, *261*(12), 2223-2231. https://doi.org/10.1016/j.foreco.2010.09.046

García-Meneses, P. M. (2012). *Landscape-scale population dynamics: field observations and modelling of Puya hamata, a flagship plant from the Andes* [Thesis, University of Plymouth]. https://doi.org/10.24382/4466

García-Meneses, P. M., & Ramsay, P. M. (2014). PUYA HAMATA DEMOGRAPHY AS AN INDICATOR OF RECENT FIRE HISTORY IN THE PÁRAMO OF EL ÁNGEL AND VOLCÁN CHILES, ECUADOR-COLOMBIA. *Caldasia*, *36*(1), 53-69. https://doi.org/10.15446/caldasia.v36n1.43891

Gómez-González, S., Torres-Díaz, C., Bustos-Schindler, C., & Gianoli, E. (2011). Anthropogenic fire drives the evolution of seed traits. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(46), 18743-18747. https://doi.org/10.1073/pnas.1108863108

Gouda, E. J., Butcher, D., & Dijkgraff, L. (2023). *Encyclopaedia of Bromeliads, Version 5.* Utrecht University Botanic Gardens. https://bromeliad.nl/encyclopedia/

Guerrero Forero, E. (1996, enero 1). *Survey of Mycorrhiza in a High Andean Paramo*.

Gui, H., Wang, J., Hu, M., Zhou, Z., & Wan, S. (2023). Impacts of fire on soil respiration and its components: A global meta-analysis. *Agricultural and Forest Meteorology*, *336*, 109496. https://doi.org/10.1016/j.agrformet.2023.109496

Hajek, P., Hertel, D., & Leuschner, C. (2013). Intraspecific variation in root and leaf traits and leaf-root trait linkages in eight aspen demes (Populus tremula and P. tremuloides).

Frontiers in Plant Science, *4*. https://www.frontiersin.org/articles/10.3389/fpls.2013.00415

Hawkins, C. D. B. (2004). TEMPERATE AND MEDITERRANEAN FORESTS | Northern Coniferous Forests. En J. Burley (Ed.), *Encyclopedia of Forest Sciences* (pp. 1377-1383). Elsevier. https://doi.org/10.1016/B0-12-145160-7/00182-4

Heinselman, M. L. (1973). Fire in the Virgin Forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research*, *3*(3), 329-382. https://doi.org/10.1016/0033-5894(73)90003-3

Hetrick, B. A. D. (1991). Mycorrhizas and root architecture. *Experientia*, *47*(4), 355-362. https://doi.org/10.1007/BF01972077

Hofstede, R., Coppus, R., Vásconez, P. M., Segarra, P., Wolf, J., & Sevink, J. (2002). El estado de conservación de los páramos de pajonal en el Ecuador. *Ecotropicos*, *15*(1), 3-18.

Hogan, J. A., Valverde-Barrantes, O., Ding, Q., Xu, H., & Baraloto, C. (2020). Morphological variation of fine root systems and leaves in primary and secondary tropical forests of Hainan Island, China. *Annals of Forest Science*, *77*. https://doi.org/10.1007/s13595-020-00977-7

Horn, S. P., & Kappelle, M. (2009). Fire in the páramo ecosystems of Central and South America. En M. A. Cochrane (Ed.), *Tropical Fire Ecology: Climate Change, Land Use, and Ecosystem Dynamics* (pp. 505-539). Springer. https://doi.org/10.1007/978-3-540-77381-8_18

Hornung-Leoni, C. T., González-Gómez, P. L., & Troncoso, A. J. (2013). Morphology, nectar characteristics and avian pollinators in five Andean Puya species (Bromeliaceae). *Acta Oecologica*, *51*, 54-61. https://doi.org/10.1016/j.actao.2013.05.010

Husson, F., Josse, J., Le, S., & Mazet, J. (2023). *FactoMineR: Multivariate Exploratory Data Analysis and Data Mining* (2.9). https://cran.r-project.org/web/packages/FactoMineR/index.html

Jabaily, R. S., & Sytsma, K. J. (2010). Phylogenetics of Puya (Bromeliaceae): Placement, major lineages, and evolution of Chilean species. *American Journal of Botany*, *97*(2), 337-356. https://doi.org/10.3732/ajb.0900107

Kassambara, A., & Mundt, F. (2020). *factoextra: Extract and Visualize the Results of Multivariate Data Analyses* (1.0.7). https://cran.r-project.org/web/packages/factoextra/index.html

Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J., & Bradstock, R. A. (2011). Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, *16*(8), 406-411. https://doi.org/10.1016/j.tplants.2011.04.002

Koske, R. E., & Gemma, J. N. (1989). A modified procedure for staining roots to detect VA mycorrhizas. *Mycological Research*, *92*(4), 486-488. https://doi.org/10.1016/S0953-7562(89)80195-9

Krishnaraj, S. J., Baker, T. G., Polglase, P. J., Volkova, L., & Weston, C. J. (2016). Prescribed fire increases pyrogenic carbon in litter and surface soil in lowland Eucalyptus forests of south-eastern Australia. *Forest Ecology and Management, 366,* 98-105. https://doi.org/10.1016/j.foreco.2016.01.038

Leon, D., Peyre, G., Zobel, M., Moora, M., Meng, Y., Diaz, M., & Bueno, C. G. (2023). Mycorrhizal symbioses in the Andean paramo. *Mycorrhiza*. https://doi.org/10.1007/s00572-023-01133-5

Leon-Garcia, I. V., & Lasso, E. (2019). High heat tolerance in plants from the Andean highlands: Implications for paramos in a warmer world. *PloS One*, *14*(11), e0224218. https://doi.org/10.1371/journal.pone.0224218

Liechty, H. O., & Hooper, J. J. (2016). Long-term effect of periodic fire on nutrient pools and soil chemistry in loblolly-shortleaf pine stands managed with single-tree selection. *Forest Ecology and Management*, *380*, 252-260. https://doi.org/10.1016/j.foreco.2016.08.045

Liese, R., Alings, K., & Meier, I. C. (2017). Root Branching Is a Leading Root Trait of the Plant Economics Spectrum in Temperate Trees. *Frontiers in Plant Science*, *8*. https://www.frontiersin.org/articles/10.3389/fpls.2017.00315

Liu, L., Zhang, Y.-Q., Tumi, L., Suni, M. L., Arakaki, M., Burgess, K. S., & Ge, X.-J. (2022). Genetic markers in Andean Puya species (Bromeliaceae) with implications on plastome evolution and phylogeny. *Ecology and Evolution*, *12*(8), e9159. https://doi.org/10.1002/ece3.9159

Liu, X., & Pan, C. (2019). Effects of recovery time after fire and fire severity on stand structure and soil of larch forest in the Kanas National Nature Reserve, Northwest China. *Journal of Arid Land*, *11*(6), 811-823. https://doi.org/10.1007/s40333-019-0022-9

Longo, M. S., Urcelay, C., & Nouhra, E. (2011). Long term effects of fire on ectomycorrhizas and soil properties in Nothofagus pumilio forests in Argentina. *Forest Ecology and Management*, *262*(3), 348-354. https://doi.org/10.1016/j.foreco.2011.03.041

Longo, S., Nouhra, E., Goto, B. T., Berbara, R. L., & Urcelay, C. (2014). Effects of fire on arbuscular mycorrhizal fungi in the Mountain Chaco Forest. *Forest Ecology and Management*, *315*, 86-94. https://doi.org/10.1016/j.foreco.2013.12.027

Luther, H. E. (2014). *AN ALPHEBETICAL LIST OF BROMELIAD BINOMIALS* (14.ª ed.). https://www.bsi.org/new/wp-content/uploads/2015/01/2014-Binomial-XIV.pdf

Madriñán, S. (2015). Una nueva especie de Puya (Bromeliaceae) de los páramos cercanos a

Bogotá, Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, *39*(152), Article 152. https://doi.org/10.18257/raccefyn.223

Magnani, M., Díaz-Sierra, R., Sweeney, L., Provenzale, A., & Baudena, M. (2023). Fire Responses Shape Plant Communities in a Minimal Model for Fire Ecosystems across the World. *The American Naturalist*, *202*(3), E83-E103. https://doi.org/10.1086/725391

Maracahipes, L., Carlucci, M. B., Lenza, E., Marimon, B. S., Marimon, B. H., Guimarães, F. A. G., & Cianciaruso, M. V. (2018). How to live in contrasting habitats? Acquisitive and conservative strategies emerge at inter- and intraspecific levels in savanna and forest woody plants. *Perspectives in Plant Ecology, Evolution and Systematics, 34,* 17-25. https://doi.org/10.1016/j.ppees.2018.07.006

Messier, Julie & Lechowicz, Martin & Mcgill, Brian & Violle, Cyrille & Enquist, Brian. (2017). Interspecific integration of trait dimensions at local scales: The plant phenotype as an integrated network. Journal of Ecology. 105. 10.1111/1365-2745.12755.

Metcalf, C. J. E., Rees, M., Alexander, J. M., & Rose, K. (2006). Growth–survival trade-offs and allometries in rosette-forming perennials. *Functional Ecology*, *20*(2), 217-225. https://doi.org/10.1111/j.1365-2435.2006.01084.x

Miller, G., & Silander, J. A. (1991). Control of the Distribution of Giant Rosette Species of Puya (Bromeliaceae) in the Ecuadorian Paramos. *Biotropica*, *23*(2), 124-133. https://doi.org/10.2307/2388297

Miller, R., Tangney, R., Enright, N. J., Fontaine, J. B., Merritt, D. J., Ooi, M. K. J., Ruthrof, K. X., & Miller, B. P. (2019). Mechanisms of Fire Seasonality Effects on Plant Populations. *Trends in Ecology & Evolution*, *34*(12), 1104-1117. https://doi.org/10.1016/j.tree.2019.07.009

Mirzaei, J., Heydari, M., Omidipour, R., Jafarian, N., & Carcaillet, C. (2023). Decrease in Soil Functionalities and Herbs' Diversity, but Not That of Arbuscular Mycorrhizal Fungi, Linked to Short Fire Interval in Semi-Arid Oak Forest Ecosystem, West Iran. *Plants*, *12*(5), Article 5. https://doi.org/10.3390/plants12051112

Mitchell, R. M., Ames, G. M., & Wright, J. P. (2021). Intraspecific trait variability shapes leaf trait response to altered fire regimes. *Annals of Botany, 127*(4), 543-552. https://doi.org/10.1093/aob/mcaa179

Mora, F., Chaparro, H., Bonilla, M., & Vargas Ríos, O. (2005). *Rasgos de historia de vida de Puya cryptantha una bromelia monocárpica perenne* (pp. 289-306).

Moreno, C. (2001). *Métodos para medir la biodiversidad* (Vol. 1).

Moretti, M., & Legg, C. (2009). Combining plant and animal traits to assess community functional responses to disturbance. *Ecography, 32*(2), 299-309. https://doi.org/10.1111/j.1600-0587.2008.05524.x

Neary, D. G. (2009). Post-Wildland Fire Desertification: Can Rehabilitation Treatments Make a Difference? *Fire Ecology, 5*(1), Article 1. https://doi.org/10.4996/fireecology.0501129

Odland, M. C., Goodwin, M. J., Smithers, B. V., Hurteau, M. D., & North, M. P. (2021). Plant community response to thinning and repeated fire in Sierra Nevada mixed-conifer forest understories. *Forest Ecology and Management*, *495*, 119361. https://doi.org/10.1016/j.foreco.2021.119361

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M. D., Durand, S., … Weedon, J. (2022). *vegan: Community Ecology Package* (2.6-4). https://cran.r-project.org/web/packages/vegan/index.html

Ondik, M. M., Bennell, M., Davies, R. J.-P., Ooi, M. K. J., & Muñoz-Rojas, M. (2022). Fire and land use impact soil properties in a Mediterranean dry sclerophyll woodland. *Journal of Environmental Management*, *324*, 116245. https://doi.org/10.1016/j.jenvman.2022.116245

Pattinson, G. S., Hammill, K. A., Sutton, B. G., & Mcgee, P. A. (1999). Simulated fire reduces the density of arbuscular mycorrhizal fungi at the soil surface. *Mycological Research*, *103*(4), 491-496. https://doi.org/10.1017/S0953756298007412

Paula, S., & Pausas, J. G. (2011). Root traits explain different foraging strategies between resprouting life histories. *Oecologia*, *165*(2), 321-331. https://doi.org/10.1007/s00442-010-1806-y

Pausas, J. G., Alessio, G. A., Moreira, B., & Corcobado, G. (2012). Fires enhance flammability in Ulex parviflorus. *New Phytologist*, *193*(1), 18-23. https://doi.org/10.1111/j.1469-8137.2011.03945.x

Pausas, J. G., & Schwilk, D. (2012). Fire and plant evolution. *New Phytologist*, *193*(2), 301-303. https://doi.org/10.1111/j.1469-8137.2011.04010.x

Perez, T. M., Rodriguez, J., & Mason Heberling, J. (2020). Herbarium-based measurements reliably estimate three functional traits. *American Journal of Botany*, *107*(10), 1457-1464. https://doi.org/10.1002/ajb2.1535

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., Vos, A. C. de, … Cornelissen, J. H. C. (2016). Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *64*(8), 715-716. https://doi.org/10.1071/bt12225_co

Perez-Lamarque, B., Petrolli, R., Strullu-Derrien, C., Strasberg, D., Morlon, H., Selosse, M.-

A., & Martos, F. (2022). Structure and specialization of mycorrhizal networks in phylogenetically diverse tropical communities. *Environmental Microbiome*, *17*(1), 38. https://doi.org/10.1186/s40793-022-00434-0

Pico, A. (2020). *Germinación, crecimiento y desarrollo ex situ de Puya bicolor Mez (BROMELIACEAE) durante 32 meses en Bogotá, Colombia | BISTUA Revista de la Facultad de Ciencias Básicas*. https://ojs.unipamplona.edu.co/index.php/bistua/article/view/269

Pierick, K., Leuschner, C., & Homeier, J. (2021). Topography as a factor driving small-scale variation in tree fine root traits and root functional diversity in a species-rich tropical montane forest. *New Phytologist*, *230*(1), 129-138. https://doi.org/10.1111/nph.17136

Premauer, J. (2004). PATRONES DE DIVERSIDAD EN VEGETACIÓN PASTOREADA Y QUEMADA EN UN PARAMO HUMEDO. *ECOTROPICOS*, *17*(1-2), 52-66.

Quensen, J., Simpson, G., & Oksanen, J. (2023). *ggordiplots: Make «ggplot2» Versions of Vegan's Ordiplots* (0.4.2). https://cran.r-project.org/web/packages/ggordiplots/index.html

R Core Team. (2023). *_R: A Language and Environment for Statistical Computing_*. R Foundation for Statistical Computing. <https://www.R-project.org/>

Ramírez, P., Villaseñor, R., Eyzaguirre, A., Morales, N., & Muñoz, A. (2017). *ANATOMIA FOLIAR DE PUYA CHILENSIS MOLINA (BROMELIACEAE), UNA PLANTA QUE RESISTE AL FUEGO*. *1*. http://www.chlorischile.cl/Puya%20chilensis-Ramirez-villase%C3%B1or-/Ramirez-villase%C3%B1or-Puya%20chilensis.htm

Raz, L., & Agudelo-Zamora, H. D. (s. f.). *Herbario Nacional Colombiano (COL)*. https://doi.org/10.15472/ea8sek

Rendon-Espinosa, M., Bottin, M., Sanchez, A., Vargas, C., Raz, L., & Corrales, A. (In review). *DIVERSITY OF MYCORRHIZAL TYPES ALONG ALTITUDINAL*

GRADIENTS IN THE TROPICAL ANDES.

Renvoize, S., Luteyn, J., Churchill, S., Iii, D., Gradstein, S., Sipman, H., & A., M. (2000). Paramos: A Checklist of Plant Diversity, Geographical Distribution, and Botanical Literature (Memoirs of the New York Botanical Garden Volume 84). *Kew Bulletin*, *55*, 1017. https://doi.org/10.2307/4113659

Rivadeneira, G., Ramsay, P. M., & Montúfar, R. (2020). Fire regimes and pollinator behaviour explain the genetic structure of Puya hamata (Bromeliaceae) rosette plants. *Alpine Botany*, *130*(1), 13-23. https://doi.org/10.1007/s00035-020-00234-7

Santacruz-García, A. C., Bravo, S., del Corro, F., & Ojeda, F. (2019). A comparative assessment of plant flammability through a functional approach: The case of woody species from Argentine Chaco region. *Austral Ecology*, *44*(8), 1416-1429. https://doi.org/10.1111/aec.12815

Sayre, R., Martin, M., Karagulle, D., Frye, C., Breyer, S., Wright, D., Butler, K., VanGraafeiland, K., Boucher, T., McGowan, J., Touval, J., Wolff, N. H., Sotomayor, L., Game, E. T., & Possingham, H. (2020). World Terrestrial Ecosystems. En M. I. Goldstein & D. A. DellaSala (Eds.), *Encyclopedia of the World's Biomes* (pp. 31-34). Elsevier. https://doi.org/10.1016/B978-0-12-409548-9.12474-1

Schwilk, D. W., & Caprio, A. C. (2011). Scaling from leaf traits to fire behaviour: community composition predicts fire severity in a temperate forest. *Journal of Ecology*, *99*(4), 970-980. https://doi.org/10.1111/j.1365-2745.2011.01828.x

Seethepalli, A., & York, L. M. (2020). *RhizoVision Explorer - Interactive software for generalized root image analysis designed for everyone (Version 2.0.3)* (2.0.3). Zenodo. http://doi.org/10.5281/zenodo.4095629

Shao, X., Wang, L., Zhang, Q., Liu, Y., & Yang, X. (2019). Future direction of searching for root economics spectrum: focusing on the fibrous roots "absorptive unit". *Ecosphere,* *10*. https://doi.org/10.1002/ecs2.2716

Shi, Y.-F., Shi, S.-H., Jiang, Y.-S., & Liu, J. (2022). A global synthesis of fire effects on soil seed banks. *Global Ecology and Conservation*, *36*, e02132. https://doi.org/10.1016/j.gecco.2022.e02132

Sklenář, P., Dušková, E., & Balslev, H. (2011). Tropical and Temperate: Evolutionary History of Páramo Flora. *The Botanical Review*, *77*(2), 71-108. https://doi.org/10.1007/s12229-010-9061-9

Strydom, T., Riddell, E. S., Rowe, T., Govender, N., Lorentz, S. A., le Roux, P. A. L., & Wigley-Coetsee, C. (2019). The effect of experimental fires on soil hydrology and nutrients in an African savanna. *Geoderma*, *345*, 114-122. https://doi.org/10.1016/j.geoderma.2019.03.027

Suarez, L. (1988). Seasonal distribution and food habits of spectacled Bears Tremarctos ornatus in the highlands of Ecuador. *Studies on Neotropical Fauna and Environment*, *23*(3), 133-136. https://doi.org/10.1080/01650528809360755

Tangney, R., Merritt, D. J., Fontaine, J. B., & Miller, B. P. (2019). Seed moisture content as a primary trait regulating the lethal temperature thresholds of seeds. *Journal of Ecology*, *107*(3), 1093-1105. https://doi.org/10.1111/1365-2745.13095

Toledo-Aceves, T., García-Hernández, M. & Paz, H. Leaf functional traits predict cloud forest tree seedling survival along an elevation gradient. *Annals of Forest Science* **76**, 111 (2019). https://doi.org/10.1007/s13595-019-0900-5

Varner, J. M., Shearman, T. M., Kane, J. M., Banwell, E. M., Jules, E. S., & Stambaugh, M. C. (2022). Understanding flammability and bark thickness in the genus Pinus using a phylogenetic approach. *Scientific Reports*, *12*, 7384. https://doi.org/10.1038/s41598-022-11451-x

Vásquez, D. L. A., Balslev, H., & Sklenář, P. (2015). Human impact on tropical-alpine plant diversity in the northern Andes. *Biodiversity and Conservation*, *24*(11), 2673-2683. https://doi.org/10.1007/s10531-015-0954-0

Verdú, M., & Pausas, J. G. (2007). Fire drives phylogenetic clustering in Mediterranean Basin woody plant communities. *Journal of Ecology*, *95*(6), 1316-1323. https://doi.org/10.1111/j.1365-2745.2007.01300.x

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*(5), 882-892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Wang, Y., Thorup-Kristensen, K., Jensen, L., & Magid, J. (2016). Vigorous Root Growth Is a Better Indicator of Early Nutrient Uptake than Root Hair Traits in Spring Wheat Grown under Low Fertility. *Frontiers in Plant Science*, *7*. https://doi.org/10.3389/fpls.2016.00865

Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E., & Eriksson, O. (1999). Challenging Theophrastus: A common core list of plant traits for functional ecology. *Journal of Vegetation Science*, *10*(5), 609-620. https://doi.org/10.2307/3237076

Wickham, H., Chang, W., Henry, L., Pedersen, T. L., Takahashi, K., Wilke, C., Woo, K., Yutani, H., Dunnington, D., Posit, & PBC. (2023). *ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics* (3.4.4). https://cran.r-project.org/web/packages/ggplot2/index.html

Withington, J. M., Reich, P. B., Oleksyn, J., & Eissenstat, D. M. (2006). Comparisons of Structure and Life Span in Roots and Leaves Among Temperate Trees. *Ecological Monographs*, *76*(3), 381-397. https://doi.org/10.1890/0012-9615(2006)076[0381:COSALS]2.0.CO;2

Zomer, M. A., & Ramsay, P. M. (2021). Post-fire changes in plant growth form composition and diversity in Andean páramo grassland. *Applied Vegetation Science*, *24*(1), e12554. https://doi.org/10.1111/avsc.12554

Supporting Information

Table S1. Soil analysis for each of the fire regime zones: 1988, 2002, No fire.

		Fire		
Variable	Abbreviation	1988	2002	No Fire
pH	pH	4.58	4.35	4.3
Electric conductivity (dS/M)	CE	0.2	0.38	0.41
Effective Cation exchange capacity (meq/100g)	CICE	10.6	9.31	12.4
Average humidity saturation (%)	N.A	48	45.6	48.3
Oxidizable Organic carbon (%)	COOx	12.5	12.3	11.1
Organic Matter (%)	MO	21.6	21.2	19.1
Total Nitrogen (%)	N Total	1.04	1.02	0.925
Density (g/cm3)	d.a.	632	657	662
Interchangeable Potassium (mg/Kg)	K	123	99.5	170
Interchangeable Calcium (mg/Kg)	Ca	22.2	27.6	34.7
Interchangeable Magnesium (mg/Kg)	Mg	39.1	32.4	35.6
Interchangeable Sodium (mg/Kg)	Na	6.4	17.3	28
Interchangeable Acidity (mg/Kg)	Ac.inter.	886	772	1030
Phosphorus (mg/Kg)	P	14	11.18	15.2
Sulfur (mg/Kg)	S	4.71	8.67	6.15
Texture				
Clay (%)		12	16	10
Sand (%)		16	12	18
Lime (%)		72	72	72
Texture		Silt Loam	Silt Loam	Silt Loam

Table S2. List of traits used in this study with their units and functions.

Traits	**Unit**	**Function**	**Reference**
Leaf Area (LA)	cm^2	Related to energy and water balance	Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2016
Specific Leaf Area (SLA)	cm^2 g^{-1}	Related to growth and photosynthetic rate	
Leaf Dry Matter Content (LDMC)	mg g^{-1}	Positive relation with life-span, and negative with potential growth rate	
Leaf thickness (LT)	mm	Related to disturbance response, competitive ability and dispersal	Weiher et al., 1999
Plant Height (H)	cm		
Rosette Diameter (RD)	cm	A proxy to biomass	Metcalf et al., 2006
Root Tissue Density (RTD)	g mm^3	Related to root lifespan	Withington et al., 2006
Specific Root Area (SRA)	mm^2 g^{-1}	Related to increased root soil exploration, increased resource uptake, and mycorrhizal associations	Hajek et al., 2013
Specific Root Length (SRL)	mm g^{-1}		
Root Branching Frequency (BF)	mm	Intense branching tends to indicate an acquisitive strategy	Liese et al., 2017
Root Branching Index (BI)	root tips cm^{-1}	A decrease in BI reflects a conservative strategy	Pierick et al., 2021
Root Average Diameter (AD)	mm	Proxy to root size and related to mycorrhizal colonization	Costa et al., 2000
Root Surface Area (SA)	mm^2	Related to the uptake of minerals	Wang et al., 2016

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., Steege, H. ter, Morgan, H. D., Heijden, M. G. A. van der, Pausas, J. G., & Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany, 51(4), 335-380. https://doi.org/10.1071/bt02124

Costa, C., Dwyer, L., Hamilton, R., Hamel, C., Nantais, L., & Smith, D. (2000). A Sampling Method for Measurement of Large Root Systems with Scanner-Based Image Analysis. Agron J, 92, 621-627. https://doi.org/10.2134/agronj2000.924621x

Hajek, P., Hertel, D., & Leuschner, C. (2013). Intraspecific variation in root and leaf traits and leaf-root trait linkages in eight aspen demes (Populus tremula and P. tremuloides). Frontiers in Plant Science, 4. https://www.frontiersin.org/articles/10.3389/fpls.2013.00415

Liese, R., Alings, K., & Meier, I. C. (2017). Root Branching Is a Leading Root Trait of the Plant Economics Spectrum in Temperate Trees. Frontiers in Plant Science, 8. https://www.frontiersin.org/articles/10.3389/fpls.2017.00315

Metcalf, C. J. E., Rees, M., Alexander, J. M., & Rose, K. (2006). Growth–survival trade-offs and allometries in rosette-forming perennials. Functional Ecology, 20(2), 217-225. https://doi.org/10.1111/j.1365-2435.2006.01084.x

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., Vos, A. C. de, … Cornelissen, J. H. C. (2016). Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany, 64(8), 715-716. https://doi.org/10.1071/bt12225_co

Pierick, K., Leuschner, C., & Homeier, J. (2021). Topography as a factor driving small-scale variation in tree fine root traits and root functional diversity in a species-rich tropical montane forest. New Phytologist, 230(1), 129-138. https://doi.org/10.1111/nph.17136

Wang, Y., Thorup-Kristensen, K., Jensen, L., & Magid, J. (2016). Vigorous Root Growth Is a Better Indicator of Early Nutrient Uptake than Root Hair Traits in Spring Wheat Grown under Low Fertility. Frontiers in Plant Science, 7. https://doi.org/10.3389/fpls.2016.00865

Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E., & Eriksson, O. (1999). Challenging Theophrastus: A common core list of plant traits for functional ecology. Journal of Vegetation Science, 10(5), 609-620. https://doi.org/10.2307/3237076

Withington, J. M., Reich, P. B., Oleksyn, J., & Eissenstat, D. M. (2006). Comparisons of Structure and Life Span in Roots and Leaves Among Temperate Trees. Ecological Monographs, 76(3), 381-397. https://doi.org/10.1890/0012-9615(2006)076[0381:COSALS]2.0.CO;2

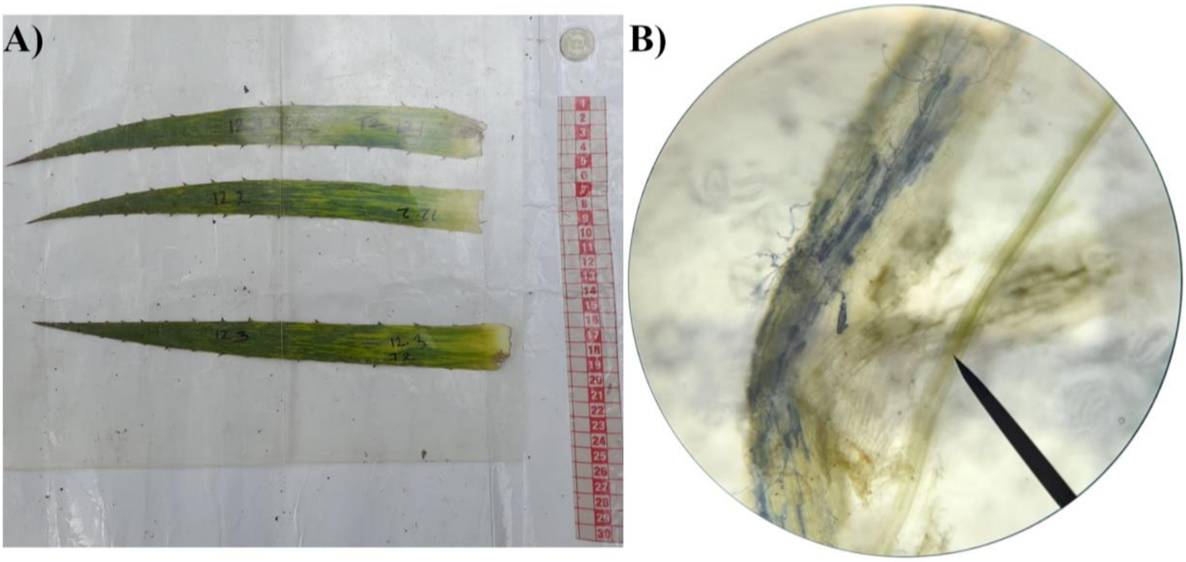

Figure S1. A) Example of how photographs were taken of *Puya* leaves, to determine leaf area (LA). B) Dyed vesicles, present in *P. goudotiana* roots.

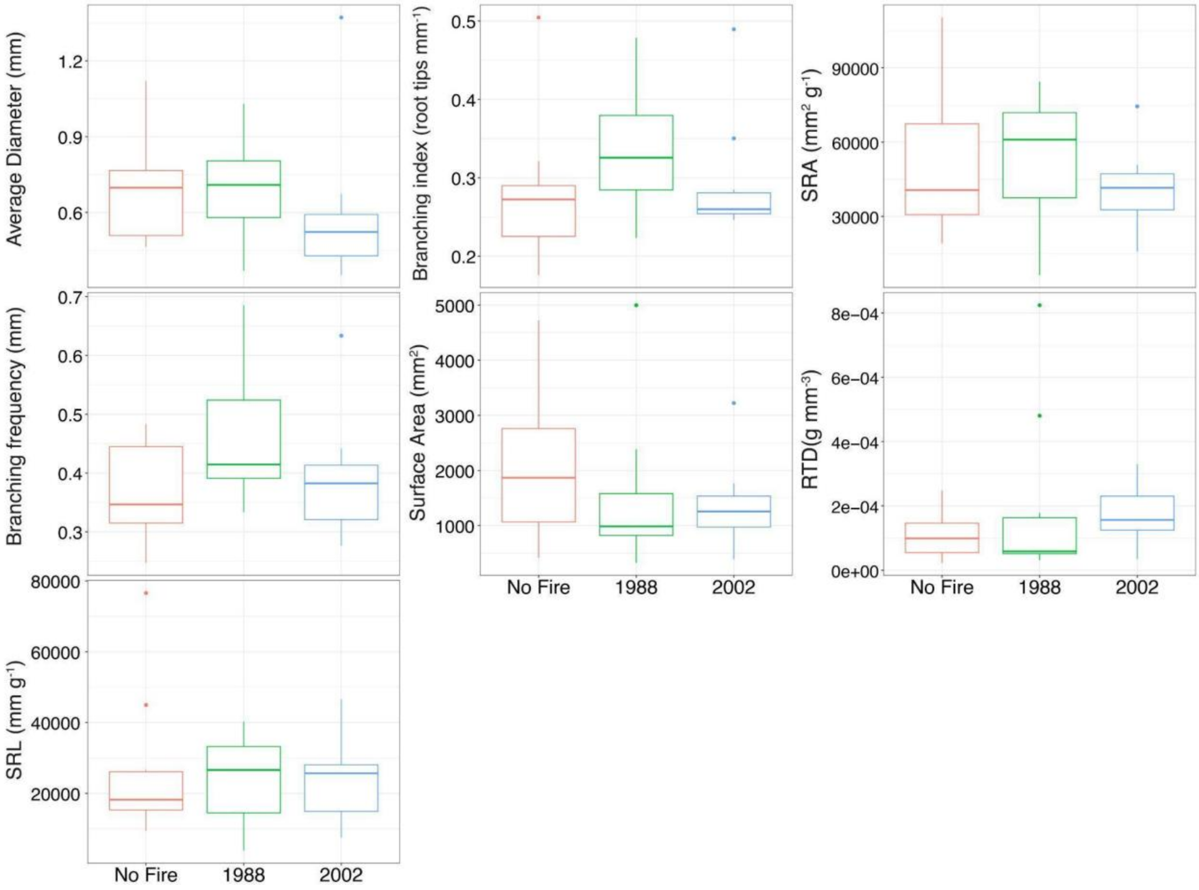

Figure S2. *Puya goudotiana* root traits from left to right, Average diameter (mm), Bi: Branching index (root tips mm^{-1}), SRA: Specific root area (mm^{2} g^{-1}), Surface Area (mm^{2}), Branching frequency per (mm), RTD: Root tissue density (g mm^{-3}), SRL: Specific root length (mm g^{-1}).

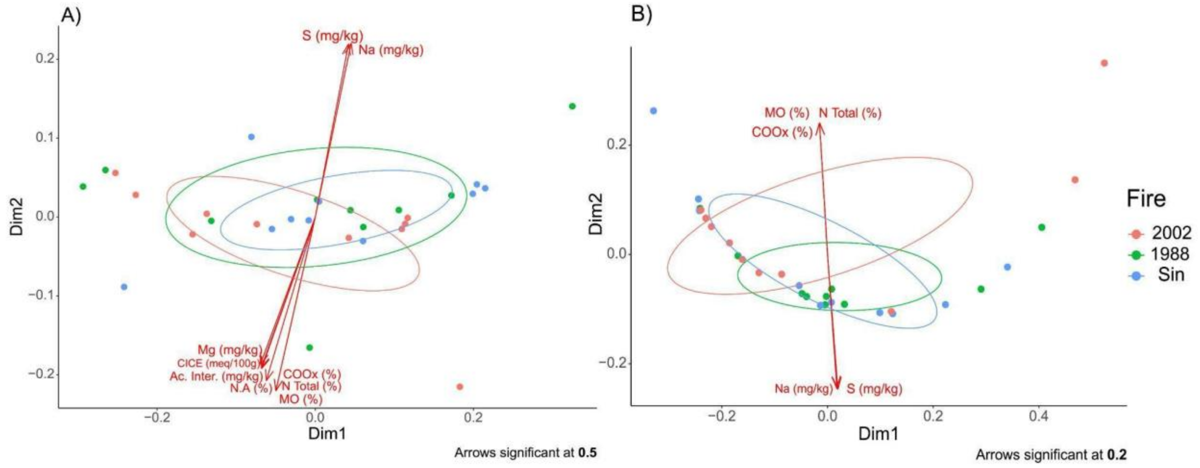

Figure S3. Ordination of A) Aboveground traits y B) Aboveground and radicular traits, for *P. goudotiana*, with minimum significance level for soil characteristics influencing traits. Ellipses showing the confidence interval for the individual in each fire category, red: 1988, green: 2002, blue: No fire. Red arrows show the soil characteristics that influence the traits at a given significant level (A: 0.5, B: 0.2). Arrows in A) correspond to Interchangeable sodium (Na, mg kg^{-1}), Interchangeable sulfur (S, mg kg^{-1}), Effective Cation exchange capacity (CICE, meq/100g), Interchangeable magnesium (Mg, mg kg^{-1}), I, Interchangeable acidity (Ac. Inter, mg kg^{-1}), Oxidizable organic carbon (COOx, %), Total nitrogen (N Total, %). B) N Total (%), COOx (%), Na (mg kg^{-1}), S (mg kg^{-1}), Organic matter (MO, %).

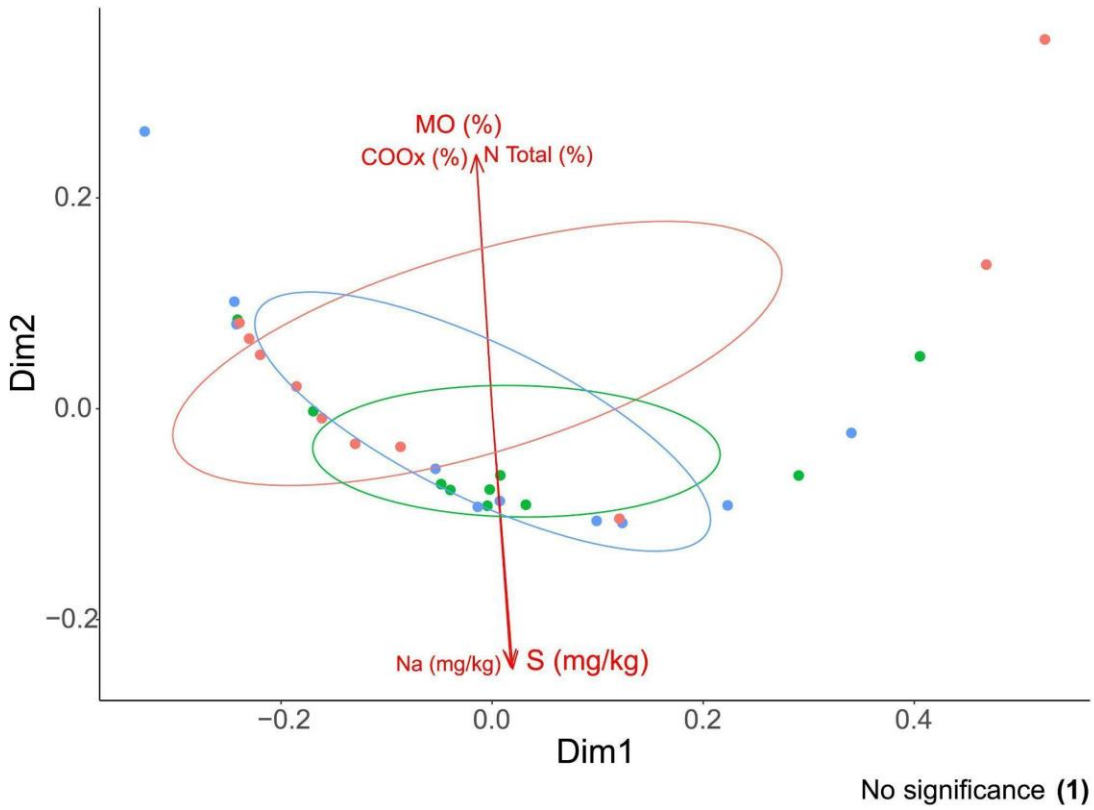

Figure S4. Ordination of radicular traits for *P. goudotiana*, without significance level for soil characteristics influencing traits. Ellipses show the confidence interval for the individual in each fire category, red: 1988, green: 2002, blue: No fire. Red arrows show the soil characteristics: N Total (%), COOx (%), Na (mg kg^{-1}), S (mg kg^{-1}).

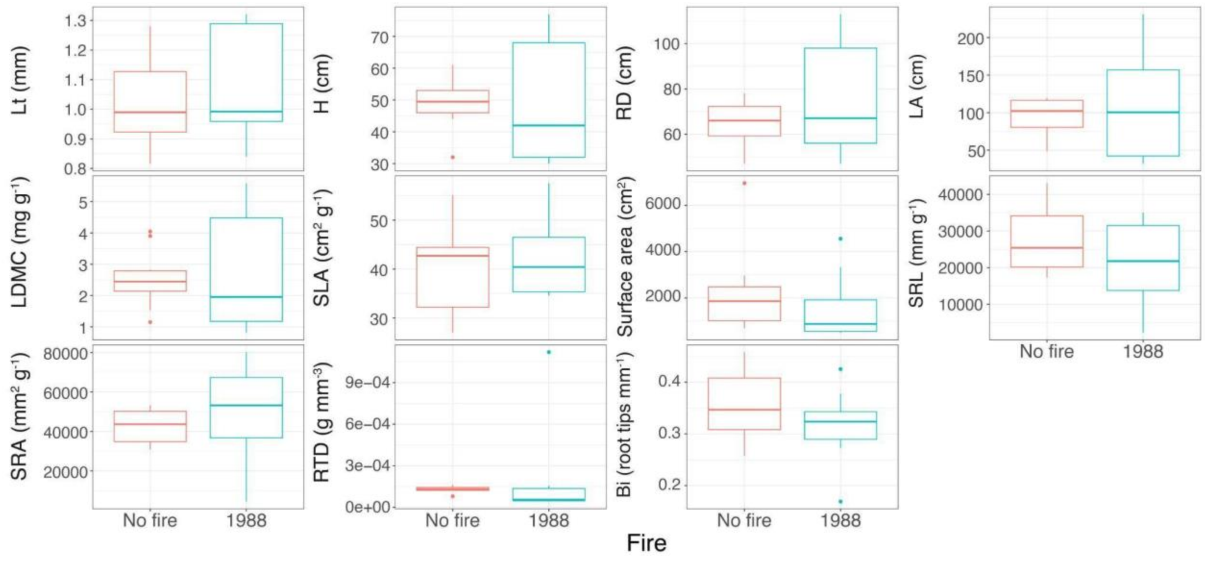

Figure S5. *Puya nitida* traits from left to right: H: Plant height; Lt: Leaf thickness (mm), RD: Rosette diameter (cm), LA: Leaf area (cm^2), LDMC: Leaf dry matter content (mg g^{-1}), SLA:

Specific leaf area (cm^{2} g^{-1}), Surface Area (cm^{2}), SRL: Specific root length (mm g^{-1}), SRA: Specific root area (mm^{2} g^{-1}), RTD: Root tissue density (g mm^{-3}), Bi: Branching index (root tips mm^{-1}), in two fire regime categories: No fire and 1988.