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EDITED BY
Manfred J. Lexer,
University of Natural Resources and Life Sciences Vienna, Austria

REVIEWED BY
Aseesh Pandey,
Govind Ballabh Pant National Institute of Himalayan Environment and Sustainable Development, India
Mariasole Calbi,
University of Florence, Italy

*CORRESPONDENCE
Yessica D. Hoyos
✉ yessica.hoyos@urosario.edu.co
Adriana Sanchez
✉ adriana.sanchez@urosario.edu.co

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Different functional responses in populations of *Polylepis quadrijuga* (Rosaceae) as a consequence of anthropogenic disturbance

Yessica D. Hoyos*, Natalia Vargas and Adriana Sanchez*

Departamento de Biología, Facultad de Ciencias Naturales, Universidad del Rosario, Bogotá, Colombia

The monodominant forests of *Polylepis quadrijuga*, endemic to the páramos of the eastern cordillera in the Colombian Andes, are among the most threatened in South America due to fragmentation and anthropogenic degradation. Despite their role in regulating water flow and forming biodiverse, endemic biotic communities, there are few studies on their functional responses to stress caused by anthropogenic disturbance and climate change. In this study, we evaluate how six different populations of *P. quadrijuga* with distinct levels of anthropogenic disturbance (low and high) change 11 foliar, stem, and root functional traits. Also, the physicochemical properties of the soils were analyzed, and mycorrhizal colonization was quantified to evaluate how each population responds to the stress conditions. The results indicated that populations with lower disturbance levels exhibit a conservative leaf trait configuration, whereas those with higher disturbance levels adopt an acquisitive strategy, potentially making them more vulnerable. Additionally, we found no functional coordination between above- and belowground traits. The results also highlight a lower percentage of arbuscular mycorrhizarl fungi (AMF) colonization in sites with a high level of disturbance. Our findings show *P. quadrijuga's* sensitivity to anthropogenic disturbance and its resilience, demonstrated by high plasticity in aboveground traits. Conservation efforts for this endangered species should focus on fragmented populations and those under stress from grazing or agriculture, aiming to create connectivity and promote its establishment

KEYWORDS

abiotic factors, disturbance, fragmentation, functional coordination, nutrients, treeline

1 Introduction

The mountainous region of the Andes is a center of biodiversity and endemism (Myers et al., 2000). In particular, the high Andean forests and páramos contain a high number of plant species in a small area, displaying unique adaptations to extreme environmental conditions (Valencia et al., 2020; Caballero-Villalobos et al., 2021). However, the plants inhabiting these ecosystems are highly threatened by changes in hydrological cycles, temperature increases, and habitat loss, due to anthropogenic activities such as land use change and expansive agriculture (Espitia Villarraga, 2018; Caballero-Villalobos et al., 2021). These activities have also been magnified worldwide by the effects of climate change (Toivonen et al., 2011; Montalvo et al., 2018; Chacón-Moreno et al., 2021; Singh et al., 2021).

Polylepis quadrijuga Bitter is a native tree of the Eastern Cordillera of Colombia and is cataloged as critically endangered (Boza Espinoza, 2023). These plants grow above the treeline (ca. 3,200–3,600 m.a.s.l), below or interspersed with the páramo ecosystem, and despite their limited geographical distribution, they form monodominant but highly diverse forests. It has been documented that these forests contain a variety of endemic and endangered avifauna, such as *Diglossa gloriosissima* or the yellow-eared parrot (*Leptosittaca branickii*) (Peña and Rangel, 2007). The trunks of *Polylepis* harbor numerous species of bryophytes (mosses) and lichens (Pulido Herrera, 2016). Additionally, species of *Polylepis* provide ecosystem services, acting as carbon sinks, protecting water sources through runoff regulation, reducing soil erosion, and aiding in the retention of nutrients and sediments (Peña and Rangel, 2007; Cuyckens and Renison, 2018; Montalvo et al., 2018; Boza Espinoza and Kessler, 2022).

Despite their importance, *Polylepis* forests have been exploited for centuries for dendroenergetic purposes (Cuyckens and Renison, 2018; Boza Espinoza and Kessler, 2022). Additionally, the ongoing expansion of agricultural and livestock frontiers has led to the fragmentation and isolation of species such as *P. quadrijuga* (Ramos et al., 2013; Caballero-Villalobos et al., 2021). These relicts or man-made patches (Toivonen et al., 2011; Rangel and Arellano Peña, 2010) are highly susceptible to climate change due to the stressful conditions caused by high altitudes, low temperatures, and high humidity (Macek et al., 2009; Kessler et al., 2014; Caballero-Villalobos et al., 2021). One approach to understand and identify how different populations of *P. quadrijuga* respond to the current climatic conditions and anthropogenic disturbance is through the study of functional traits (Violle et al., 2007; Garnier et al., 2015).

Functional traits are morphological, physiological or phenological characteristics that are inherited and that influence fitness (Garnier et al., 2015). Therefore, functional traits help us understand how populations respond to the biotic and abiotic factors of a specific habitat. For instance, it has been found that altitudinal gradients (Rozman et al., 2013; Pandey et al., 2018), fragmentation (Ramos et al., 2013), mining, agricultural and livestock activities (Ding et al., 2012; Soteras et al., 2016; Ji et al., 2022), and the composition and interactions of soil microbiological communities can alter the functional diversity (Soteras et al., 2016; Gazol et al., 2017) and increase the intraspecific variability of species (Aubin et al., 2016; Gazol et al., 2022). Additionally, anthropogenic disturbances, such as land use changes and fragmentation, significantly impact abiotic conditions such as soil nutrients and moisture, temperature, and light levels (Vitousek et al., 1997). These disturbances can favor species or individuals with specific functional traits and reduce trait diversity in a population or community, which can in turn, affect ecosystem functioning and increase competitive exclusion (e.g., Flynn et al., 2011; Laliberté and Tylianakis, 2012; Mouillot et al., 2013).

Previous studies on functional traits in *Polylepis* species, such as *P. tarapacana* (distributed in Peru, Chile, Bolivia, and Argentina), which has a near threatened conservation status (Boza Espinoza, 2023), have found a complex interplay between water stress, elevation (Hertel and Wesche, 2008; Macek et al., 2009; Toivonen et al., 2018), nutrient availability (Toivonen et al., 2014) and seasonality (Kessler et al., 2014). These factors have a greater effect on trees than anthropogenic disturbance (e.g., fire, fragmentation and/or agricultural practices; Soteras et al., 2015; Soteras et al., 2016). *Polylepis tarapacana* is distributed in countries with stronger temperature seasonality and in drier conditions, therefore, we expect a different functional response compared to *P. quadrijuga*. Additionally, the severe fragmentation experienced by *P. quadrijuga* populations, will likely cause a different functional response, compared to *P. tarapacana*. Plants exposed to higher abiotic stress in response to low temperatures and high solar radiation, rather than recent anthropogenic disturbance (Ramos et al., 2013; Weemstra et al., 2016) will show conservative trait values. This would be reflected in higher specific leaf area (SLA) (Weemstra et al., 2016), wood density (WD) (Garnier and Navas, 2012; Reich, 2014), leaf thickness (LT) (Macek et al., 2009) and leaf dry matter content (LDMC) (Garnier and Navas, 2012), and lower values of leaf area (LA) (Ramos et al., 2013; Macek et al., 2009) and branching frequency (BF) (Semchenko et al., 2018). Conversely, plants associated with anthropogenic disturbance will tend to have acquisitive functional trait values, such as high values of specific root length (SRL) (Wright et al., 2004; Weemstra et al., 2016; Bergmann et al., 2020), root tip abundance (RTA) (Hertel and Wesche, 2008), root branching index (RBI) (Pierick et al., 2021) and low values of root diameter (ARD) (Ma et al., 2018; Bergmann et al., 2020) and root tissue density (RTD) (Bergmann et al., 2020) (Supplementary Table S1).

There are also substantial knowledge gaps regarding the belowground symbiosis in the genus *Polylepis*, such as the association with mycorrhizae, which has only been assessed in *P. australis* (Menoyo et al., 2007; Menoyo et al., 2009; Soteras et al., 2013; Soteras et al., 2014; Soteras et al., 2015; Soteras et al., 2016). Colonization by symbionts, such as N-fixing bacteria and mycorrhizae are key to enhance the nutrient uptake capacity of plants and is considered as a belowground functional trait (Pérez-Harguindeguy et al., 2013). In *P. australis*, the arbuscular mycorrhizal fungi (AMF) communities are present under various types of disturbances, such as grazing or fire, and no significant differences in colonization have been found between these disturbances. However, other studies in tropical mountains have shown that anthropogenic disturbance, such as intensive land use (Barnola and Montilla, 1997) and fertilization (Jefwa et al., 2012), significantly reduces fungal communities and colonization (Ji et al., 2022). This could decrease, in turn, the nutrient uptake by plants and affect their growth and survival (e.g., Begum et al., 2019).

Regardless of whether populations experience human disturbance, we expect individuals of *P. quadrijuga* to exhibit a coordinated functional response (e.g., Messier et al., 2017; Carvalho et al., 2020). This expectation is supported by the fact that traits are interlinked in a plant's growth, survival and reproduction, and these share similar environmental pressures. Therefore, both sets of traits should respond in unison (Violle et al., 2007; Reich, 2014; Messier et al., 2017). Previous studies at the local scale (Hu et al., 2019) have shown a coordination between leaf and root traits, aligning with the "do it yourself" strategy (Bergmann et al., 2020). These traits have proven to be reliable indicators of plant metabolic activity in response to environmental factors such as temperature in temperate regions (Ding et al., 2024) and the degree of succession (Hu et al., 2019). Generally, traits tend to be more conservative in colder climates and later successional stages.

In this study, we aim to evaluate the intraspecific functional trait variability between different populations of *Polylepis quadrijuga* (Rosaceae) with two levels of disturbance (measured as the proximity to anthropogenic activity and fragmentation) and conservation in high-Andean forests of the Colombian eastern mountain range. We expect to find (1) a functional conservation strategy for populations with high abiotic stress and low anthropogenic disturbance, and an acquisitive strategy for high anthropogenic disturbance sites. (2) We also hypothesize that AMF colonization will be impacted by anthropogenic disturbance, similar to what has been shown in species from tropical mountains. (3) We anticipate a functional coordination between above- (leaves and stems) and belowground traits (roots) of *P. quadrijuga*. This knowledge is critical in the establishment of conservation strategies for an endangered species such as *P. quadrijuga*, taking into account the anthropogenic pressures experienced by different populations.

2 Materials and methods

2.1 Study area

The study was conducted at six páramo sites located in the Eastern Cordillera of the Colombian Andes (Figure 1): Santuario de Fauna y Flora Guanentá alto Río Fonce (SFF), surroundings of the Parque Nacional Natural (PNN) El Cocuy, Laguna de Palchacual and La Rusia Páramo Complex in the Departments of Boyacá and Santander, as well as Sumapaz and Guerrero páramos in the Department of Cundinamarca. At the Cocuy site we collected in two different areas: Parada de Romero and Laguna de San Pablín (less than 10 km away). Collections were carried out during the rainy season between April–May and September–November 2022. Areas with a high density of adult individuals of *P. quadrijuga* forming closed-canopy forests (control areas) or located along roadsides and pastures (anthropogenic disturbance) were selected for sampling. The sampling was conducted at elevations ranging from 3,400 to 4,000 m.a.s.l. in at least 0.3 ha per site (Table 1).

2.2 Description of *Polylepis quadrijuga*

Polylepis quadrijuga is a tree endemic to the eastern Andean Cordillera of Colombia, found at an elevational range between 2,200 to 4,000 m.a.s.l. It is usually found in fairly humid areas near water bodies (Boza Espinoza and Kessler, 2022). This species can reach ca. 10 m in height, and flowering occurs approximately in August, while fruiting occurs in October (Velez et al., 1998). *Polylepis quadrijuga* growth rate (like that of other species of the genus) is slow, growing approximately 1 mm per year, and its germination is characterized by a long dormancy and by being thermally dependent (maximum germination at 20°C) (Boza Espinoza and Kessler, 2022).

2.3 Experimental design and data collection

In each páramo site, we randomly selected at least 10 adult individuals (defined by their height and/or the presence of inflorescences) per site (Table 1), and growing more than 2 m away from each other. A level of disturbance (low or high) was also assigned based on the anthropogenic accessibility (Figure 2).

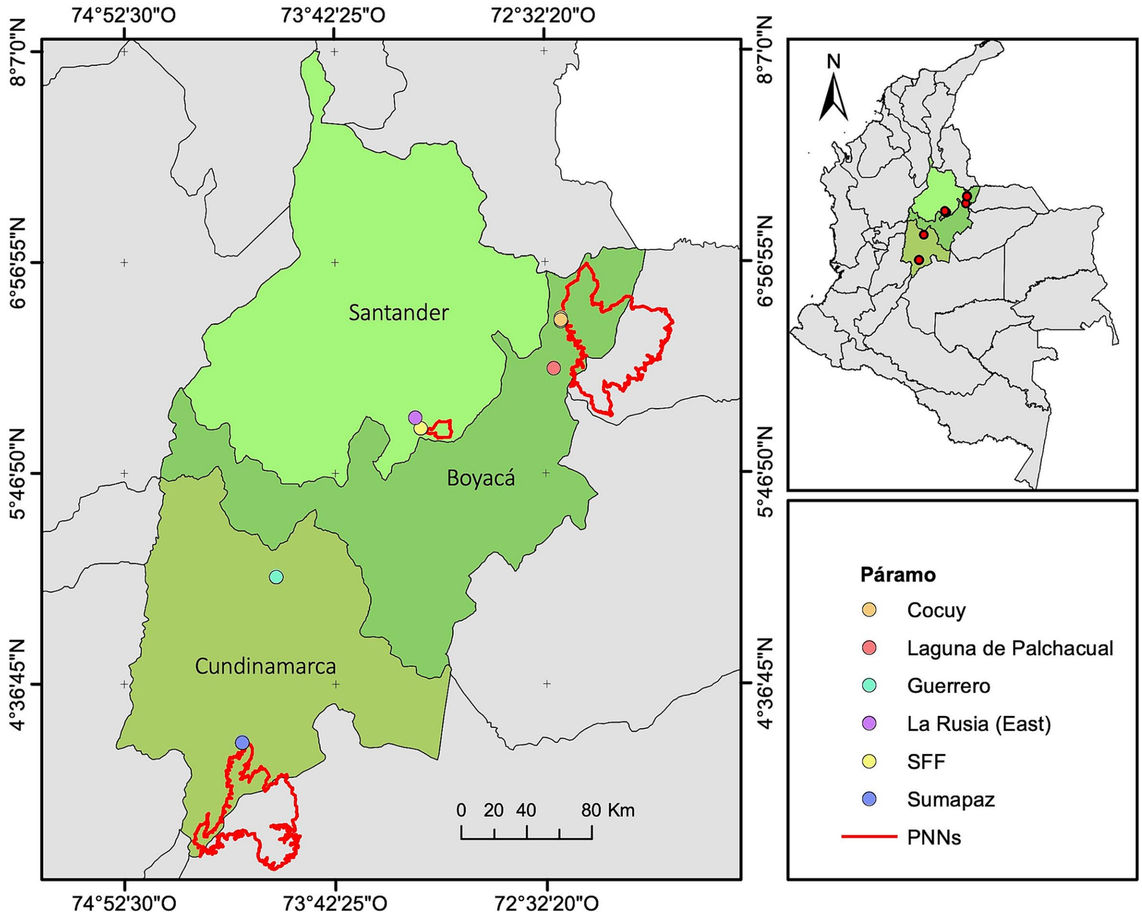

FIGURE 1
Populations of *Polylepis quadrijuga* sampled in this study. The symbols and colors represent the location of each páramo site, and the red lines represent the boundary of the protected areas: Parque Nacional Natural (PNN) Sumapaz, PNN Cocuy and Santuario de Fauna y Flora (SFF) Guanentá-Alto Río Fonce. The maps were created based on the Colombian administrative maps obtained from the HUMANITARIAN DATA EXCHANGE (https://data.humdata.org/dataset/cod-ab-col; Creative Commons Attribution 4.0 International license) and from the Parques Nacionales Naturales (PNN) de Colombia website (https://www.parquesnacionales.gov.co/). The PNN shapefiles are licensed under the terms specified at: https://portaldatosabiertos-pnnc.hub.arcgis.com/pages/trminos-y-condiciones.

TABLE 1 Collection sites for the study of intraspecific functional trait variability in *Polylepis quadrijuga* (Figure 2).

Collection sites	*N*	Patches	Sampled area	Elevation	Disturbance level
Santuario de Fauna y Flora (SFF) Guanentá Alto Río Fonce	40	2	2.00	3,687–3,770	Low
PNN Sumapaz	12	1	0.70	3,708–3,740	Low
PNN Cocuy	22	2	1.70	3,920–4,003	Low
Guerrero	10	1	0.34	3,492–3,593	High
La Rusia (East)	12	1	0.61	3,652–3,726	High
Laguna de Palchacual	11	1	0.35	3,656–3,670	High

Number of sampled individuals (N), number of patches sampled per site, approximate sampled area (ha), forest elevation (m.a.s.l.), and disturbance level assigned to each population. A total of 107 individuals were sampled.

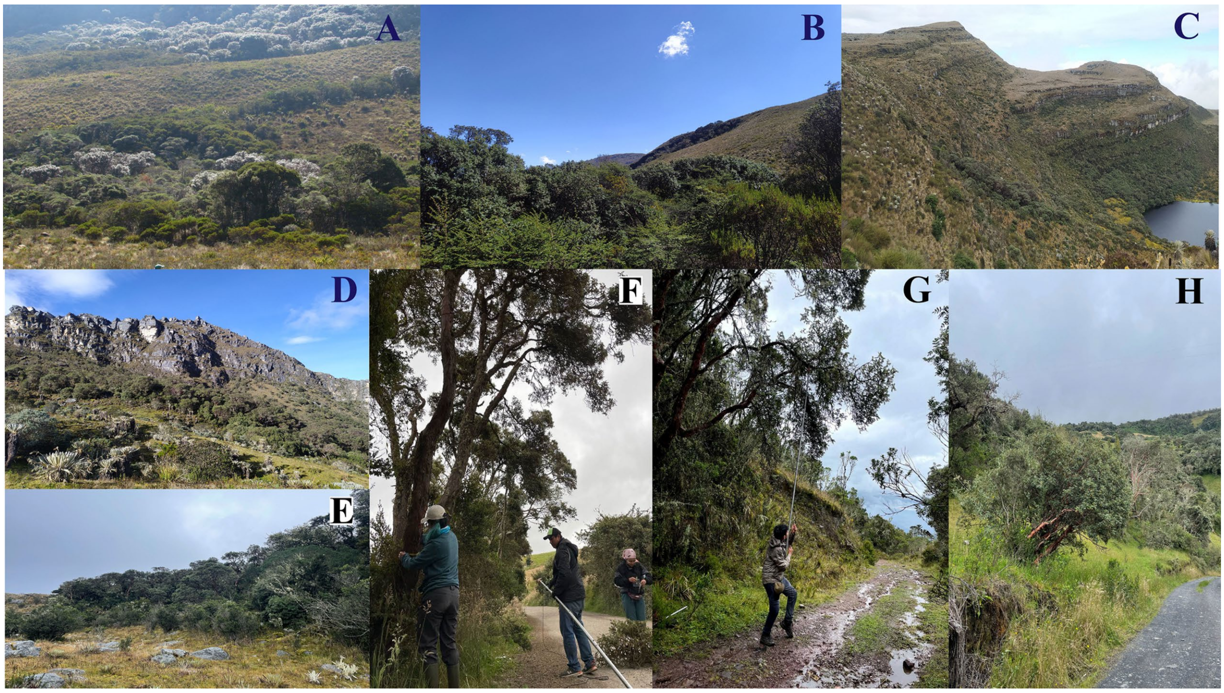

FIGURE 2
Photos of the different study sites: **(A)** Forest near Laguna Agua Clara within the Santuario de Fauna y Flora Guanentá Alto Río Fonce; **(B)** Forest near Laguna de Media Luna within the Santuario de Fauna y Flora Guanentá Alto Río Fonce; **(C)** Forest located west of Laguna Cajitas in the Sumapaz complex; **(D)** Forest located near La Parada de Romero in the municipality of Güicán; **(E)** Patch located near the Laguna San Pablín in the municipality of Güicán; **(F)** Individuals located along the road in the Guerrero complex; **(G)** Individuals located along the road on the east side of the La Rusia páramo complex, near the Laguna de Patos; **(H)** Individuals located along the road near the Laguna Palchacual in the municipality of Cocuy. Sites from **(F-H)** correspond to high disturbance. Photographs **(C, D, F-G)** and **(H)** by Adriana Sanchez; **(B, E)** by Yessica Hoyos; **(A)** by Camilo Márquez.

Accessibility refers to the distance from the individuals' growth location to anthropogenic activities such as livestock, agriculture and fertilization, mining, fragmentation by roads, and housing. The surrounding vegetation of the site was also taken into account because monodominant forests did not form on sites with a high level of disturbance. We considered the proximity to the outer limits of National protected areas, such as national parks (PNN), as an additional indicator of disturbance. In this context, sites categorized as having low disturbance levels were located close (< 2 km) to PNN boundaries (PNN Cocuy and Sumapaz) or within a protected area (SFF Guantentá Alto Río Fonce). If a group of individuals was growing at the edge of a road with a matrix of pastures and other trees around them, a "high" level of disturbance was assigned; for example, at the Guerrero site (Table 1 and Figure 2F). Each individual plant sampled was georreferenced.

2.4 Sampling and functional traits measurement

Samples of leaves, trunks, and roots were collected, and the diameter at breast height (DBH) was recorded in 107 adult individuals. A total of 11 functional traits related to plant growth and survival (Supplementary Table S1) were measured using standardized protocols (Pérez-Harguindeguy et al., 2013).

Four foliar traits were measured: leaf area (LA, mm^2), specific leaf area (SLA, $mm^2\ mg^{-1}$), leaf thickness (LT, mm), and leaf dry matter content (LDMC, $mg\ g^{-1}$) and the measurements were taken on three healthy, sun-exposed leaves per individual (excluding the petiole). We weighed leaves in the field. To calculate LA, we took photos of the leaves using a tripod and processed them with ImageJ software (Schneider et al., 2012). The SLA value was determined by dividing LA by the dry weight of the leaf. The leaves were dried at 70°C for 48 h and weighed immediately after removing them from the oven. Using a Vernier caliper, we measured LT values in the field. Since *P. quadrijuga* has compound leaves, three leaflets per leaf were chosen for LT measurements. These leaflets always corresponded to one closest to the petiole, one from the middle, and the tip leaflet. We always measured LT in the middle of each leaflet. For LDMC, the dry weight value was calculated based on the fresh weight measured in the field. In the stem, we measured wood density (WD, $mg\ mm^{-3}$) and was calculated based on three stem pieces per individual. These were dried at 70°C for 96 h to weigh and calculate WD as the ratio of their dry weight to volume.

For the six root traits average root diameter (ARD, mm), specific root length (SRL, $m\ g^{-1}$), root tip abundance (RTA, $n\ mg^{-1}$), root tissue density (RTD, $g\ mm^{-3}$), branching frequency (BF, mm) and root branching index (RBI, $n\ cm^{-1}$), we sampled fine roots (10–25 cm depth) per individual and stored them in Ziplock bags. Subsequently, we scanned the samples with an Epson Perfection V19 scanner at a resolution of 300 DPI and dried them in an oven at 70°C for 48 h. The images were analyzed using RhizoVision Explorer V2.0.3 (Seethepalli et al., 2020), where each sample was divided into three categories based on its diameter (0–2 mm, 2–5 mm, and > 5 mm). In this study, we only used fine roots (0–2 mm) to estimate functional traits. Following this criterion, we eliminated five individuals with roots >2 mm. Root traits were therefore analyzed in 102 individuals. Measurements of root length (RL), fine root volume (RV), the number of tips (NT), BF, and ARD were taken based on the software. SRL was calculated as the ratio of RL to its dry weight; RTA as the ratio of NT to its dry weight; RTD as the ratio of dry weight to RV, and RBI as the ratio of NT to RL.

2.5 Arbuscular mycorrhizal colonization (AMF)

Colonization by bacteria and/or fungi has also been considered as a functional trait ("Nutrient uptake strategy" in Pérez-Harguindeguy et al., 2013). Given that disturbed areas could impact the colonization by symbionts (Barnola and Montilla, 1997; Jefwa et al., 2012; Ji et al., 2022), and that the symbiosis with *P. quadrijuga* had not been described, we explored the fungal colonization and included an estimate of fungal colonization. We used two fine-root samples per individual (10 per each páramo site), removed soil and organic particles from the roots collected for colonization, stored them in alcohol (90%) and later cleared and stained for observation (Grace and Stribley, 1991). We cleared the roots with 10% KOH (20 min at 90°C) and rinsed the sample three times with water. We bleached the roots with 3% H_2O_2 (15 min at 90°C) and rinsed the sample twice with water. Then, we acidified them with 1% HCl (5 min at room temperature) and stained them with 0.05% black ink (5% acetic acid +0.05% black ink). Finally, we rinsed three times with water and stored them with a destain solution (50% glycerol +45% water +5% HCl). We mounted each sample for examination under a LEICA-DM750 4-100x microscope. We employed the grid line intersection method (Giovannetti and Mosse, 1980) to record the presence of arbuscules, vesicles, and hyphae as well as the absence of mycorrhizal structures at a magnification of x40 and a 6 × 5 grid line. For estimating colonization percentage (Col %), we calculated the total number of infected roots divided into the total number of roots intersecting grid lines.

2.6 Soil analyses

We collected soil samples near each individual plant to create a composite soil sample (~1,000 g) for each páramo site (two for SFF and Cocuy, one for the other sampling sites; Table 1). The soils were air-dried for a week and then sieved. The physicochemical analysis was conducted by Agrilab Environmental and Agricultural Services (Bogotá, Colombia) for the following variables: pH and electrical conductivity (EC, $dS\ m^{-1}$) were measured using the conductimetry technique, with a saturation paste as the extractant; oxidizable organic carbon (COOX, %) was obtained through a colorimetric analysis using potassium dichromate as the extractant; average humidity saturation (Humidity, %) was measured using a gravimetric analysis with a saturation paste as the extractant; effective cation exchange capacity (ECEC, meq/100 g), organic matter (OM, %), total nitrogen (N, %), and apparent density (DA, $g\ cm^{-3}$) were calculated; potassium (K, $mg\ kg^{-1}$), calcium (Ca, $mg\ kg^{-1}$), magnesium (Mg, $mg\ kg^{-1}$), and sodium (Na, $mg\ kg^{-1}$) were obtained using inductively coupled plasma optical emission spectrometry (ICP-OES) with ammonium acetate as the extractant; phosphorus (P, $mg\ kg^{-1}$) was also obtained through a colorimetric technique using Bray II solution as the extractant; sulfur (S, $mg\ kg^{-1}$) was measured using turbidimetry, with monobasic calcium phosphate as the extractant; and finally, exchangeable acidity (EA) was determined using volumetric analysis with 1 N potassium chloride as the extractant.

2.7 Statistical analysis

In order to have a general climatic characterization of the sites and compare between disturbance levels, we used WorldClim[1] with a spatial resolution of 30 s (~1 km^2). We included seven environmental variables that describe the conditions of each site: precipitation seasonality (Pr_season), temperature seasonality (TM_season), wet season precipitation (Pr_Wet), dry season precipitation (Pr_Dry), maximum temperature in the hottest month (MaxTM_Hot), minimum temperature in the coldest month (MinTM_Cold), and annual mean precipitation (Annual_Pr). A Principal Component Analysis (PCA) was performed using the FactoMineR v1.34 package (Husson et al., 2008) and factoextra v1.0.7 package (Kassambara and Mundt, 2020) in R v4.2.0 (R Core Team, 2020). In each of the páramo sites we sampled multiple individuals, and in some cases more than one patch (Table 1). These individuals were all georreferenced.

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[1] http://www.worldclim.org, accessed in February 2023

Additionally, we performed two additional PCAs to observe trends and patterns for each disturbance level in: (1) Aboveground functional traits and (2) belowground functional traits. We also compared the physicochemical soil properties between highly and less disturbed sites using a pairwise test (Student's *t*-test or *U* Mann–Whitney), depending on normality and homoscedasticity.

For each functional trait, we checked for normality and homoscedasticity. For RTA, we normalized values using the logarithmic function to conduct parametric comparison tests (Student's *t*-test) between disturbance levels (high and low). A Wilcoxon test was conducted when the transformation did not meet the assumptions of normality and/or homoscedasticity. We also performed a logistic model to evaluate which functional traits were significantly affected by the level of disturbance: 1 = low level of disturbance and 0 = high level of disturbance (R Core Team, 2020). Then, we used the function "stepAIC" from the MASS v7.3–58.1 package (Venables and Ripley, 2002) to perform a stepwise model selection by Akaike Information Criterion (AIC). The best model with the lowest AIC (56.37) (Equation 1) was:

$$\log\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1(LT) + \beta_2(LA) + \beta_3(LDMC) + \beta_4(SRL) + \beta_5(RTD) + \beta_6(BF) + \beta_7(ARD) + \beta_8(COL) \tag{1}$$

Where p is the probability that the dependent variable "Level of Disturbance" is equal to 1, β_X are the coefficients of the model which are multiplied by each of the independent variables that contributed significantly to the model.

3 Results

3.1 Functional variability between levels of disturbance

The principal component analysis (PCA) showed climatic differences between the páramo sites, but not between disturbance levels (Supplementary Figure S1). We also found that *P. quadrijuga* exhibited high intraspecific functional trait variability. The clustering pattern of aboveground functional traits, which explained 70.1% of the variability (44.9 and 25.2% for each axis, respectively), showed a different response depending on the disturbance level (Figure 3A). In contrast, we found that the clustering pattern of belowground functional traits was similar between different disturbance levels (Figure 3B). This PCA explained 65.8% of the variation (43.2 and 22.6%, respectively).

Populations with high disturbance levels had significantly higher values of LT, LA, and SLA and populations with low disturbance levels had high WD and LDMC values (Figure 4; Supplementary Table S2; $p < 0.05$). Although belowground traits showed high overlap in the PCA, there were significant differences in ARD, BF, and Col % between disturbance levels (Figure 4; Supplementary Table S2; $p < 0.05$). Populations with lower disturbance had lower ARD values but higher BF compared to high disturbance sites (Figure 4). The other functional traits evaluated had no significant differences (SRL, RTA, RTD, RBI; $p > 0.05$).

AMF colonization (Col %) was significantly higher in lower disturbance (mean = 65.27, $p = 0.026$; Figure 4) and lower in higher disturbance sites (mean = 56.10; Figure 4). Also, we found a vesicle percentage of 13.11%, arbuscles of 0.14%, and hyphae of 42.50% for

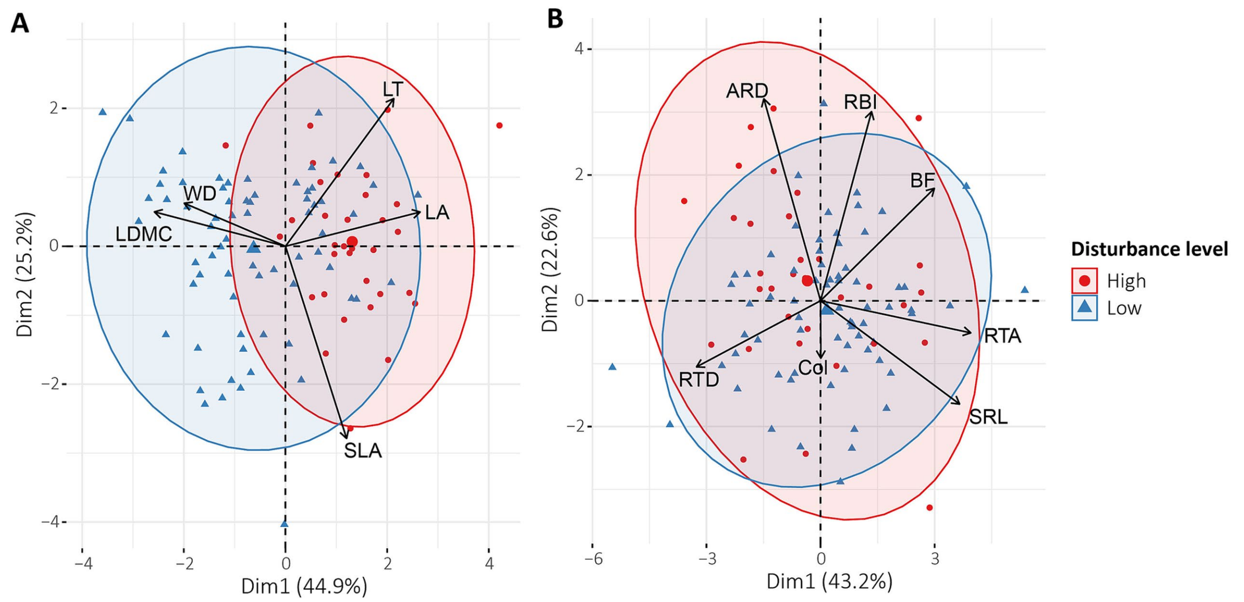

FIGURE 3
PCAs showing the relationships between functional traits of *Polylepis quadrijuga* **(A)** Aboveground functional traits from two disturbance levels: leaf area (LA, mm^2), specific leaf area (SLA, mm^2 g^{-1}), leaf thickness (LT, mm), leaf dry matter content (LDMC, mg g^{-1}) and wood density (WD, mg mm^{-3}). **(B)** Belowground functional traits from two levels of disturbance: average root diameter (ARD, mm), specific root length (SRL, m g^{-1}), root tip abundance (RTA, n mg^{-1}), root tissue density (RTD, g mm^{-3}), branching frequency (BF, mm), root branching index (RBI, n cm^{-1}) and colonization percentage (Col %).

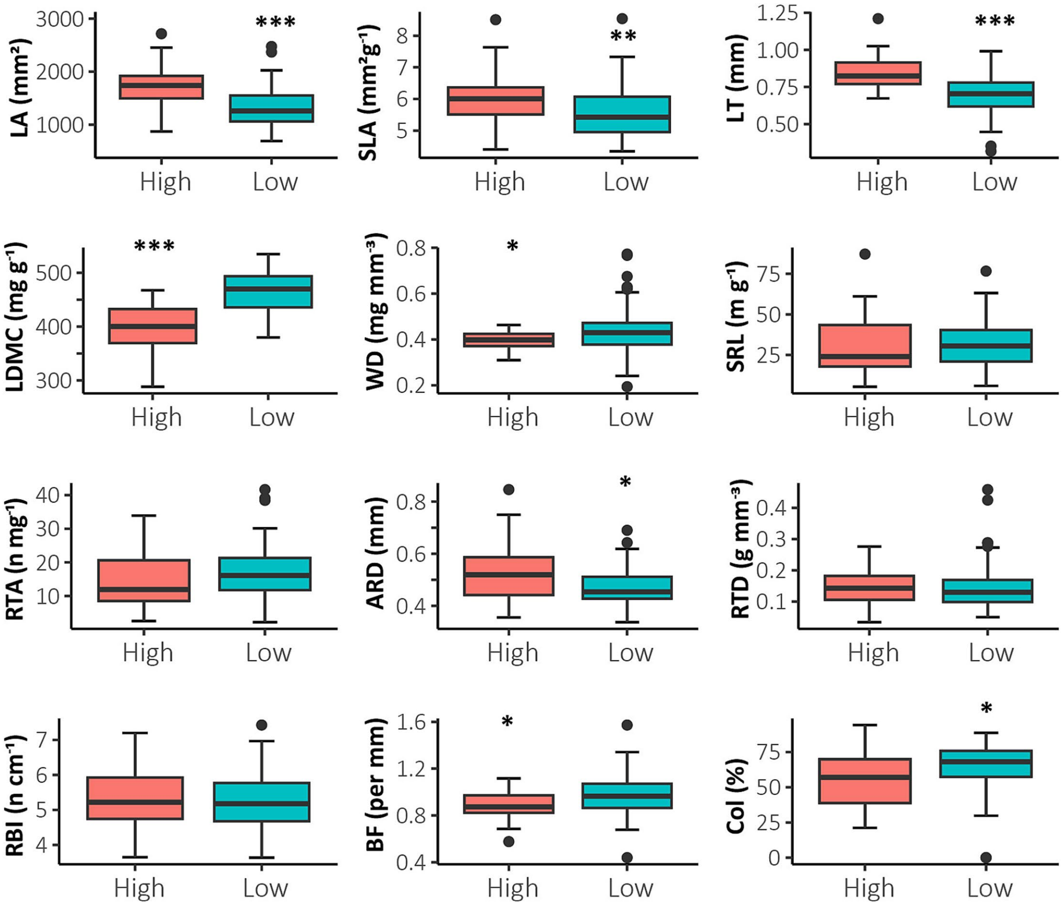

FIGURE 4
Comparison of *Polylepis quadrijuga* functional traits between the different disturbance levels (High, Low) using boxplots. The median value of each trait and its corresponding patch is shown (box: standard error; whisker: standard deviation): leaf area (LA, mm^2), specific leaf area (SLA, $mm^2\ g^{-1}$), leaf thickness (LT, mm), leaf dry matter content (LDMC, $mg\ g^{-1}$), wood density (WD, $mg\ mm^{-3}$), average root diameter (ARD, mm), specific root length (SRL, $m\ g^{-1}$), root tip abundance (RTA, $n\ mg^{-1}$), root tissue density (RTD, $g\ mm^{-3}$), branching frequency (BF, mm), root branching index (RBI, $n\ cm^{-1}$) and colonization percentage (Col, %). Significant differences between the two different disturbance levels are indicated as follows: $p < 0.001$: ***; $p < 0.01$: **; $p < 0.05$: *.

high-disturbance sites. For low disturbance sites we found a vesicle percentage of 15.64%, arbuscles of 0.38%, and hyphae of 46.36%.

We also found that the functional traits that significantly influence the differentiation between high and low disturbance sites in the logarithmic model were: LA, LDMC, SRL, RTD, ARD, BF, Col and LT. Although LT did not have a significant influence, the best model included it as a variable (Supplementary Table S3). In summary, we found that functional traits such as lower LA, SLA, LT, and ARD were associated with sites experiencing low disturbance levels and reflect a conservative strategy. In contrast, sites with high disturbance level showed functional traits such as lower LDCM, WD, BF, and colonization percentage (Col), which indicates an acquisitive strategy.

3.2 Physicochemical properties of soils with high and low levels of disturbance

We found a significant difference in three of the fifteen physicochemical properties analyzed between sites with high and low levels of disturbance (Supplementary Table S4). Soils from high disturbance sites were characterized by being less acidic (mean = 4.52, $t = 2.302$, $p = 0.06$) than low disturbance (mean = 4.08). In contrast, sites with lower disturbance levels had higher EC ($t = -3.078$, $p = 0.021$), and higher humidity (77.1 vs. 48.5 in high disturbance) ($t = -3.167$, $p = 0.019$).

4 Discussion

Our analyses show that *Polylepis quadrijuga* responds to different environmental changes caused by anthropogenic disturbance. According to our first hypothesis, we expected that individuals under high disturbance (road fragmentation, near crops and livestock) would have trait values reflecting an acquisitive strategy. Based on our results, populations exposed to a high disturbance level mainly differed in aboveground functional traits and had higher values of leaf area (LA) and specific leaf area (SLA), and lower values of leaf dry matter content (LDMC) and wood density (WD), compared to populations with a low disturbance level. These traits are characteristic of an acquisitive functional strategy (Wright et al., 2004; Reich, 2014), which is in line with our hypothesis. In the second hypothesis, we expected less AMF colonization in highly disturbed sites in response to land use change, which our results corroborated (Figure 4). For the last hypothesis, we had proposed that there would be coordination between above- and belowground traits. We found that these traits are not coordinated, and root traits are more similar between disturbance levels (Figure 3).

Climate was similar for páramo sites that were located nearby (Supplementary Figure S1). Therefore, locations such as SFF-La Rusia (East) and Sumapaz-Guerrero only differed in their levels of disturbance (low and high, respectively), yet displayed varying responses in both above- and belowground functional traits. This response aligns with findings from previous studies in *Polylepis* (Toivonen et al., 2014), indicating that functional traits not only respond to shifts in climate but also to the specific requirements of each species (Martínez-Vilalta et al., 2010). In this case, to stress conditions that may be caused by anthropogenic activities. Likewise, increased disturbance levels in tropical mountain ecosystems (e.g., shifting cultivation and logging) intensify the impact of abiotic filters, leading to the emergence of species with traits tailored to such disturbances (Ding et al., 2012; Feng et al., 2014; Singh et al., 2021). In this regard, *P. quadrijuga* populations exhibit a functional response to the anthropogenic alterations they have undergone in recent decades, including deforestation (Caballero-Villalobos et al., 2021) and fragmentation for agricultural purposes (Ramos et al., 2013; Boza Espinoza and Kessler, 2022). As a result of these anthropogenic activities, most *Polylepis* forests are currently restricted to areas that are difficult to access (Kessler et al., 2014; Toivonen et al., 2018).

On the one hand, individuals in sites with high disturbance levels may exhibit significantly different functional traits, potentially facilitating rapid growth and reproduction (an acquisitive strategy). This could be attributed to intense trait filtering, which enables them to mitigate the diverse environmental changes induced by the disturbance (Schellenberger Costa et al., 2017). High trait values of LA, SLA and LT had been reported in fragmented populations of *P. quadrijuga* as a strategy for light harvesting (Velez et al., 1998; Ramos et al., 2013). Individuals exposed to the edge also changed their leaf composition by increasing the lignin content in the parenchyma, antioxidant and flavonoids substance to reduce photo-oxidation damage (Velez et al., 1998; Ramos et al., 2013). Nevertheless, the trend of increasing leaf size with leaf thickness represents a unique functional pattern observed in *P. quadrijuga*. In other *Polylepis* species, an increase in leaf size is typically accompanied by a decrease in leaf thickness (Macek et al., 2009; Toivonen et al., 2014).

On the other hand, sites with low disturbance have conservative functional traits: plants invest more carbon in leaf and stem tissues, so their growth is slow as a response to the abiotic filters of their environment (Reich, 2014; Firn et al., 2019). Populations of *P. quadrijuga* in these sites also tend to have thinner leaves (Figure 4: LA). Interestingly, this pattern contrasts with previous findings where low SLA and high LDMC were associated with low water and nutrient availability in *P. rugulosa, P. tarapacana* and *P. tomentella* (Macek et al., 2009). However, recent studies have shown that SLA is not a good indicator of the nutrient amount in the soil because it also changes with light intensity (Hodgson et al., 2011; Singh and Negi, 2018; Firn et al., 2019). The observed high LDMC values in this study may represent a response to environmental conditions that could potentially cause damage, such as wind, sun, or hail (Pérez-Harguindeguy et al., 2013). Structural responses to environmental harshness such as low temperatures, rather than by anthropogenic disturbance, have also been observed in *P. subsericans* (Toivonen et al., 2018), *P. racemosa, P. pauta, P. sericea, P. pepei* (Kessler et al., 2014), *P. tomentella, P. rugulosa* and *P. tarapacana* (Macek et al., 2009).

The lack of coordination between the leaf economic spectrum (LES) and root economic spectrum (RES) observed in our study could be attributed to root traits responding multidimensionally to biotic and abiotic factors (Weemstra et al., 2016). Interestingly, sites with low disturbance levels have more compact soils (high apparent density) and display roots with lower root diameter (ARD) and higher branching frequency (BF) values (Ma et al., 2018; Semchenko et al., 2018). Such traits are typically suited for soils that are easy to explore, which is not ideal for compact soils (Weemstra et al., 2016; Bergmann et al., 2020). Consequently, the roots of these populations may rely on the colonization of arbuscular mycorrhizae (AMF) to acquire the necessary nutrients (Barnola and Montilla, 1997). Therefore, root responses may not align as clearly with the LES gradient. Additionally, of the seven belowground functional traits evaluated, only three showed significant differences between high and low disturbance sites. This finding is consistent with other studies on *Polylepis*, which have noted that belowground traits do not tend to vary as much as the aboveground and do not clearly align with a RES strategy (Hertel and Wesche, 2008; Toivonen et al., 2014; Valverde-Barrantes, et al., 2016).

Previous findings have shown that AMF colonization does not necessarily correlate with an increase in ARD (Maherali, 2014) and, in more acidic soils, AMF plays an important role in nitrogen (N) uptake (Camenzind et al., 2016). Although, in our study there was no evidence of differences in soil N content between sites, there is a greater limitation of N at higher elevations in tropical mountains (Soethe et al., 2008; Fisher et al., 2013). Additionally, we found a lower percentage of AMF colonization in sites with a high level of disturbance. It is possible that the colonization of AMF in *P. quadrijuga* is less resilient to anthropogenic disturbance compared to *P. australis* (Soteras et al., 2015; Soteras et al., 2016). One possible reason for this difference could be the specific environmental conditions of tropical mountains where *P. quadrijuga* is found. Previous studies have shown that AMF colonization in tropical mountains subjected to agrochemicals, tillage, or human management significantly decreases their colonization rate (Barnola and Montilla, 1997; Jefwa et al., 2012).

This is the first study (we know of) exploring the intraspecific functional trait variability of *P. quadrijuga* under different disturbance levels. Our findings underscore the sensitivity of this species to anthropogenic disturbance, but also its resilience. *Polylepis quadrijuga* exhibits high plasticity in its aboveground functional traits, enabling it to adjust its ecological performance in response to both abiotic and anthropogenic disturbances, such as land use change and fragmentation. This plasticity may be crucial for resisting stress and invasive species (Ferrero et al., 2022; Kaushik et al., 2022). We recommend conducting more detailed studies on the effects of anthropogenic activities such as cattle ranching, fire, or mining on the functional traits and interactions between foliar and root traits of each *Polylepis* species. In addition, it is important to study the AMF associated with *P. quadrijuga* and to evaluate how the identity of the fungi changes with disturbance. This information could be key in restoration efforts of *P. quadrijuga's* monodominant forests. Further research is also needed to enhance our understanding of the microclimate in these populations. Studies on

P. quadrijuga have used platforms like WorldClim (Fajardo-Gutiérrez et al., 2018; Caballero-Villalobos et al., 2021; Bedoya-Canas et al., 2024), which may not yield precise results for an accurate climatic characterization of these populations. Therefore, it is important to use on-site climatic sensors to understand the microclimatic conditions of these populations. As observed in this and other studies in *Polylepis* (e.g., Hertel and Wesche, 2008; Macek et al., 2009; Toivonen et al., 2011; Toivonen et al., 2014; Ramos et al., 2013), the functional traits of *P. quadrijuga* adjust to various biotic and abiotic conditions. It is crucial to determine and implement conservation and restoration strategies for these forests, which provide numerous ecosystem services. Conservation efforts for *P. quadrijuga* should prioritize fragmented populations or those facing stressful conditions such as livestock grazing or agricultural activities. These strategies should aim to create microhabitats that promote the establishment of this endangered species.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://doi.org/10.5281/zenodo.13377113.

Author contributions

YH: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. NV: Methodology, Writing – original draft, Writing – review & editing. AS: Conceptualization, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2024.1488389/full#supplementary-material

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