CONSERVATION

REVISTA DE Biología Tropical

https://doi.org/10.15517/rev.biol.trop..v73i1.61916

Human disturbance promotes an increasing abundance of shrubby plants in the páramo landscape of Southern Ecuador

Pedro X. Astudillo[1]*; https://orcid.org/0000-0002-9945-9414
Paul Porras[1]; https://orcid.org/0000-0002-0428-9070
David C. Siddons[1]; https://orcid.org/0000-0003-3305-2969
Eduardo Barnuevo[1]; https://orcid.org/0000-0001-8946-2081
Santiago Barros[1]; https://orcid.org/0000-0003-2647-6579

1. Laboratorio de Ecología, Escuela de Biología, Universidad del Azuay, Cuenca, Ecuador; pastudillow@uazuay.edu.ec (Correspondence*); paulporraspolo@gmail.com; dsiddons@uazuay.edu.ec; barflo93@gmail.com; jsanty.b1@gmail.com

Received 17-IX-2024. Corrected 13-II-2025. Accepted 30-V-2025.

ABSTRACT

Introduction: The páramo grassland ecosystem is an important center of plant diversity and endemism. However, human activities, such as burning and livestock grazing, are altering the plant composition of the páramos. These changes may be associated with an increase in the abundance of shrubby species and a corresponding decrease in native grass cover.

Objective: To evaluate the effects of human disturbance on the composition of woody plant species in páramo habitats.

Methods: We conducted 36 transects across the páramo landscape of the Macizo del Cajas Biosphere Reserve in Southern Ecuador between April 2017 and November 2019, recording woody plant species (e.g., bushes and shrubs) along each transect. To explore variations in woody plant composition, we employed non-metric multidimensional scaling, using the proportion of disturbed area, páramo grassland, and elevation as predictor variables.

Results: We recorded a total of 13 377 woody plants. The proportion of disturbed areas has an influence on the composition of the woody plant species. Shrubby species such as *Diplostephium ericoides*, *Hypericum quitense*, *Valeriana microphylla,* and *Valeriana hirtella* are more prevalent in transects with a greater proportion of disturbed areas.

Conclusion: There was a greater presence of fast-growing woody plant species in response to human-induced disturbance. This suggests that native herbaceous species are gradually being replaced by woody encroachment, particularly in human-accessible páramos. Conservation and restoration efforts should take this phenomenon into account to prevent the accelerated spread of woody encroachment and enhance the availability of páramo grassland habitats.

Key words: high Andes; woody plant encroachment; plant community composition; grasslands; biosphere reserve.

RESUMEN

Las perturbaciones humanas promueven el incremento en la abundancia de plantas arbustivas en el paisaje de páramo del sur de Ecuador

Introducción: El ecosistema de páramo herbáceo es un importante centro de diversidad y endemismo de plantas. Sin embargo, las actividades humanas como el pastoreo y las quemas están alterando la composición de plantas

de los páramos. Estos cambios pueden estar asociados a un incremento en la abundancia de especies arbustivas y una menor cobertura de pastizales nativos.

Objetivo: Evaluar los efectos de la alteración humana sobre la composición de plantas leñosas en hábitats de páramo.

Métodos: Entre abril de 2017 y noviembre de 2019, recorrimos 36 transectos a través del paisaje de páramo de la Reserva de la Biósfera del Macizo del Cajas en el sur de Ecuador, registrando las especies de plantas leñosas (e.g., arbustos y matorrales) a lo largo de cada transecto. Para explorar las diferencias en la composición de las plantas leñosas, usamos un escalamiento multidimensional no métrico, con la proporción en la cobertura de área alterada, páramo herbáceo y elevación como variables predictoras.

Resultados: En total, registramos 13 337 plantas leñosas. La proporción de área alterada influye en la composición de las especies de plantas leñosas. Las especies arbustivas como *Diplostephium ericoides*, *Hypericum quitense*, *Valeriana microphylla* y *Valeriana hirtella* tiene mayor presencia en transectos con un incremento en la proporción de las áreas alteradas.

Conclusiones: Hay una mayor presencia de especies de plantas leñosas de crecimiento rápido en respuesta al efecto de la alteración inducida por los humanos. Esta observación sugiere que las especies herbáceas nativas están siendo gradualmente reemplazadas por un engrosamiento con plantas leñosas, particularmente en páramos con acceso humano. Los esfuerzos de conservación y restauración deberían tener en cuenta este fenómeno para evitar una aceleración de la invasión de plantas leñosas y, asegurar la disponibilidad de hábitats de páramo herbáceo.

Palabras clave: altos Andes; engrosamiento de plantas leñosas; composición de la comunidad de plantas; pastizales; reserva de la biósfera.

INTRODUCTION

The Tropical Andes is an important center of biodiversity and endemism (Jiménez-Rivillas et al., 2018; Myers et al., 2000). The region is one of the most biological diverse hotspots globally (Baquero et al., 2004; Jiménez-Rivillas et al., 2018; Neill, 1999; Sarmiento, 2000), harboring one sixth of the terrestrial plant diversity on less than 1 % of the global surface (Myers et al., 2000). Páramo is the major vegetation type in the high Andes (> 3 000 m.a.s.l.) of Northern South America (Llambí et al., 2012). In Ecuador, the páramos are a mosaic of habitats, mainly characterized by native tussock grasses (páramo grassland), but also associated with small woody plants within marshes, bog plants in more humid areas (cushion páramo), taller vegetation in semi-open shrubland (shrubby páramo), and numerous patches of *Polylepis* woodlands (García et al., 2020; Neill, 1999; Sklenár & Ramsay, 2001).

This páramo ecosystem, like other biodiversity hotspots, is impacted by human activities such as burning to facilitate pastures for grazing, agricultural expansion and habitat modification at roadsides (Bagchi et al., 2018; Barros et al., 2020; Hofstede & Llambí, 2020; Matson & Bart, 2013; Sylvester et al., 2017). In Southern Ecuador, livestock grazing is the main activity affecting the páramo landscape (Astudillo et al., 2017; Suárez & Medina, 2001) resulting in the homogenization (i.e., botanically and structurally) of páramo vegetation (Astudillo et al., 2017; García et al., 2020; Hofstede & Llambí, 2020; Jørgensen et al., 2011; Smart et al., 2006; Sylvester et al., 2017). This region is also expected to experience changes in habitat structure and composition due to climate change (Carrillo-Rojas et al., 2019; Hofstede & Llambí, 2020). It is predicted that vegetation adaptable to more extreme climate ranges (e.g., longer and more intense droughts with shorter and more intense rainfalls) will become more dominant (Foster, 2001; Hudson et al., 2014). These actual and future pressures have led the páramo ecosystem to become a priority for biological conservation (Astudillo et al., 2024; Hofstede & Llambí, 2020; Madriñán et al., 2013).

The intensity and frequency of human-induced disturbances have been shown to result in changes to plant composition (González et al., 2023; He et al., 2019; Hofstede & Llambí, 2020;

Suárez & Medina, 2001; Sylvester et al., 2017). For example, research shows that excluding fire leads to an increase in woody plants, such as shrubs and bushes (Brandt et al., 2013; Matson & Bart, 2014) with a consequent reduction of available grazing areas (Matson & Bart, 2014; Montané et al., 2007). Here, following a fire, the regeneration of vegetation typically begins with the establishment of species that have a patchy distribution, such as those belonging to the Poaceae family (Jantz & Behling, 2012; Sarango-Cobos et al., 2019). However, in the long term, woody plants colonize páramo soils when they are left to regenerate, mainly occupying areas lacking native grass cover (Matson & Bart, 2014). This final phenomenon occurs in conjunction with irregular topography (e.g., along elevation gradients and on steep slopes with minimal grass cover) and facilitates the encroachment of woody shrubs and bushes across the páramo landscape (Matson & Bart, 2013). Furthermore, in more extreme climate regime scenarios, plants with a wider geographic range, rapid dispersion, and presence in the montane forest tree line close to the lower limit of the páramo will also contribute to woody encroachment (Caballero-Villalobos et al., 2021; Foster, 2001; Jantz & Behling, 2012; Loughlin et al., 2018; McKinney & Lockwood, 1999; Montaño-Centellas et al., 2024). Nevertheless, the natural presence of shrubs may also create favorable conditions (e.g., shade and protection from the wind), which in turn may lead to an increase in the species richness of páramo plant communities (Sylvester et al., 2017; Vargas-Ríos & Ávila-Rodríguez, 2021).

Therefore, there is an urgent need to monitor páramo habitats to fully understand the effects of human disturbance and their associated changes in plant composition in order to improve conservation and restoration strategies for natural resource managers. Specifically, it is important to address how the increasing cover of woody plants is affecting páramo vegetation communities. Consequently, in the páramos of Southern Ecuador, an important region for plant diversity (Jiménez-Rivillas et al., 2018), we evaluated the effects of human disturbance on the vegetation composition of páramo habitats. We expected an increasing abundance of woody bushes and shrubs in areas with greater disturbance (mainly influenced by burning and livestock grazing). Principally, we expected disturbed areas to have a higher prevalence of widely distributed, generalist woody plant species (i.e., faster growing plants and those associated with the lower limits of páramo and the upper limits of montane forest).

MATERIALS AND METHODS

Study area: This study was conducted in the highlands (> 3 500 m.a.s.l.) of the Macizo del Cajas Biosphere Reserve in SouthWestern Ecuador (2°55'25" S & 79°21'57" W) (Fig. 1), a priority region for biological conservation (e.g., Astudillo et al., 2024). The study area is dominated by páramo grassland ecosystem and covers ~166 000 ha. The Macizo del Cajas has two protected areas forming the core area of this reserve, Cajas National Park (2°50'45"' S & 79°14'33" W) and Quimsacocha National Recreation Area (3°00'45" S & 79°14'12" W) (Rodríguez et al., 2014). These two protected areas encompass ~19 % of the total area of páramos within Macizo del Cajas (Fig. 1) (Barros et al., 2020). The average monthly temperature ranges between 5 and 12 °C. Average annual precipitation ranges between 1 200 and 1 500 mm, with two rainy seasons; intense precipitation between March and May and a second, less intense peak, between September and February. The lowest precipitation occurs between June and August (Ballari et al., 2018; Celleri et al., 2007).

The study area has an elevation range between 3 600 and 4 050 m. The vegetation is dominated by tussock grasses of species of *Calamagrostis* and *Festuca* with cushion plants and rosette species, such as *Plantago* and *Oreobolus,* in smaller humid areas (Minga et al., 2016; Sklenár et al., 2005). In more heterogeneous páramo, the vegetation is associated with native shrub species mainly of the family Asteraceae such as *Chuquiraga jussieui* J.F. Gmel, *Monticalia arbutifolia* (Kunth) C. Jeffrey,

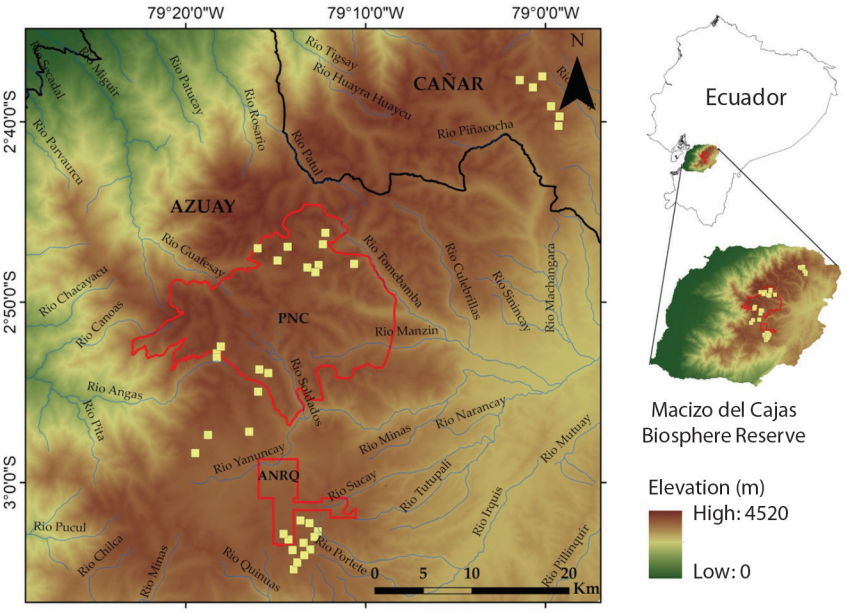

Fig. 1. Study area and location of 36 transects for vegetation sampling in the páramo landscape of the Macizo del Cajas Biosphere Reserve, Southern Andes of Ecuador. The yellow squares represent the central coordinate of each 1 km transect. The red polygons are the protected areas within the reserve (PNC = Cajas National Park. ANRQ = Quimsacocha National Recreation Area). / **Fig. 1.** Área de estudio y ubicación de los 36 transectos para el muestreo de vegetación en el paisaje de páramo de la Reserva de la Biosfera Macizo del Cajas, sur de los Andes de Ecuador. Los cuadrados amarillos representan la coordenada central de cada transecto de 1 km. Los polígonos rojos son las áreas protegidas dentro de la reserva (PNC = Parque Nacional Cajas. ANRQ = Área Nacional de Recreación Quimsacocha).

Gynoxys miniphylla Cuatrec. (Ansaloni et al., 2022; Baquero et al., 2004; Minga et al., 2016; Neill, 1999). In addition, the páramo is interspersed with patches of *Polylepis* woodlands (Astudillo et al., 2020; Pinos, 2020). The main human activity is livestock grazing associated with burning to enhance pasture (Astudillo et al., 2017) with evident negative effects on páramo habitats (e.g., less complex habitat structure with lower plant diversity).

Vegetation sampling: We randomly established, in a suitable area (i.e., avoiding extreme slopes or mountain tops), 36 transects across protected areas and surrounding zones within the páramo ecosystem (Fig. 1). Each transect was 1 km in length and spaced at least 400 m apart and located in páramo habitats (e.g., páramo grassland, shrubby páramo, cushion páramo). All sampling was carried out between April 2017 and November 2019.

We used the vegetation sampling protocol provided by Astudillo et al. (2017), Astudillo et al. (2019) and Barros et al. (2020). These protocols have been widely used in monitoring páramo habitats and woody plants across the regional páramo. Thus, along each transect, ten circular plots with a radius of 12 m were installed, covering a total sampling area of 452.39 m². These plots were regularly spaced 100 m apart. In each circular plot, the proportion of two habitat types was visually estimated (Fig. 2): (i) páramo grassland (Fig. 2A), a natural open habitat with herbaceous vegetation (Ansaloni et al., 2022; Barros et al., 2020; Hofstede et al., 2002) dominated by tussock grasses, including species of *Calamagrostis*, *Festuca*, and *Stipa*, as well as cushion and bog plants, such as *Azorella*, *Oreobolus*, and *Plantago* (Beltrán et al., 2009; Minga et al., 2016) and (ii) disturbed area (Fig. 2B), defined as human-modified habitat with signs of paths, trails, exotic plants

Fig. 2. Examples of photos of vegetation monitored in the páramo landscape of Macizo del Cajas Biosphere Reserve. We present two examples per habitat (upper and lower panels): **A.** A less human disturbed páramo grassland (e.g., without evidence of burns and grazing) located inside of Cajas National Park. **B.** A more human disturbed páramo grassland (e.g., with evidence of burns and eroded soils resulting in more presence of certain faster growing woody plants) located outside of the national system of protected areas. All habitat examples are located at the relatively same elevation (~3 750 m.a.s.l.). / **Fig. 2.** Fotos de ejemplo de la vegetación monitoreada en el paisaje de páramo de la Reserva de la Biósfera Macizo del Cajas. Presentamos dos ejemplos por hábitat (paneles superior e inferior): **A.** Un páramo herbáceo menos alterado por el humano (e.g., sin evidencia de quemas y pastoreo) localizado dentro del Parque Nacional Cajas. **B.** Un páramo herbáceo más alterado por el humano (e.g., con evidencia de quemas y de suelo erosionado que resulta en una mayor presencia de ciertas plantas leñosas de crecimiento rápido) localizado fuera del sistema nacional de áreas protegidas. Todos los hábitats de ejemplo están localizados relativamente a la misma elevación (~3 750 m.s.n.m.).

(e.g., *Pinus* sp., *Polylepis racemosa* Ruiz & Pav.), burns, evidence of livestock grazing (e.g., feces), and eroded soils. Additionally, within each circular plot, we established four 12 m sub-transects, oriented along the cardinal directions. Along each sub-transect, we sampled the vegetation by counting and identifying shrubs (< 3 cm diameter at breast height [DBH]) and trees (> 3 cm DBH) touched by an observer walking with arms extended along the transect.

Data analysis: In order to evaluate the adequacy of the sampling effort, a species-accumulation curve was used based on the total abundance of shrubs, bushes and trees recorded across all transects (n = 36). We used rarefaction to standardize the observed richness (Colwell et al., 2012). The Chao 1 estimator was calculated based on 1 000 random permutations (Chao, 1984) to evaluate whether the observed richness was representative of the regional diversity (Colwell et al., 2012).

Community ordination: We used a non-metric multidimensional analysis (NMDS) to explore differences in the composition of

woody plant species (2D solution). The NMDS used Bray-Curtis dissimilarity with the total abundance of shrub, bushes and tree species recorded across the 36 transects (i.e., samples). Samples closer in the ordination represent less dissimilarity in vegetation composition. In order to investigate differences in the community, the average the proportion of páramo grassland, the proportion of disturbed area, as well as the mean elevation (meters above the sea level) per transect were post-hoc linearly fitted and their significance was tested via random permutations (1 000 iterations). Correlations among the predictors (proportion of páramo grassland, proportion of disturbed area and elevation) were evaluated. We found a negative correlation between the proportion of disturbed area and the proportion of páramo grassland (R = -0.77). Consequently, to obtain an approximation of the 'proportion of the páramo grassland' independent of the proportion of the disturbed area, we performed a linear model on páramo grassland with disturbed area as a predictor and used the residuals as the predictor variable. Therefore, all predictors showed no correlation (R-range = -0.28 to 0.17). All analyses were carried out in R 4.4.1 (R Core Team, 2024). For estimators and species accumulation curves we used the 'iNext' package (Chao et al., 2024), while for community ordination we used the 'vegan' package (Oksanen et al., 2024).

RESULTS

In total, we recorded 13 377 woody plants. The records are grouped in 29 species, 17 genera and 10 families (Table 1). The most

Table 1

Total abundance and codes of woody plant species recorded across 36 transects located in the páramo landscape of the Macizo del Cajas Biosphere Reserve, Southern Andes of Ecuador / **Tabla 1.** Abundancia total y códigos de las especies leñosas registradas a través de 36 transectos ubicados en el paisaje de páramo de la Reserva de la Biosfera Macizo del Cajas, sur de los Andes de Ecuador.

Family	Scientific name	Species code	Abundance
Asteraceae	*Baccharis tricuneata* (L. f.) Pers.	BATR	476
	Chuquiraga jussieui J.F. Gmel.	CHJU	660
	Diplostephium oblanceolatum S.F. Blake	DIOB	402
	Diplostephium rupestre (Kunth) Wedd.	DIRU	900
	Diplostephium ericoides (Lam.) Cabrera	DIER	178
	Diplostephium glandulosum Hieron.	DIGL	45
	Gynoxys miniphylla Cuatrec.	GYMI	789
	Gynoxys cuicochensis Cuatrec.	GYCU	188
	Gynoxys baccharoides (Kunth) Cass.	GYBA	19
	Loricaria thuyoides (Lam.) Sch. Bip.	LOTH	1 420
	Monticalia arbutifolia (Kunth) C. Jeffrey	MOAR	1 637
	Monticalia vaccinioides (Kunth) C. Jeffrey	MOVA	864
	Monticalia andicola (Turcz.) C. Jeffrey	MOAN	76
	Monticalia empetroides (Cuatrec.) C. Jeffrey	MOEM	137
Berberidaceae	*Berberis lutea* Ruiz & Pav.	BELU	101
	Berberis rigida Hieron.	BERI	43
Caprifoliaceae	*Valeriana microphylla* Kunth	VAMI	753
	Valeriana hirtella Kunth	VAHI	64
Ericaceae	*Pernettya prostrata* (Cav.) Sleumer	PEPR	41
Grossulariaceae	*Ribes lehmannii* Jancz.	RILE	73
Hypericaceae	*Hypericum aciculare* Kunth	HYAC	2 964
	Hypericum quitense R. Keller	HYQU	221

Family	Scientific name	Species code	Abundance
Melastomataceae	*Brachyotum jamesonii* Triana	BRJA	767
	Miconia salicifolia Bonpl. ex Naudin	MISA	267
Polygalaceae	*Monnina crassifolia* (Bonpl.) Kunth	MOCR	46
Rosaceae	*Hesperomeles obtusifolia* (Pers.) Lindl.	HEOB	21
	Polylepis reticulata Hieron.	PORE	111
	Polylepis incana Kunth	POIN	56
Rubiaceae	*Arcytophyllum vernicosum* Standl.	ARVE	58

abundant species was *Hypericum aciculare* Kunth (Hypericaceae) (22 %) followed by *M. arbutifolia* (Asteraceae) (12 %), *Loricaria thuyoides* (Lam.) Sch. Bip. (Asteraceae) (11 %), *Diplostephium rupestre* (Kunth) Wedd. (Asteraceae) (7 %) and *Monticalia vaccinioides* (Kunth) C. Jeffrey (Asteraceae) (6 %) (Table 1). The proportion of páramo grassland ranged from 30 % to 88 % (mean = 63 %) and the proportion of disturbed areas ranged from 0 % to 45 % (mean = 20 %) (Table 2).

The species accumulation curve reached its asymptote (Fig. 3), indicating that the sampling effort was sufficient and therefore,

Table 2

Locality name, transect code, average proportions (see methods) of páramo grassland as well as disturbed area and mean elevation of the 36 transects located in the páramo landscape of the Macizo del Cajas Biosphere Reserve, Southern Andes of Ecuador / **Tabla 2.** Nombre de la localidad, código de los transectos, el promedio de las proporciones (véase los métodos) de páramo herbáceo así también de área alterada y la elevación media en los 36 transectos ubicados en el paisaje de páramo de la Reserva de la Biósfera Macizo del Cajas, sur de los Andes de Ecuador.

Locality	Transect code	Páramo grassland (%)	Disturbed area (%)	Elevation (m)
Bermejos	BER001	80.5	12.3	3 794
Bermejos	BER002	74.4	14.05	3 842
Bermejos	BER003	75.31	14.9	3 795
Burgay	BUR001	63.3	17.9	3 627
Burgay	BUR002	67.6	25.1	3 818
Burgay	BUR003	62.2	20.4	3 754
Dublaicocha	DUB001	30.05	27.85	3 840
Dublaicocha	DUB002	38.6	30.25	3 876
Dublaicocha	DUB003	46.35	30.75	3 842
Galgal	GAL001	53.8	36.7	3 767
Galgal	GAL002	44.6	44.95	3 730
Galgal	GAL003	42.25	46	3 684
Miguir	MIG001	30.43	30.67	3 803
Miguir	MIG002	66.1	9.3	4 049
Miguir	MIG003	64.8	13.02	3 929
Patococha	PAT001	58.35	28.85	3 910
Patococha	PAT002	66.3	18.35	3 803
Patococha	PAT003	61.5	25.3	3 812
Rircay	RIR001	67.7	11.4	3 759
Rircay	RIR002	75.35	9.73	3 782
Rircay	RIR003	74.4	11.3	3 685
Santa Ana	SAN001	65.25	24.85	3 787
Santa Ana	SAN002	62.6	13.9	3 704
Santa Ana	SAN003	62.2	31.2	3 797

Locality	Transect code	Paramo grassland (%)	Disturbed area (%)	Elevation (m)
Taitachugo	TAI001	62.5	13.1	4 032
Taitachugo	TAI002	57.9	16.2	3 941
Taitachugo	TAI003	81.8	9.3	3 919
Tarqui	TAR001	84.6	11.75	3 998
Tarqui	TAR002	60.6	17.1	3 646
Tarqui	TAR003	82.9	0	3 789
Tomebamba	TOM001	71.78	10.5	3 809
Tomebamba	TOM002	87.83	2.8	3 909
Tomebamba	TOM003	50.25	23.7	3 733
Ventanas	VEN001	53.3	25.35	3 841
Ventanas	VEN002	62.85	7.74	3 865
Ventanas	VEN003	63.75	23.5	3 898

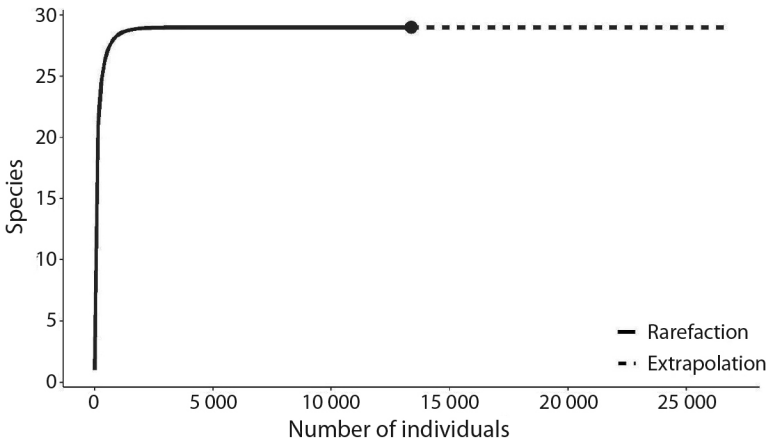

Fig. 3. Species-accumulation curve of woody plant species recorded in 36 transects located in the páramo landscape of the Macizo de Cajas Biosphere Reserve, Southern Andes of Ecuador. The solid line represents the accumulation of observed species via rarefaction. The dashed line shows the Chao 1 estimation. / **Fig. 3.** Curva de acumulación de especies de plantas leñosas registradas en 36 transectos ubicados en el paisaje de páramo de la Reserva de la Biósfera Macizo de Cajas, sur de los Andes de Ecuador. La línea continua representa la acumulación de especies observadas a través de rarefacción. La línea discontinua muestra la estimación Chao 1.

representative of the richness within the study area. Furthermore, the observed richness was the same as the estimated richness (observed richness = 29; Chao 1 estimator = 29).

Community composition of woody plant species: The NMDS analysis showed a tendency to separate the woody plant community in relation to the proportion of disturbed area (2D solution, stress = 0.2, $R^2 = 0.33$, $p < 0.001$) (Fig. 4), while the proportion of páramo grassland ($R^2 = 0.07$, p =0.32) and elevation ($R^2 = 0.10$, $p < 0.16$) were not significant. Transects with a higher proportion of disturbed area were situated towards the central-bottom of the ordination, and were associated with a greater presence of *D. ericoides*, *H. quitense*, *V. microphylla* and *Valeriana hirtella* Kunth., and transects with a lower proportion of disturbed area were located towards the central-top of the plot, and were associated with a greater presence of *M. arbutifolia*, *G. miniphylla*, *M. vaccinioides* and, *Hesperomeles obtusifolia* (Pers.) Lindl. (Fig. 4).

However, we included elevation in the ordination plot (via contour lines) as it followed the same tendency as disturbed area

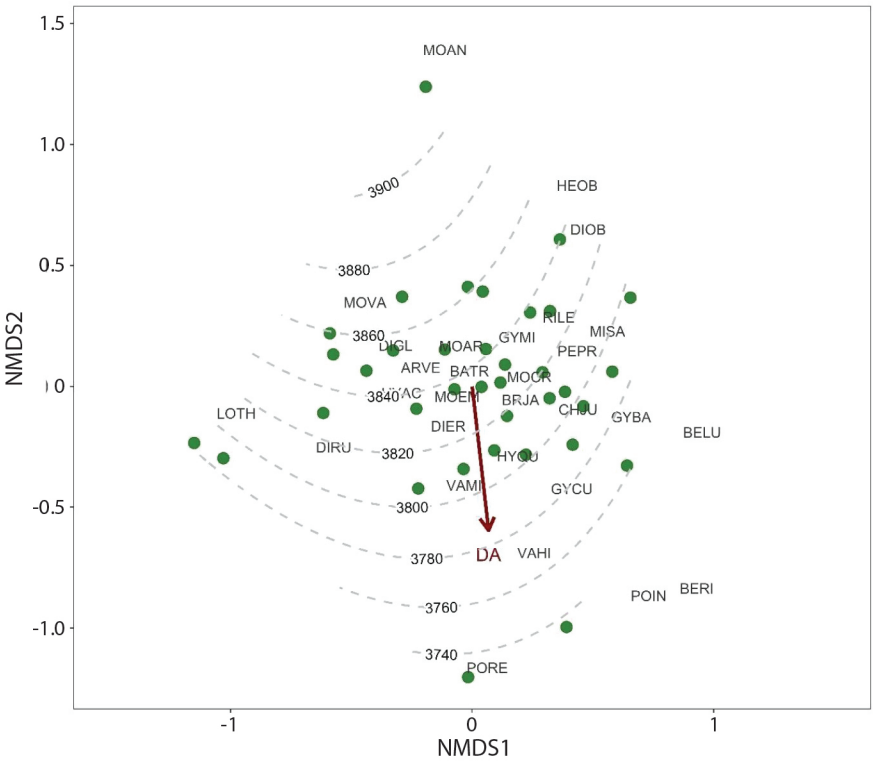

Fig. 4. Non-metric multidimensional scaling (NMDS) of the community of woody plant species recorded across 36 transects (green circles) located in the páramo landscape of the Macizo del Cajas Biosphere Reserve, Southern Andes of Ecuador. The red arrow represents the proportion of disturbed area (DA) as the environmental variable significantly influencing the ordination ($p < 0.001$). The elevation (contour lines) is also shown, although it is not significant ($p > 0.05$). The four-letter codes are the scientific names of the woody plant species (see Table 1). / **Fig. 4.** Escalamiento multidimensonal no métrico (NMDS) para la comunidad de plantas leñosas registradas a través de 36 transectos (círculos verdes) ubicados en el paisaje de páramo de la Reserva de la Biósfera del Macizo del Cajas, sur de los Andes del Ecuador. La flecha roja representa la proporción del área alterada (DA) como una variable ambiental que influye significativamente en la ordenación ($p < 0.001$). La elevación (curvas de nivel) también se muestra, aunque no influye significativamente ($p > 0.05$). Los códigos de cuatro letras son los nombres científicos de las especies de plantas leñosas (véase Tabla 1).

(i.e., from the central-top to the central-bottom of the ordination) (Fig. 4). This facilitates the interpretation of the spatial distribution of the transects and the description of woody plant species associations in relation to elevation. Thus, from ~3 800 m to ~4 000 m (in the central-top of the ordination) there is greater prevalence of *Diplostephium oblanceolatum M. arbutifolia*, *M. vaccinioides*, *H. obtusifolia* and *Monticalia andicola* (Turcz.) C. Jeffrey., while at lower elevations (i.e., from ~3 600 to 3 800 m) (in the central-bottom of the ordination) the woody plant community is associated with more presence of *D. ericoides*, *V. microphylla*, *H. quitense* and *V. hirtella* (Fig. 4).

DISCUSSION

Our findings showed significant changes in the composition of the woody plant community along the increasing proportion of disturbed areas in the monitored transects. The proportion of páramo grassland and elevation did not affect the plant composition. Dense shrub species such as *V. microphylla*, *H. quitense* and *V. hirtella* were more dominant in transects with

higher proportions of disturbed areas. Smaller shrub species such as *M. arbutifolia*, *M. vaccinioides* and *H. obtusifolia* are associated with transects with less disturbance. These changes in the plant composition of the páramo ecosystem suggests that the greater prevalence of some dense and fast-growing woody plant species is a response to human disturbance and could indicate that the native herbaceous species are gradually replaced by woody encroachment, particularly in human-accessible páramos.

Our approximation of the distribution of the woody plant community reveals that dense shrubs (e.g., *H. quitense*) are frequently observed in groups characterized as dwarf scrub and are adapted to rocky outcrops and hills where the evidence of human disturbance is higher. In fact, some *Hypericum* species are reported as opportunistic species that recover quickly after human disturbance such as fires (Matson & Bart, 2014). Their presence here may be related to an increasing cover of shrubs and a reduction in the cover of native grasses (e.g., Renison et al., 2006) due to human disturbance reducing the dominance of the tussock grasses and providing more opportunity for fast-growing woody plants (Sylvester et al., 2017).

In general, across the small valleys in the study region, páramo grassland is often associated with shrubby plants (Hofstede et al., 2002; Minga et al., 2016) creating a botanically and structurally diverse páramo (Gareca et al., 2010; Hofstede et al., 2002). However, woody encroachment is a common effect in disturbed grassland systems, including high elevation grasslands such as páramo (Matson & Bart, 2014). Our results, controlling for the proportion of the disturbed area, highlight that some transects are still characterized by a greater presence of woody plants such as *H. quitense*, *V. hirtella* and *V. microphylla*. Besides, more human accessible páramos (e.g., close to roads, lower elevations, outside of protected areas) are more prone to habitat disturbance such as fires and livestock grazing leading to less availability of native tussock grasses as well as cushion and bog plants. Consequently, in unprotected páramos of the study region, the native grasses are more sensitive to human disturbance (Astudillo et al., 2017; Hofstede & Llambí, 2020). Here, our findings suggest that fast-growing woody plant species are fostering changes in the plant community leading to more complex páramos (e.g., height profile vegetation) but with less availability of open habitats such as tussock grasses and cushion bogs.

A potential explanation for the pattern of woody plant species dispersal into the páramo grassland is the proximity to the tree line of Andean forests (Matson & Bart, 2013) across the lower páramo. In the study region, large and dense shrubs such as *V. hirtella* and *V. microphylla* are commonly found in the tree line of Andean forests and *Polylepis* woodlands (Minga et al., 2016). The frequent association of forest plants with herbaceous flora of páramo ecosystems has been reported previously (Domic & Capriles, 2021; Montalvo et al., 2018; Quispe-Melgar et al., 2020) and indeed, some native shrubs have been found to be positively associated with greater habitat complexity of páramos surrounding *Polylepis* forest within the Cajas National Park (Astudillo et al., 2019; Astudillo et al., 2020). However, as with other disturbance scenarios found outside the limit of protected areas (Caballero-Villalobos et al., 2021; Toivonen et al., 2011), our results highlight that some woody plant species are becoming more dominant. Within this framework, conservation and restoration efforts across the páramo should consider the dynamics between shrubs and other fast-growing plants with native grasses.

Conservation implications: In the high Andes, the restoration of disturbed habitats has been based on the importance of woody plant species for important pollinators (i.e., hummingbirds) (Cárdenas-Calle et al., 2020; Crespo et al., 2022; Hazlehurst et al., 2016) with a few shrubby plant species being identified as central for the restoration of high Andean ecosystems (Crespo et al., 2022). However, some of these identified woody plant species are characterized by faster growing strategies (i.e., year-round flowering) (e.g., Cárdenas-Calle et al.,

2020; Hazlehurst et al., 2016) and are already widely distributed between the limit of Andean forests and the páramo ecosystem (Minga et al., 2016; Suárez et al., 2022). Furthermore, mutualistic interactions in disturbed páramos, such as seed dispersal by birds, are seen as a mechanism that facilitates increasing cover of shrubby plant species and subsequent woody encroachment (Matson & Bart, 2013; Matson & Bart, 2014). In consequence, habitat restoration focused on fast-growing plants may promote an acceleration of woody encroachment in human-accessible páramos with evident negative effects on native grasses and organisms that depend on more open páramo grassland habitats. Further studies are needed in order to generate conservation strategies more compatible to the páramo region. For instance, in open páramos of the study region, small, endemic rodents (e.g., *Phyllotis haggardi*) have been observed foraging on flowers of herbaceous species (i.e., *Taraxacum officinale* (Weber), *Xenophyllum humile* (Kunth) V.A. Funk and *Eryngium humile* Cav.) and are considered as potential pollinators (Nivelo-Villavicencio et al., 2021). Our findings indicate that the availability of páramo grassland habitats is declining in disturbed areas, while the presence of fast-growing shrubs is increasing. This ecological information could be crucial for improving restoration and conservation efforts aimed at enhancing the availability of páramo grasslands.

Ethical statement: The authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

ACKNOWLEDGMENTS

We are grateful for the constant support of our research by Raffaella Ansaloni, Andrés López and Francisco Salgado of the Universidad del Azuay. We thank Boris Landázuri for his field support. We also acknowledge Guillermo Salgado, Vicente Jaramillo, and Ramiro Jiménez from Dundee Precious Metals Ecuador (DPMECUADOR S.A.) for their continued support of our research. Logistical support came from Hari González, park management, and staff of Cajas National Park and Quimsacocha National Recreation Area, as well as Empresa Pública de Telecomunicaciones, Agua Potable, and Alcantarillado y Saneamiento de Cuenca (ETAPA-EP). PXA was funded by DPMECUADOR S.A., ETAPA-EP (Grant No. 78010200001) and the Vicerrectorado de Investigaciones of the Universidad del Azuay (2018-0003; 2019-0090; 2021-0167). All activities were conducted under permits 196-2019-DPAA/MA and 183-2018-DPAA/MA issued by the Ecuadorian Ministry of Environment, Water and Ecological Transition.

REFERENCIAS

Ansaloni, R., Izco, J., Amigo, J., & Minga, D. (2022). Analysis of the páramo vascular flora in the Cajas National Park (Central Andes, Ecuador). *Mediterranean Botany, 43*, e76491. https://doi.org/10.5209/mbot.76491

Astudillo, P. X., Barros, S., Mejía, D., Villegas, F. R., Siddons, D. C., & Latta, S. C. (2024). Using surrogate species and MaxEnt modeling to prioritize areas for conservation of a páramo bird community in a tropical high Andean biosphere reserve. *Arctic, Antarctic, and Alpine Research*, *56*(1). https://doi.org/10.1080/15230430.2023.2299362

Astudillo, P. X., Barros, S., Siddons, D. C., & Zárate, E. (2017). Influence of habitat modification by livestock on páramo bird abundance in southern Andes of Ecuador. *Studies on Neotropical Fauna and Environment, 53*(1), 29–37. https://doi.org/10.1080/01650521.2017.1382122

Astudillo, P. X., Grass, I., Siddons, D. C., Schabo, D. G., & Farwig, N. (2020). Centrality in species-habitat networks reveals the importance of habitat quality for high-andean birds in *Polylepis* woodlands. *Ardeola, 67*(2), 307–324. https://doi.org/10.13157/arla.67.2.2020.ra5

Astudillo, P. X., Schabo, D. G., Siddons, D. C., & Farwig, N. (2019). Patch-matrix movements of birds in the páramo landscape of the southern Andes of Ecuador. *Emu, 119*(1), 53–60. https://doi.org/10.1080/01584197.2018.1512371

Bagchi, R., Brown, L. M., Elphick, C. S., Wagner, D. L., & Singer, M. S. (2018). Anthropogenic fragmentation of landscapes: mechanisms for eroding the specificity of plant–herbivore interactions. *Oecologia, 187*(2), 521–533. https://doi.org/10.1007/s00442-018-4115-5

Ballari, D., Giraldo, R., Campozano, L., & Samaniego, E. (2018). Spatial functional data analysis for regionalizing precipitation seasonality and intensity in a sparsely monitored region: unveiling the spatio-temporal dependencies of precipitation in Ecuador. *International Journal of Climatology*, *38*(8), 3337–3354. https://doi.org/10.1002/joc.5504

Baquero, F., Sierra, R., Ordoñez, L., Tipán, M., Espinosa, L., Rivera, M. B., & Soria, P. (2004). *La vegetación de los Andes del Ecuador: Memoria explicativa de los mapas de vegetación, potencial y remanente a escala 1:250 000 y del modelamiento predictivo con especies indicadoras* (1a ed.). EcoCiencia; EcoPar; MAG SIGAGRO; CDC-Jatun Sacha; División Geográfica-IGM.

Barros, S., Astudillo, P. X., Landázuri, B. O., Porras, P., Siddons, D. C., & Latta, S. C. (2020). Habitat heterogeneity rather than the limits of protected areas influence bird communities in an Andean biosphere reserve. *Ecología Austral, 30*(3), 454–464. https://doi.org/10.25260/ea.20.30.3.0.1068

Beltrán, K., Salgado, S., Cuesta, F., León-Yánez, S., Romoleroux, K., Ortiz, E., Cárdenas, A., & Velástegui, A. (2009). *Distribución espacial, sistemas ecológicos y caracterización florística de los páramos en el Ecuador*. EcoCiencia; Proyecto Páramo Andino; Herbario QCA. https://biblio.flacsoandes.edu.ec/libros/digital/43576.pdf

Brandt, J. S., Haynes, M. A., Kuemmerle, T., Waller, D. M., & Radeloff, V. C. (2013). Regime shift on the roof of the world: alpine meadows converting to shrublands in the southern Himalayas. *Biological Conservation, 158*, 116–127. https://doi.org/10.1016/j.biocon.2012.07.026

Caballero-Villalobos, L., Fajardo-Gutiérrez, F., Calbi, M., & Silva-Arias, G. A. (2021). Climate change can drive a significant loss of suitable habitat for *Polylepis quadrijuga*, a treeline species in the sky islands of the northern Andes. *Frontiers in Ecology and Evolution*, *9*, 661550. https://doi.org/10.3389/fevo.2021.661550

Cárdenas-Calle, S., Cárdenas, J. D., Landázuri, B. O., Mogrovejo, G., Crespo, A. M., Breitbach, N., Schleuning, M., & Tinoco, B. A. (2020). Pollinator effectiveness in the mixed-pollination system of a Neotropical Proteaceae, *Oreocallis grandiflora*. *Journal of Pollination Ecology, 26*. https://doi.org/10.26786/1920-7603(2020)601

Carrillo-Rojas, G., Silva, B., Rollenbeck, R., Celleri, R., & Bendix, J. (2019). The breathing of the Andean highlands: net ecosystem exchange and evapotranspiration over the páramo of southern Ecuador. *Agricultural and Forest Meteorology*, *265*, 30–47. https://doi.org/10.1016/j.agrformet.2018.11.006

Celleri, R., Willems, P., Buytaert, W., & Feyen, J. (2007). Space-time rainfall variability in the Paute basin, Ecuadorian Andes. *Hydrological Processes, 21*(24), 3316–3327. https://doi.org/10.1002/hyp.6575

Chao, A. (1984). Nonparametric restimation of the number of classes in a population. *Scandinavian Journal of Statistics, 11*(4), 265–270.

Chao, A., Ma, K. H., & Hsieh, T. C. (2024). *iNEXT: Interpolation and Extrapolation for Species Diversity, version 3.0.1* [Software]. Anne Chao's website. http://chao.stat.nthu.edu.tw/wordpress/software_download/

Colwell, R. K., Chao, A., Gotelli, N. J., Lin, S. Y., Mao, C. X., Chazdon, R. L., & Longino, J. T. (2012). Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology, 5*(1), 3–21. https://doi.org/10.1093/jpe/rtr044

Crespo, A., Aguilar, J. M., Pintado, K., & Tinoco, B. A. (2022). Key plant species to restore plant–hummingbird pollinator communities in the southern Andes of Ecuador. *Restoration Ecology, 30*(4), e13557. https://doi.org/10.1111/rec.13557

Domic, A. I., & Capriles, J. M. (2021). Distribution shifts in habitat suitability and hotspot refugia of Andean tree species from the last glacial maximum to the Anthropocene. *Neotropical Biodiversity, 7*(1), 297–309. https://doi.org/10.1080/23766808.2021.1957652

Foster, P. (2001). The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Science Reviews*, *55*(1–2), 73–106. https://doi.org/10.1016/S0012-8252(01)00056-3

García, V. J., Márquez, C. O., Rodríguez, M. V., Orozco, J. J., Aguilar, C. D., & Ríos, A. C. (2020). Páramo ecosystems in Ecuador's southern region: conservation state and restoration. *Agronomy, 10*(12), 1922. https://doi.org/10.3390/agronomy10121922

Gareca, E. E., Hermy, M., Fjeldså, J., & Honnay, O. (2010). *Polylepis* woodland remnants as biodiversity islands in the Bolivian high Andes. *Biodiversity and Conservation, 19*, 3327–3346. https://doi.org/10.1007/s10531-010-9895-9

González, A., Chase, J. M., & O'Connor, M. I. (2023). A framework for the detection and attribution of biodiversity change. *Philosophical Transactions of the Royal Society B*, *378*(1881), 20220182. https://doi.org/10.1098/rstb.2022.0182

Hazlehurst, J., Cardenas, S., Tinoco, B., & Karubian, J. (2016). Pollination ecology of *Oreocallis grandiflora* (Proteaceae) at the northern and southern ends of its geographic range. *Journal of Pollination Ecology*, *19*, 71–80. https://doi.org/10.26786/1920-7603(2016)4

He, T., Lamont, B. B., & Pausas, J. G. (2019). Fire as a key driver of Earth's biodiversity. *Biological Reviews, 94*(6), 1983–2010. https://doi.org/10.1111/brv.12544

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

Hofstede, R. G. M., Groenendijk, J. P., Coppus, R., Fehse, J. C., & Sevink, J. (2002). Impact of pine plantations on soils and vegetation in the Ecuadorian high Andes. *Mountain Research and Development*, *22*(2), 159–167. https://doi.org/10.1659/0276-4741(2002)022[0159:IOPPOS]2.0.CO;2

Hofstede, R. G., & Llambí, L. D. (2020). Plant diversity in Páramo-Neotropical high mountain humid grasslands. In M. I. Goldstein, & D. A. DellaSala (Eds.), *Encyclopedia of the World's Biomes* (vol. 1–5, pp. 362–372). Elsevier. http://dx.doi.org/10.1016/B978-0-12-409548-9.11858-5

Hudson, L. N., Newbold, T., Contu, S., Hill, S. L., Lysenko, I., De Palma, A., Phillips, H. R. P., Senior, R. A., Bennett, D. J., Booth, H., Choimes, A., Correia, D. L. P., Day, J., Echeverría-Londoño, S., Garon, M., Harrison, M. L. K., Ingram, D. J., Jung, M., Kemp, V., ... & Purvis, A. (2014). The predicts database: a global database of how local terrestrial biodiversity responds to human impacts. *Ecology and Evolution*, *4*(24), 4701–4735. https://doi.org/10.1002/ece3.1303

Jantz, N., & Behling, H. (2012). A Holocene environmental record reflecting vegetation, climate, and fire variability at the páramo of Quimsacocha, southwestern Ecuadorian Andes. *Vegetation History and Archaeobotany, 21*(3), 169–185. https://doi.org/10.1007/s00334-011-0327-x

Jiménez-Rivillas, C., García, J. J., Quijano-Abril, M. A., Daza, J. M., & Morrone, J. J. (2018). A new biogeographical regionalisation of the Páramo biogeographic province. *Australian Systematic Botany, 31*(4), 296–310. https://doi.org/10.1071/SB18008

Jørgensen, P. M., Ulloa, C., León, B., Leon-Yánez, S., Beck, S. G., Nee, M., Zarucchi, J. L., Celis, M., Bernal, R., & Gradstein, R. (2011). Regional patterns of vascular plant diversity and endemism. In S. K. Herzog, R. Martínez, P. M. Jørgensen, & H. Tiessen (Eds.), *Climate change and diodiversity in the Tropical Andes* (pp. 192–203). IAI and SCOPE.

Llambí, L. D., Soto-W, A., Celleri, R., De Bievre, B., Ochoa, B., & Borja, P. (2012). *Ecología, hidrología y suelos de páramos* (1a ed.). Proyecto Páramo Andino; CONDESAN; GEF-UNEP.

Loughlin, N. J. D., Gosling, W. D., Mothes, P., & Montoya, E. (2018). Ecological consequences of post-Columbian indigenous depopulation in the Andean–Amazonian corridor. *Nature Ecology & Evolution*, *2*(8), 1233–1236. https://doi.org/10.1038/s41559-018-0602-7

Madriñán, S., Cortés, A. J., & Richardson, J. E. (2013). Páramo is the world's fastest evolving and coolest biodiversity hotspot. *Frontiers in Genetics, 4,* 1–7. https://doi.org/10.3389/fgene.2013.00192

Matson, E., & Bart, D. J. (2013). Interactions among fire legacies, grazing and topography predict shrub encroachment in post-agricultural páramo. *Landscape Ecology, 28*(9), 1829–1840. https://doi.org/10.1007/s10980-013-9926-5

Matson, E., & Bart, D. J. (2014). Plant-community responses to shrub cover in a páramo grassland released from grazing and burning. *Austral Ecology, 39*(8), 918–928. https://doi.org/10.1111/aec.12157

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, *14*(11), 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

Minga, D., Ansaloni, R., Verdugo, A., & Ulloa-Ulloa, C. (2016). *Flora del páramo del Cajas, Ecuador*. Universidad del Azuay. Editorial Don Bosco-Centro Gráfico Salesiano. http://dspace.uazuay.edu.ec/handle/datos/8786

Montalvo, J., Minga, D., Verdugo, A., López, J., Guazhambo, D., Pacheco, D., Siddons, D., Crespo, A., & Zárate, E. (2018). Características morfológico-funcionales, diversidad arbórea, tasa de crecimiento y de secuestro de carbono en especies y ecosistemas de Polylepis del sur de Ecuador. *Ecología Austral, 28*(1-bis), 249–261. https://doi.org/10.25260/EA.18.28.1.1.557

Montané, F., Rovira, P., & Casals, P. (2007). Shrub enroachment into mesic mountain grasslands in the Iberian Peninsula: effects of plant and quality and temperature on soil C and N stocks. *Global Biogeochemical Cycles, 21*(4), 1–10. https://doi.org/10.1029/2006GB002853

Montaño-Centellas, F., Fuentes, A. F., Cayola, L., Macía, M. J., Arellano, G., Loza, M. I., Nieto-Ariza, B., Tello, J. S. (2024). Elevational range sizes of woody plants increase with climate variability in the Tropical Andes. *Journal of Biogeography*, *51*(5), 814–826. https://doi.org/10.1111/jbi.14783

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature, 403*(6772), 853–858. https://doi.org/10.1038/35002501

Neill, D. A. (1999). Vegetación. In P. M. Jørgensen & S. León-Yánez (Eds.), *Catalogue of the vascular plants of Ecuador* (pp. 13–25). Monographs in Systematic Botany from the Missouri Botanical Garden.

Nivelo-Villavicencio, C., Timbe, B., & Astudillo, P. X. (2021). Observaciones de forrajeo en recursos florales por *Phyllotis haggardi* (Rodentia: Cricetidae) en un ecosistema de páramo al sur del Ecuador. *Neotropical*

Biodiversity, *7*(1), 376–378. https://doi.org/10.1080/23766808.2021.1964912

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., 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., De Caceres, M., Durand, S., ... & Borman, T. (2024). *Vegan: community ecology package, R package, version 2.6-6.1* [Software]. CRAN. https://doi.org/10.32614/CRAN.package.vegan

Pinos, J. (2020). Challenges and conservation implications of woodlands in the Andean region: defining actions for sustainable management. *Hacquetia*, *19*(2), 143–153. https://doi.org/10.2478/hacq-2020-0001

Quispe-Melgar, H. R., Sevillano-Ríos, C. S., Navarro-Romo, W. C., Ames-Martínez, F. N., Camel, V., Fjeldså, J., & Kessler, M. (2020). The Central Andes of Peru: a key area for the conservation of *Polylepis* forest biodiversity. *Journal of Ornithology, 161*(1), 217–228. https://doi.org/10.1007/s10336-019-01703-5

R Core Team. (2024). *A Language and Environment for Statistical Computing, version 4.4.1* [Software]. R Foundation for Statistical Computing. https://www.r-project.org/

Renison, D., Hensen, I., Suárez, R., & Cingolani, A. M. (2006). Cover and growth habit of *Polylepis* woodlands and shrublands in the mountains of central Argentina: human or environmental influence? *Journal of Biogeography*, *33*(5), 876–887. https://doi.org/10.1111/j.1365-2699.2006.01455.x

Rodríguez, S., Rodas, F., Schubert, A., & Vasco, S. (2014). Área de biosfera macizo del Cajas, experiencias de desarrollo sostenible para el buen vivir/ GAD Cuenca, ETAPA EP, SENPLADES zona 6, MAE (Ministerio del Ambiente de Ecuador), zona 6, Cooperación Alemana GIZ (1a ed.). Gobierno Autónomo Descentralizado Municipal de Cuenca.

Sarango-Cobos, J., Muñoz, J., Muñoz, L., & Aguirre, Z. (2019). Impacto ecológico de un incendio forestal en la flora del páramo antrópico del Parque Universitario "Francisco Vivar Castro", Loja, Ecuador. *Bosques Latitud Cero, 9*(2), 101–114.

Sarmiento, F. O. (2000). Breaking mountain paradigms: ecological effects on human impacts in man-aged tropandean landscapes. *AMBIO: A Journal of the Human Environment*, *29*(7), 423–431. https://doi.org/10.1579/0044-7447-29.7.423

Sklenár, P., & Ramsay, P. M. (2001). Diversity of zonal páramo plant communities in Ecuador. *Diversity and Distributions, 7*(3), 113–124. https://doi.org/10.1046/j.1472-4642.2001.00101.x

Sklenár, P., Luteyn, J., Ulloa-Ulloa, C., Jørgensen, P. M., & Dillon, M. O. (2005). *Flora genérica de los Páramos: guía ilustrada de las Plantas vasculares (Memoirs of the New York Botanical Garden, 92)*. The New York Botanical Garden Press. https://academic.oup.com/botlinnean/article/154/4/609/2420189

Smart, S. M., Thompson, K., Marrs, R. H., Le Duc, M. G., Maskell, L. C., & Firbank, L. G. (2006). Biotic homogenization and changes in species diversity across human-modified ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1601), 2659–2665. https://doi.org/10.1098/rspb.2006.3630

Suárez, E., & Medina, G. (2001). Vegetation structure and soil properties in Ecuadorian páramo grasslands with different histories of burning and grazing. *Arctic, Antarctic, and Alpine Research*, *33*(2), 158–164. https://doi.org/10.2307/1552216

Suárez, E., Chimbolema, S., Jaramillo, R., Zurita-Arthos, L., Arellano, P., Chimner, R. A., Stanovick, J. S., & Lilleskov, E. A. (2022). Challenges and opportunities for restoration of high-elevation Andean peatlands in Ecuador. *Mitigation and Adaptation Strategies for Global Change, 27*(4), 1–17. https://doi.org/10.1007/s11027-022-10006-9

Sylvester, S. P., Heitkamp, F., Sylvester, M. D. P. V., Jungkunst, H. F., Sipman, H. J. M., Toivonen, J. M., Gonzáles-Inca, C. A., Ospina, J. C., & Kessler, M. (2017). Relict high-Andean ecosystems challenge our concepts of naturalness and human impact. *Scientific Reports*, *7*(1), 1–13. https://doi.org/10.1038/s41598-017-03500-7

Toivonen, J. M., Kessler, M., Ruokolainen, K., & Hertel, D. (2011). Accessibility predicts structural variation of Andean *Polylepis* forests. *Biodiversity and Conservation, 20*(8), 1789–1802. https://doi.org/10.1007/s10531-011-0061-9

Vargas-Ríos, O., & Ávila-Rodríguez, L. A. (2021). Dinámica de la vegetación de los páramos. In O. Vargas-Ríos (Ed.), *Bases ecológicas y sociales para la restauración de los páramos* (1a ed., pp. 87–141). Facultad de Ciencias, Universidad Nacional de Colombia.