



Habitat and population structure of rare and endemic Andean *Espeletia pycnophylla* subsp. *llanganatensis* (Asteraceae) in an Ecuadorian biodiversity hotspot

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Abstract High-elevation neotropical environments of the Andes include the Páramo, a biodiversity hotspot with fast speciation rates. The genus *Espeletia* is distinctive of this ecosystem in the northern Andes. Its southern distribution limit lies in Ecuador, with the endemic *E. pycnophylla* subsp. *llanganatensis* being the only known representative south of the equator. This study presents the distribution, population structure and co-occurring flora of the subspecies *llanganatensis* in the Valle de los Frailejones (VFL), Cordillera de los Llanganates. Four clusters totalling ~ 20 ha could be identified at elevations of 3400–3550 m above sea level. *Espeletia pycnophylla* subsp. *llanganatensis* occurred amidst the sub-Páramo upper elevational limits of montane forests and within transitional areas between forest margins and waterlogged terrains. This habitat preference was

a distinguishing ecological difference to the nearest (200 km) congener, *E. pycnophylla* subsp. *angelensis*. Plants ($N = 781$ measured) were skewed towards the smallest size classes ≤ 20 cm (28% of the population, including 17% recruits ≤ 10 cm) and reaching a total plant height of 900 cm. Synflorescences were observed in specimens ≥ 110 cm and in 51% of the mature population. The oldest specimens grew on terrains with higher edaphic stability. While local recruitment appears healthy, geographic distribution is limited suggesting vulnerability to local extinction. Co-occurring vegetation encompassed ~ 70 species, with grasses (Poaceae) and mosses (Bryophyta) dominating the ground cover, resulting in homogenous vegetation. Although *E. pycnophylla* subsp. *llanganatensis* is currently not exposed to direct human disturbance, clandestine mining activities intruding the region pose a potential threat to the survival of this Ecuadorian endemic.

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Introduction

Neotropical high-elevation ecosystems encompass grasslands between the upper limit of the closed-canopy forest at about 3500–3900 m and the upper limit of plant life at around 4600–4900 m above sea level (Smith 1981; Luteyn et al. 1992; Luteyn 1999) and referred to

as ‘Páramo’ in Ecuador (Luteyn 1999). They are characterized by tussock grasses, large rosette plants, shrubs with evergreen, coriaceous and sclerophyllous leaves, and cushion plants). The Páramo has one of the fastest speciation rates among the world’s biodiversity hotspots (Madriñán et al. 2013) and represents the most species-rich tropical alpine region (Sklenář et al. 2014; Flantua and Hooghiemstra 2018). Located in the Andes of Venezuela, Colombia, Ecuador and northern Peru (Luteyn 1999), and to lesser extent in Costa Rica and Panama (Kappelle and Horn 2016), Páramo ecosystems are discontinuous sky islands (Sklenář et al. 2014) with high levels of endemism (León-Yáñez et al. 2011; Cuesta et al. 2017) and belong to the two biodiversity hotspots in South America, namely the Tropical Andes and the Tumbes–Chocó–Magdalena Corridor (Mittermeier et al. 2011). Compared to other tropical ecosystems, such as rain forests and coral reefs, which have become part of the mainstream environmental discourse fostering conservation initiatives worldwide for decades, the Páramo’s regional and global relevance is only gradually gaining attention (UN 2020; Peyre 2021). The Páramo provides numerous cross-boundary ecosystem services including water supply and streamflow buffering (Mora-Osejo 2001; Buytaert and Beven 2011; Cárdenas et al. 2018). It is also an important carbon sink, storing more carbon per area than tropical rain forests (Hofstede and Jongsma 1997; Buytaert et al. 2011; Curiel Yuste et al. 2017). Moreover, while accelerated climate change and agricultural expansion continue to encroach on this biodiverse ecosystem (Verweij and Kok 1992; Verweij and Beekman 1995; Hughes 2017; Kovář 2001; Noh et al. 2020; Thompson et al. 2021), our knowledge base on key habitat-shaping taxa remains highly fragmented (Kleemann et al. 2022).

A distinguishing floristic component of the northern Andean Páramo is the genus *Espeletia* Bonpl. (Asteraceae; Humboldt and Bonpland 1809), commonly referred to as ‘frailejones’ in Spanish or ‘sangurima’ in Quichua (Ecuador). *Espeletia* is a perennial caulescent rosette plant (Cuatrecasas 1968, 2013; Smith 1981). Its rosettes of large leaves bear a dense bud of immature leaves around the apical meristem and are supported by unbranched or little-branched stems often covered by a thick cylindrical sheath of dry leaves. *Espeletia* is part of a monophyletic subtribe (Rauscher 2002) of three to eight genera with 72 (Diazgranados 2012) or 90

(Marávez 2021) species and numerous subspecies and hybrids. It likely originated in the Venezuelan Andes, with the Cordillera de Mérida and Colombia’s Eastern Cordillera currently at the centre of diversity, and has been reported across Colombia and northern Ecuador (Pouchon et al. 2018; Mavárez 2019). Cortés et al. (2018) linked *Espeletia*’s fast diversification rates to repeated periods of connectivity and spatial isolation during Pleistocene glacial cycling related to the Andean uplift. The evolution of ecotypes into separate species appears to be rooted in environmental heterogeneity and ecological opportunity associated with adaptation to local environmental variation (Bridle and Vines 2007; Cortés 2013, 2015; Cortés et al. 2014; Cortés and Blair 2018; Cortés and Wheeler 2018). In this scenario, rapid mutation rates have been attributed to elevated levels of ultraviolet light of high tropical mountains (Davies et al. 2004; Willis et al. 2009).

Only *Espeletia pycnophylla* subsp. *angelensis* Cuatrec. 1980 and subsp. *llanganatensis* Cuatrec. 1980 (Cuatrecasas 2013) occur in Ecuador, differing in the morphology of synflorescences and leaves (Cuatrecasas 2013). Populations of *E. pycnophylla* subsp. *angelensis* in southern Colombia (Nariño) and northern Ecuador (Carchi) are well studied (Cross 2001; Holt 2001; Foley 2001; Ramsay and Michell 2001; Sanchez 2004; Benavides et al. 2007, 2010; Noboa 2019). The plants can be considered ecosystem engineers (*sensu* Cuddington 2012) given their landscape-shaping function and across elevations from 3600 m to 4200 m they display stable population dynamics (Sanchez 2004), except where exposed to wildfires (Kovář 2001). Contrastingly, *E. pycnophylla* subsp. *llanganatensis* is the only known *Espeletia* from the Southern Hemisphere, and has remained more elusive to investigations due to the difficult access to few reported occurrences from the eastern fringes of the Cordillera de los Llanganates, within the Llanganates National Park. Conclusive accounts of the presence of *Espeletia* date to the chronicles of the Boschetti-Andrade Marín Expedition of 1933–1934 (Andrade Marín 1936). Andrade Marín observed particularly tall arboreous *Espeletia* at the foot of Cerro Negro (Yana-Llanganati), nowadays known as Valle de los Frailejones (VFL) and at nearby localities referred to as Las Torres. In 1939 Asplund collected specimens ‘near Las Torres’, including the holotype for the description of the subspecies by Cuatrecasas.

The presence of *E. pycnophylla* subsp. *llanganatensis* in the VFL was verified by Vargas et al. (2000), but its spatial distribution, population structure and approximate size remained undocumented. The aim of this study was to (a) delineate the current spatial distribution of *E. pycnophylla* subsp. *llanganatensis*, (b) describe its population structure based on macroscopic morphometric features, and (c) provide a first characterization of its co-occurring vegetation.

Material and methods

Study area

The Valle de los Frailejones (VFL) comprises the terminal three kilometres of a valley enclosed by the southern flanks of the Cordillera de los Llanganates (Cresta del Gallo) and the western and northern flanks of Cerro Negro (Yana-Llanganati, Fig. 1A–C). The valley head sources the origins of an unnamed brook, a tributary to Río Topo (draining into Rios Negro and Pastaza). Its upper half drains towards the west and its lower half towards the south. The sections are separated by a narrow passage and drop in terrain, above and below which the brook meanders forming shallow ponds surrounded by wetlands. The largest pond of approx. 4 ha ($01^{\circ} 09' 42''$ S, $78^{\circ} 15' 58''$ W) is situated in the southern half of the valley and is a

persistent landmark already mentioned by Andrade Marín (1936). The valley's humid microclimate is fed by water vapour from the Amazon basin, rising along the Río Topo valley and crossing the Las Torres massif from the Northeast. A forested belt was present at elevations between 3420 and 3600 m a.s.l. whereas grasslands and bare rock dominate the landscape above 3650 m a.s.l. The details of the access to the VFL are summarized in the electronic supplementary material.

Survey of *E. pycnophylla* subsp. *llanganatensis*

The current spatial distribution of *E. pycnophylla* subsp. *llanganatensis* at VFL was established by recording locations of occurrence, elevational distribution, and exposure. The largest cluster of *E. pycnophylla* subsp. *llanganatensis*, here named the 'central cluster', was selected for detailed surveys (Fig. 1B).

To assess the population structure of *E. pycnophylla* subsp. *llanganatensis*, eight 10 m × 10 m plots were installed. Plots 1–4 were haphazardly placed in the northeastern part of the Central Cluster, and plots 5–8 in its southwestern part. Within each plot, the following morphometric features were measured to the closest 10 cm in each *E. pycnophylla* subsp. *llanganatensis* specimen: total height, rosette height and diameter, and height of the necrotic collar. Measurements to the closest 10 cm allowed rapid surveys under the difficult climatic conditions and limited time. All plants were

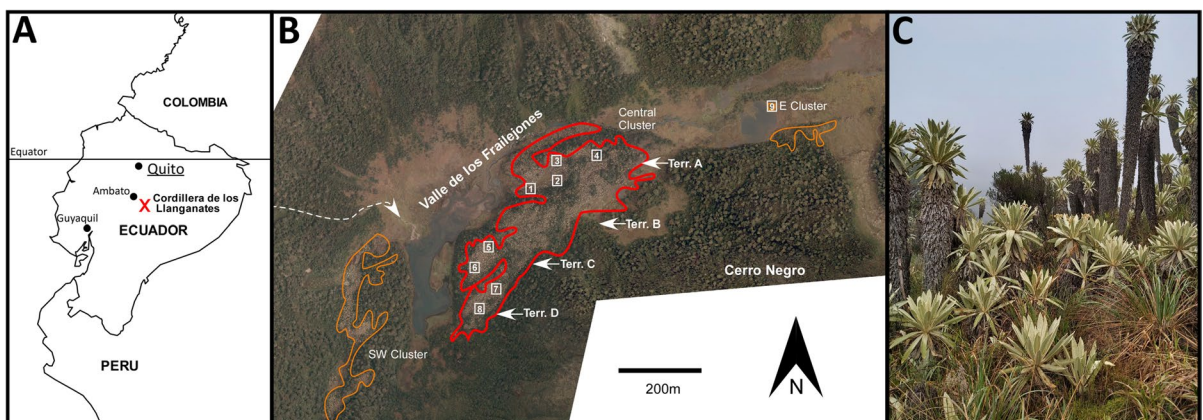


Fig. 1 **A** – General outline of Ecuador with the location of the Cordillera de los Llanganates (Tungurahua). **B** – Sentinel-2 satellite image of the Valle de los Frailejones (VFL), with the *E. pycnophylla* subsp. *llanganatensis* Central Cluster delineated in red and the SW and E cluster delineated in orange. The NE

cluster is not in the image. Arrows indicate topographic terraces A–D. The dotted white line shows the access route into the VFL. **C** – Image of *E. pycnophylla* subsp. *llanganatensis* community: specimens of 40–230 cm in total height in the foreground and up to 800 cm in the distant background

examined for signs of fires, such as charred stems. The number of synflorescences and the distance to the nearest seedling (plants ≤ 10 cm in height) from each flowering plant were recorded to gauge local recruitment. The space occupied by *Espeletia* stems (barren or covered by necrotic collars) was recorded to complement the subsequent ground cover estimates of the co-occurring vegetation. Time constraints allowed the survey of only one additional plot (9 in Fig. 1B) outside of the Central Cluster, for which only the total plant height and the synflorescences of all *E. pycnophylla* subsp. *llanganatensis* specimens were recorded.

In plots 1–8, three topsoil samples were collected with a core sampler to characterize the textural composition (hydrometric method by Bouyoucos 1962), organic matter (oxidation with H_2SO_4 as in Anderson and Ingram 1993), macronutrients N (digestion with H_2SO_4 and distillation, see Brenner 1965; Allen 1974), P (extraction via NaHCO_3 – Watable and Olsen 1965), K, Ca and Mg (digestion with H_2SO_4 and atomic absorption spectrophotometry – AAS, Allen 1974), and interchangeable aluminium ($\text{Al}^{+3} + \text{H}$, Al^{+3}) via AAS (see Hossner 2020). Samples were complemented by *in situ* pH measurements using a conductivity meter.

Description of the *E. pycnophylla* subsp. *llanganatensis* population

Plants were examined for size distribution in all plots and for presence or absence of flowers (all recruits, immature and senescent plants). Size distributions in three categories (all plants, plants with flowers, plants without flowers) were explored for each sampling area using Gaussian density plots. Information in these is similar to histograms, but kernel smoothing eliminates noise to create a more defined distribution shape.

Demographic ratios of *E. pycnophylla* subsp. *llanganatensis* in different growth phases were calculated for each sampling plot separately and across all plots, based on size classes, comparing the number of recruits (≤ 20 cm) vs the total population (TP), immatures (30–100 cm) vs TP, and mature flowering plants (≥ 110 cm) vs mature non-flowering plants, and the number of dead specimens vs TP. In addition, height and diameter of rosettes were plotted against plant height. To visualize the resulting patterns, LOESS smoothers (locally weighted scatterplot

smoothers) with a 95% confidence region, which make no assumption of an underlying growth relationship, were used.

First assessment of co-occurring vegetation

Field-based identifications of species were verified by the examination of the collected specimens at the Herbario Nacional del Ecuador (QCNE), Instituto Nacional de Biodiversidad (INABIO) and at the herbarium of the Pontificia Universidad Católica (QCA) in Quito. All specimens are currently deposited at the Herbario ECUAMZ, Universidad Estatal Amazónica (UEA), under numbers PL 1371–1412.

Co-occurring vegetation in plots 1–8 was assessed by recording the dominant growth forms and their respective ground cover, as herbaceous and arbus-tive vascular plants formed a single dense stratum of approximately 80 cm height without distinct canopy levels. The ground of the remaining open spaces was covered by bryophytes (mainly mosses), which were tallied without further taxonomic classification or specimen collection. Vascular plants were identified *in situ* and their ground cover was estimated. Ground cover data of co-occurring vegetation were examined by ranking plant frequencies from rare (lowest density = 1) to common (highest density = 9). A hierarchical, agglomerative cluster analysis was executed using the R package ‘vegan’ (Oksanen et al. 2017; R Development Core Team 2012), utilizing Euclidean distances and Ward’s method linkage, and illustrated with a heatmap (in the electronic supplementary material) sorting species content according to weighted averages on plot scores (Borcard et al. 2011).

Results

Spatial distribution and habitat

Espeletia pycnophylla subsp. *llanganatensis* grew at elevations between 3420 m and 3600 m a.s.l. within the VFL, amidst the upper elevational limit of montane tree forms characterized by *Buddleja incana*, *Monticalia andicola*, *Hesperomeles obtusifolia*, *Miconia tinifolia*, *Gaiadendron punctatum*, *Oreopanax seemannianus*, *Weinmannia pinnata*, *Escallonia myrtilloides* and the tree fern *Blechnum auratum*. *Espeletia pycnophylla* subsp. *llanganatensis*

displayed a patchy distribution and occurred in four clusters (Fig. 1B), separated from each other in distances of 200–900 m, and covered a total area of ~ 20 ha (Table 1). The clusters occupied transitional terrains between waterlogged areas or such that occasionally flood on the one side and better drained ridges and steep forested slopes on the other. Such terrains were found on terraces formed by successive landslides from the northwestern flanks of Cerro Negro and the unnamed mountain to its west (Fig. 1B, central cluster, SW cluster). All terraces drained in a southwesterly direction into the valley. The population's distribution limit towards the north and east was located at approximately 01° 09' 25" S and 78° 13' 30" W, and towards the south and west at 01° 10' 00" S, 78° 15' 09" W. No *Espeletia* were observed in the grasslands *en route* to the VFL.

The Central Cluster extended across four terraces (Fig. 1B). Surveyed plots had southwestern exposures with terrain inclinations ranging between 5° and 20°, and at elevations of 3440–3480 m a.s.l. (Table 2). All plots were characterized by a dense herbaceous stratum (i.e. *Carex bonplandii*, *Cortaderia nitida*, *Blechnum loxense*, *Equisetum bogotense*, *Desfontainia spinosa*, *Loricaria thuyoides*, *Neurolepis aristata*, *Gunnera magellanica*) approximately higher than 80 cm and intermittent 'open spaces' covered by bryophytes. Additional structural complexity of the plots was shaped to a lesser extent by arbustive forms (i.e. *Baccharis genistelloides*, *Diplostephium rhododendroides*, *D. glandulosum*) and the bromeliad *Puya eryngioides*. Arborescent growth forms were only represented by tall specimens of *E. pycnophylla*

subsp. *llanganatensis* and the tree fern *Blechnum auratum*.

Soil textures were consistently in the loam category in all plots with similar contents of sand (40%) and silt (44%), and less clay (16%). Soils were acidic (pH 4.2–4.8) with a low ionic exchange capacity based on interchangeable aluminium ($Al^{3+}+H$, 2.1 cmol · kg⁻¹) and low levels of nitrogen (0.87 %). The mean levels of organic matter were high (28.75%, see Tab. 2), Ca levels were medium (3.8 cmol · kg⁻¹), available P levels were medium to low (8.73 mg · kg⁻¹), and K (0.77 cmol · kg⁻¹) and Mg (0.71 cmol · kg⁻¹) levels were low, based on the exchangeable cation rating by Hossner (2020).

Population structure

The surveyed plots contained 781 individuals of *E. pycnophylla* subsp. *llanganatensis*, reaching a maximum total height of 900 cm, and in abundances of 40–135 individuals per plot. Dead specimens were rare, contributing ≤ 0.02% of individuals per plot. The frequency distribution of plants overall was strongly skewed towards smaller plants, with the two smallest size classes (10 cm and 20 cm) containing 137 and 221 individuals, respectively. Seedlings were observed in distances of 10–300 cm from the nearest individual in the flowering stage. Considering both classes combined as recruits, they contributed 28.3% of the total population.

Flowering plants were present in all plots. Of 781 surveyed plants, $N = 602$ (77%) had no flowers, while $N = 179$ (23%) had some. The minimum size observed among flowering plants was in size class

Table 1 Clusters of *Espeletia pycnophylla* subsp. *llanganatensis* from north to south in the VFL

Label	Exposure and Location	Area [ha]	Elevational range [m a.s.l.]	Central point coordinates
NE cluster	W exposures along the upper end of the VFL, along the brook, enclosed by the southern flanks of Cresta del Gallo and Las Torres massif and the northern flanks of the Cerro Negro.	2	3500–3550	01° 09' 29" S, 78° 13' 43" W
E cluster	NW and S exposures along the low northern flanks of Cerro Negro scared by recent landslides (survey plot 9)	1	3450–3470	01° 09' 34" S, 78° 14' 32" W
Central cluster	SW exposure on the western and northwestern flanks of Cerro Negro (survey plots 1–8)	14	3420–3510	01° 09' 44" S, 78° 14' 51" W
SW cluster	NE and W exposures, unnamed mountain across the VFL vis-à-vis Cerro Negro	3.5	3430–3490	01° 09' 48" S, 78° 15' 06" W

Table 2 Plot characteristics and vegetative cover of *Espetelia pycnophylla* subsp. *llanganatensis* (EPL), vascular plants, herbaceous (VHE) and arbustive (VAR), and bryophyte (BRY). Randomly placed plots had varying inclination and drainage with their borders. Mean inclination is given in degrees, and drainage is classified as 1 (poor), 2 (fair), 3 (good) or 4 (very good). Mean organic matter in soils in plots 1–8

Plot	Terrace	Exposure	Inclination [°]	Drainage	Organic matter [%]	Elevation [m a.s.l.]	Vegetation cover [%]				Central point coordinates	
							EPL	VHE	VAR	BRY	EPL	BRY
1	A	SW	20	1	32	3440	11.6	34.1	36.3	18	01° 09' 42" S; 78° 14' 56" W	
2	A	SW	5	2	34	3445	27	54.1	4.9	14	01° 09' 41" S; 78° 14' 53" W	
3	A	SE	25	3	33	3450	24.2	69.4	0.4	6	01° 09' 38" S; 78° 14' 42" W	
4	A	S	10	4	30	3470	14.2	66.0	13.8	6	01° 09' 39" S; 78° 14' 38" W	
5	C	SW	10	3	26	3460	23.6	57.3	9.1	10	01° 09' 45" S; 78° 14' 55" W	
6	C	SW	15	4	25	3455	12.4	76.2	5.4	6	01° 09' 47" S; 78° 14' 57" W	
7	D	SW	5	4	26	3480	10.8	67.3	11.9	10	01° 09' 49" S; 78° 14' 54" W	
8	D	SW	15	4	24	3475	8	72.9	13.1	6	01° 09' 51" S; 78° 14' 56" W	
9	n/a	Multiple	5–45	4	n/a	3450	23	n/a	n/a	n/a	01° 09' 33" S; 78° 14' 31" W	

100–110 cm ($N = 1$), followed by up to $N = 5$ in the larger size classes. If all plants equal to or larger than the observed minimum flowering size were mature, half of the population (51%) had synflorescences during the survey. Flowers were mostly wilting in late December 2020. We observed up to sixteen thyrsoïd synflorescences per individual, each bearing six to ten generally paired capitula (Fig. 2A–D).

The inverse J-shaped distribution curves of the size classes (Fig. 3), as well as the demographic ratios between individuals in different growth phases (Fig. 4), may indicate a stable population with active recruitment. From a plot perspective, most individuals were below 120 cm in all northern plots (1–4) and in one southern plot (5). The remaining southern plots (6–8) had more broadly distributed size classes and larger individuals (Fig. 3A). Distribution curves of size classes among all flowering plants revealed distinctive variation between plots. In plots 1 and 2, most flowering plants were smaller or equal to 130 cm height. In plots 5, 7 and 8 flowering plants were > 500 cm. In plots 3, 4 and 6, flowering plants had sizes between these extremes. Plot 9 had no plants taller than 300 cm (Fig. 3C).

Rosette height and diameter never surpassed 100 cm and increased consistently up to a total plant height of approximately 110 cm (Fig. 5). Collars of necrotic leaves covered the entire stalk in plants shorter than 400 cm with few exceptions ($N = 9$). In plants taller than 400 cm, 63% had lost the lower 25–50% of the necrotic collar. Signs of wildfires, such as charred stems or the presence of horizons of consistently missing necrotic collars in all size classes were not observed.

Co-occurring Vegetation

Seventy species co-occurred with *E. pycnophylla* subsp. *llanganatensis* (11–26 co-occurring species per plot), belonging to 45 genera of 30 families, mostly angiosperms and a few pteridophytes (Table 2). Groundcover was dominated by Poaceae (*Cortaderia nitida*, *Calamagrostis effusa*, *Neurolepis aristata*), Blechnaceae (*Blechnum auratum*), Asteraceae (*E. pycnophylla* subsp. *llanganatensis*, *Bacharis genistelloides*), Ericaceae (*Gaultheria amoena*), Cyperaceae (*Uncinia paludosa*) and bryophytes. Aside from

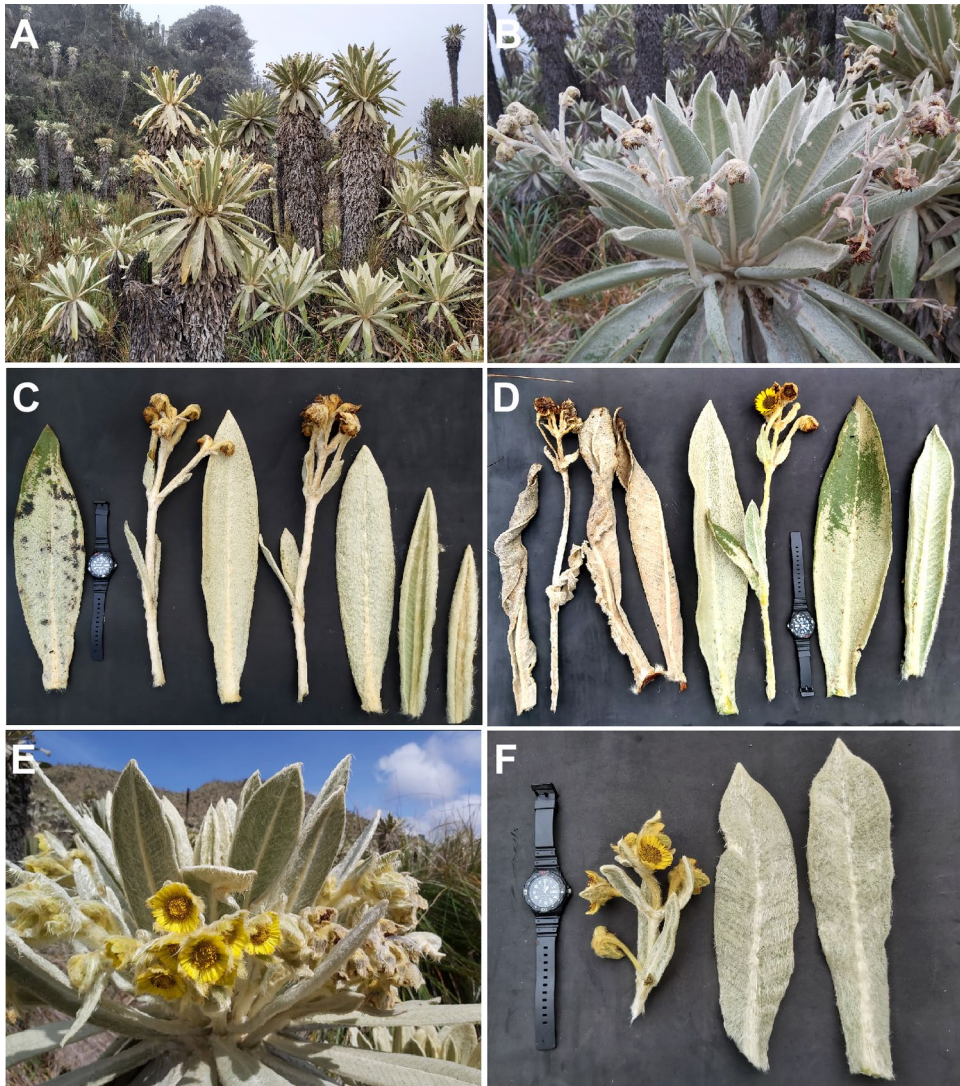


Fig. 2 A–F – *Espeletia* from the Cordillera de Los Llanganates (Tungurahua) and from El Ángel (Carchi). A–D – *E. pycnophylla* subsp. *llanganatensis*, VFL (Tungurahua), Decem-

ber 2020, *E. pycnophylla* subsp. *angelensis*. E–F – El Ángel (Carchi), March 2021. Scale: wristwatch 26 cm

E. pycnophylla subsp. *llanganatensis*, *Lachemilla llanganatensis* is also an endemic to Ecuador. The former is regarded as being endangered and the latter as vulnerable according to IUCN threat categories (see León-Yáñez et al. 2011). *Puya eryngioides* and *Elaphoglossum artisanae* were newly recorded for the Cordillera de los Llanganates. Their threat categories are ranked as of least concern and vulnerable, respectively (León-Yáñez et al. 2011). Species composition

and ground cover, compared across plots 1–8, showed minimal differentiation across four terraces and various drainage levels, as illustrated by the heatmap (in the electronic supplementary material), indicating that the samples stemmed from a largely homogeneous community. Thirteen species occurred commonly across all plots, most species occurred equally frequently at several plots, and only sixteen were unique to any one of the eight plots.

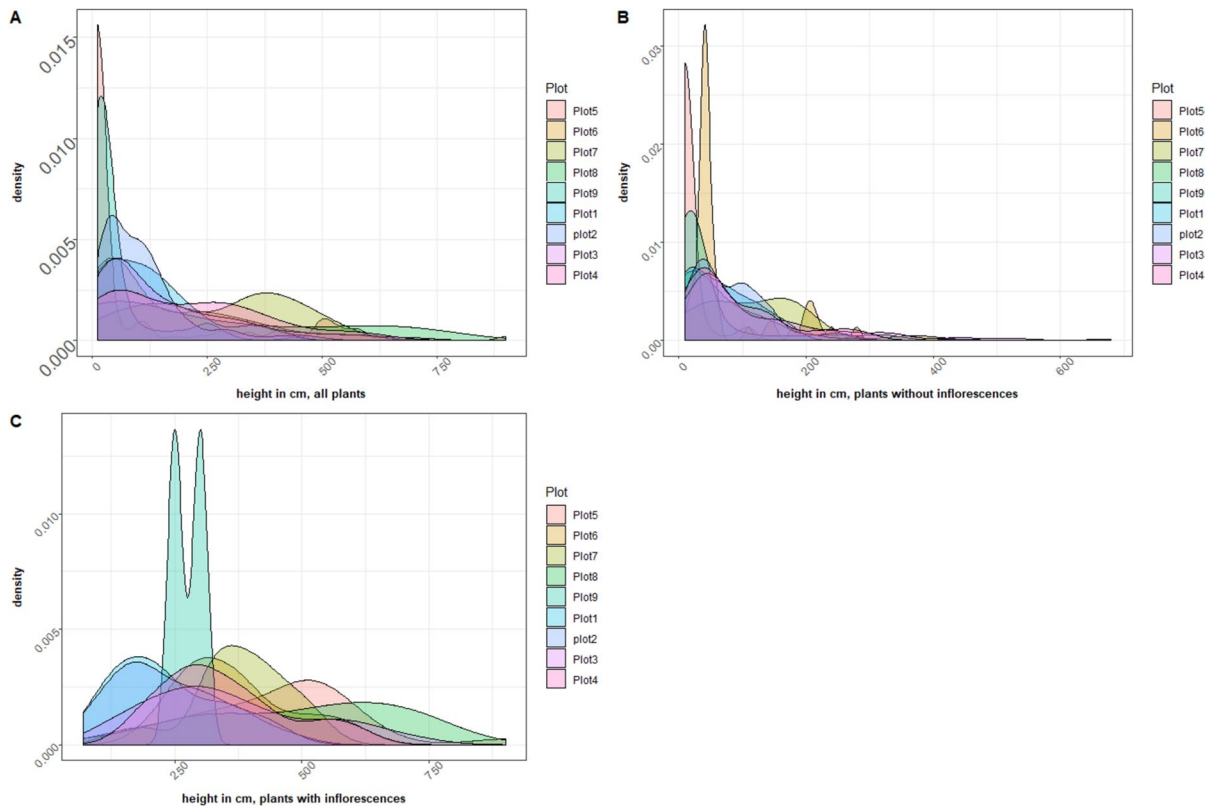


Fig. 3 Density plots of size distribution of *E. pycnophylla* subsp. *llanganatensis* in plots 1–9. **A** – All plants per plot, **B** – non-flowering plants per plot, **C** – flowering plants per plot

Discussion

Geographic distribution of *E. pycnophylla* subsp. *llanganatensis*

The observations from the Valle de los Frailejones (VFL) match Andrade Marín’s (1936) first conclusive

sighting of the arborescent *Espeletia* now known as *E. pycnophylla* subsp. *llanganatensis*. Andrade Marín described an extensively swampy valley floor, including a large ‘laguna’, surrounded by ‘billions of arboreous *sagurimas*’. His viewpoint was Cresta del Gallo (3800 m), from where he looked southward into the VFL, which he did not enter. Although he gave no

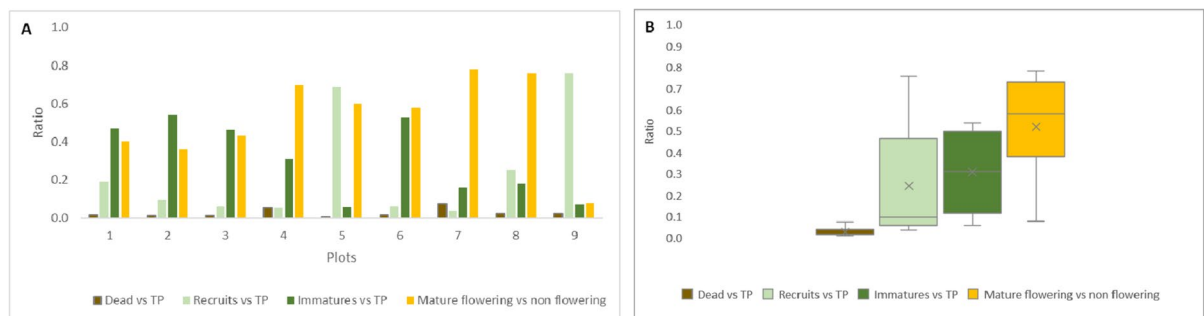


Fig. 4 **A** – Overall demographic ratios between *E. pycnophylla* subsp. *llanganatensis* in different growth phases in the VFL in plots 1–8, and **B** – dead vs. total population (TP), recruits ≤ 20 cm vs TP, immature vs total population, mature flowering plants vs mature non-flowering plants, across all plots

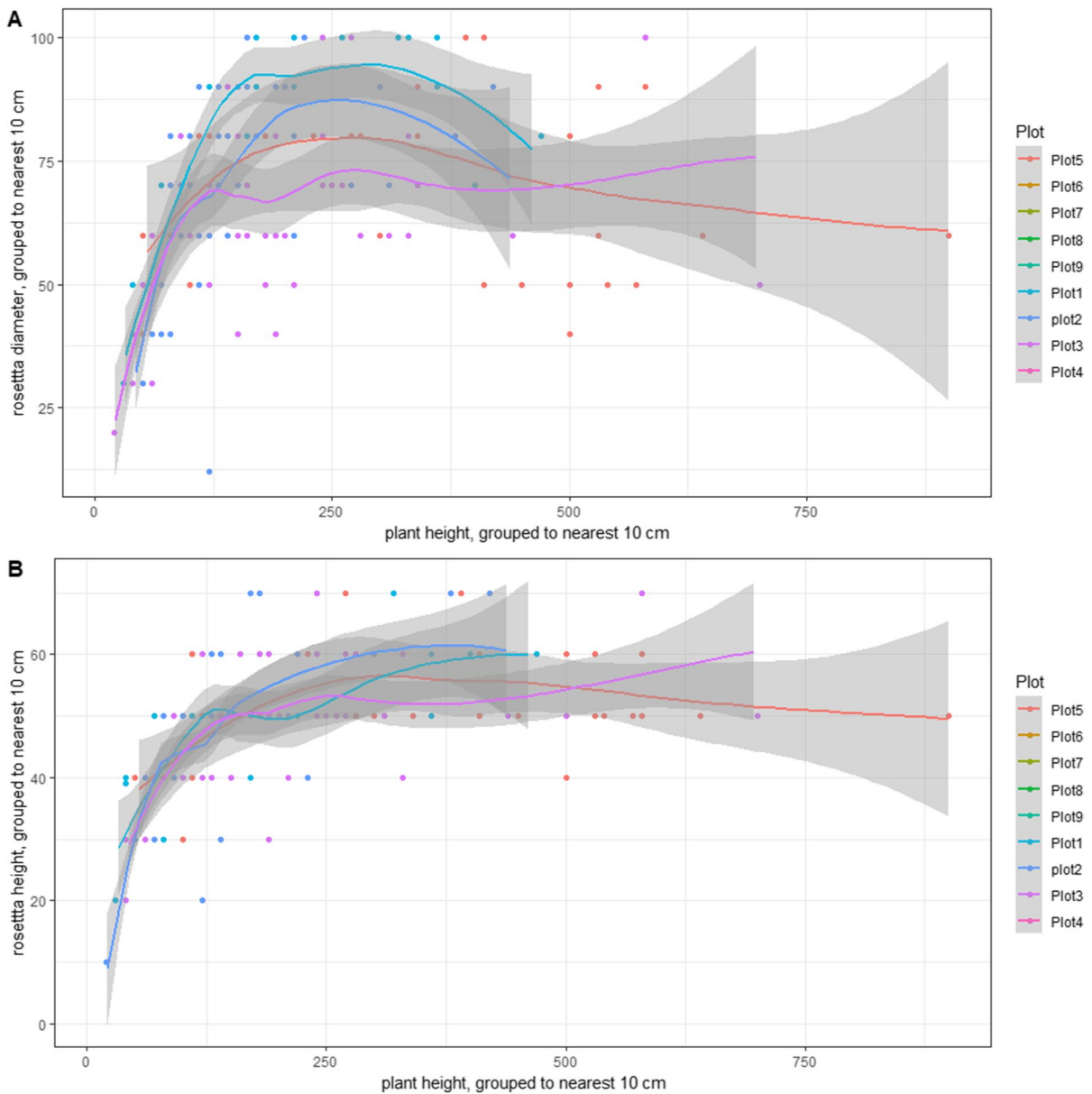


Fig. 5 **A** – Relationship between rosetta diameter and total plant height and **B** – rosetta height and total plant height of *E. pycnophylla* subsp. *llanaganatensis* from the VFL, in plots 1–9. Datapoints connected by LOESS smoother and 95% confi-

dence interval. The plateau suggests a similar maximum height of rosettes across all sample sites but marked variability in diameter. Asymptotic rosetta size is achieved by plants around 125 cm total plant height

elevational estimates for the reported communities on the northeastern flanks of Cerro Negro, these do correspond to the clusters that we identified within the upper elevational limits of the sub-Páramo arboreal zone between 3420 and 3600 m a.s.l., which have persisted to this date. In fact, Andrade Marín’s trail log proved to be the most accurate published description

on how to access the area and the vegetation to be seen *en route*.

The VFL is the only area of *E. pycnophylla* subsp. *llanaganatensis* registered by Ecuador’s governmental entities responsible for biodiversity (Vargas et al. 2000). Andrade Marín reported additional populations approximately three kilometres

northeast of the VFL, in an area referred to as Las Torres, which drains into the Río Dantayacu (downstream into R. Mulatos) on the eastern fringes of the Cordillera de los Llanganates in the Province of Napo. Andrade Marín (1936) also described other patches of *Espeletia* south of Las Torres, in an area draining into tributaries of Río Negro in Tungurahua Province and states the elevational range of *Espeletia* as being between 2300 and 3600 m a.s.l. Earlier records by Spruce (1861) mention ‘sangurimas’ in the Cordillera de los Llanganates, referring to a 1827 transcript of the Chronicles of the Royal Accountant Pedro de Valverde from 1582, but without conclusive plant descriptions (compare Andrade Marín 1936; Cuatrecasas 2013; Anhalzer 2017). This study confirms *Espeletia* clusters on the eastern flanks of Cerro Negro, but a distribution below elevations of 3000 m remains doubtful.

The absence of *E. pycnophylla* subsp. *llanganatensis* in the Páramo grasslands of the Cordillera de los Llanganates and its apparent restriction to a small area within the sub-Páramo ecotone (below the continuous tree line *sensu* Baruch 1984), in proximity of upper elevational montane-forest limits is a distinguishing ecological feature to *E. pycnophylla* subsp. *angelensis*, occurring along the Ecuador–Colombia border, Province of Carchi. The fact that no *Espeletia* have been identified between the Cordillera de los Llanganates and Carchi, may be a result of either natural or human-induced local extinction. Population growth and agricultural expansion have transformed many Páramos into anthropogenic ecosystems (Verweij and Beukema 1992; Verweij and Beekman 1995; Hofstede and Jongsma 1997; Loaiza-Usuga et al. 2021), in which remote and undisturbed valleys such as the VFL are rare, and possibly serve as refuge for *E. pycnophylla* subsp. *llanganatensis*. Known occurrences of *E. pycnophylla* subsp. *llanganatensis* were accidental finds by persons searching for the presumed hidden treasure of Atahualpa, a principal attractant of expeditions to the Cordillera de los Llanganates (Andrade Marín 1936; Anhalzer 2017) and the botanical descriptions followed later. It is thus plausible that a systematic examination of remote unpopulated valleys in nearby mountain ranges with similar habitat attributes as the VFL may lead to the identification of other populations of *E. pycnophylla* subsp. *llanganatensis* or varieties thereof.

Spatial distribution of *E. pycnophylla* subsp. *llanganatensis* in the VFL

Espeletia pycnophylla subsp. *llanganatensis* occupies transitional areas between less stable waterlogged soils and more stable, better drained areas and ridges, never intertwining with the surrounding forest. This occurrence pattern also reflects Andrade Marín’s (1936) observations from Las Torres, where *Espeletia* grew around ponds, separated from surrounding forested areas. The observed restriction of *E. pycnophylla* subsp. *llanganatensis* to such transitional areas and the sub-Páramo is in stark contrast to *E. pycnophylla* subsp. *angelensis* in northern Ecuador and southern Colombia, which occurs across a wide elevational range above the Andean tree line (see Ramsay and Michell 2001; Sanchez 2004; Benavides et al. 2007; Noboa 2019).

In terms of habitat range, *E. pycnophylla* subsp. *llanganatensis* appears stenotopic in topographically sheltered areas, influenced by weather patterns from the Amazon basin driven from the Atlantic. By contrast, *E. pycnophylla* subsp. *angelensis* inhabits more extensive and partially more arid Páramo influenced by the confluence of Pacific and Atlantic-driven weather patterns (Rangel-Churio 2006; Emck 2007). Rapid environmental changes, such as extremes in precipitation or drought, may threaten the survival of this *E. pycnophylla* subsp. *llanganatensis* population in terms of erosion or dehydration (Valencia et al. 2020; Peyre 2022), particularly in the limited distribution within the VFL.

Population structure

Based on size structure and number of recruits, the VFL population of *E. pycnophylla* subsp. *llanganatensis* appears stable. This contrasts with the demographic structure of *E. pycnophylla* subsp. *angelensis* in northern Ecuador (Carchi), where wildfires have suppressed recruitment (Ramsay and Michell 2001). Depressed numbers of *Espeletia* recruits in Cundinamarca, Colombia (Venegas Carillo 2011) were interpreted as indications of chronic disturbance *sensu* Permauer (1999). In Colombia, fifteen species of *Espeletia* have been regarded as critically endangered, 25 as endangered (Diazgranados and Castellanos-Castro 2021), and the threat levels to *Espeletia pycnophylla* were classified as being of least concern. Given the comparatively small population of *E. pycnophylla*

subsp. *llanganatensis*, a monitoring programme of its demographic composition would be a beneficial conservation tool. Based on the overall density of individuals observed in all plots, the entire population of the four cluster may encompass 173,400 individuals.

Within the VFL, size-class distribution varied. Highly saturated grounds favoured large numbers of recruits and smaller size classes whereas better-drained substrates favoured the presence of individuals in larger size classes (400–900 cm). This may be due to ground-stability constraints, toppling being a limiting factor for tall specimens on highly saturated grounds.

Synflorescences occurred in plants > 110 cm. While successful local recruitment was evident in the ratios of recruits vs total population in VFL, more stable substrates harboured greater proportions of old reproductive individuals. The highly saturated, less stable areas favoured germination and smaller size classes. Thus, longevity of plants and their reproductive activity also decreased with ground stability. However, for the conservation of this southernmost *Espeletia* population, the existence of these habitats appears essential to local recruitment. The less stable areas seem to be recruitment areas, where plants have ample space for germination and live long enough to contribute seeds and seedlings for decades. More stable areas favour prolonged growth and fecundity.

The overall dispersal capability of *E. pycnophylla* subsp. *llanganatensis* remains unknown. Although tall florescent individuals, observed on stable grounds, may facilitate wind dispersal, this pollination mechanism appears to primarily occur at higher elevations, where animal pollinators are rare (Cruden 1972; Berry and Calvo 1989) and where self-incompatibility is predominant (Fagua and Gonzalez 2007). The secluded nature of the VFL is not conducive to strong winds but the surrounding montane forest provided ample habitat for animal pollinators (comp. Sturm 1989; Berry and Calvo 1994). We observed a hummingbird and several insects around synflorescences of the subspecies.

The height and width of rosettes increased with plant height up to ~ 130 cm, beyond which only trunk height increased. This roughly coincided with the development of inflorescences (observed only in individuals \geq 110 cm). Similar patterns are known from *E. pycnophylla* subsp. *angelensis*, but these plants rarely reach 700 cm (Benavides et al. 2007; Cuatrecasas 2013). *Espeletia barclayana* grows by

3.8 cm · yr⁻¹ in specimens taller than 60 cm (Cavelier et al. 1992), while juveniles and adults of *E. grandiflora* grow by 7.8 cm · yr⁻¹ (Fagua and Gonzalez 2007). Specimens in the VFL plots with a height of 900 cm could therefore be more than 200 years old.

Regional and site-specific distribution limits point at a narrow ecological niche occupied by *E. pycnophylla* subsp. *llanganatensis*, with good local recruitment but possibly a reduced potential for territorial expansion and a potentially pronounced vulnerability to extinction in the VFL. Peyre et al. (2020) modelled a dispersal capacity of 129 cm · yr⁻¹ for *E. pycnophylla*, based on species trait data from Colombia and Ecuador. If this were to apply to the subspecies *llanganatensis*, then habitat availability may be at the root of the restricted occurrence. As the Cordillera de los Llanganates is not populated or utilized agriculturally, direct human intervention is presently an unlikely source of disturbance. The extreme isolation of *E. pycnophylla* subsp. *llanganatensis* from established trails or roads has so far favoured this situation. Nonetheless, *Espeletia* has historically been used for fuel and rudimentary shelter structures (Diazgranados and Castellanos-Castro 2021) and if the clandestine mining activities that have already intruded the Llanganates National Park reach the VFL, a new threat to the survival of this population will emerge. Contrastingly, agricultural encroachment and wildfires have already shaped the recruitment of *E. pycnophylla* subsp. *angelensis* and the diversity of its co-occurring flora for more than a century in some parts of northern Ecuador (Kovář 2001; Noh et al. 2020).

Co-occurring vegetation

At the scale of this study, no clear differences in the composition and ground cover of the co-occurring flora were discernible across terrain gradients like distinct terraces and drainage levels, because of the spatial dominance of grasses and bryophytes, joined by many less-common species. The vegetation co-occurring with *E. pycnophylla* subsp. *llanganatensis* in the VFL was species-richer than that co-occurring with *E. pycnophylla* subsp. *angelensis* at El Angel in Carchi (comp Ramsay 2001). This was possibly a result of the pronounced differences in habitat. While *E. pycnophylla* subsp. *llanganatensis* grows in the sub-Páramo, without evidence of fires, subsp.

angelensis grows above the Andean tree line and is exposed to wildfires (Zomer and Ramsay 2020; Kovář 2001; Ramsay and Michell 2001). The examination of the flora co-occurring with *E. pycnophylla* subsp. *llanganatensis* populations east of Cerro Negro will tell whether the mentioned differences represent a consistent pattern.

Conclusion

Espeletia pycnophylla subsp. *llanganatensis* is so far the only identified *Espeletia* south of the equator and may indeed represent the austral distribution limit of the genus. The subspecies occupies a different and geographically more restricted environment than subsp. *angelensis*, 200 km to the north in the Province of Carchi along the Ecuador–Colombia border. Instead of occupying a wide elevational and territorial range in the Páramo, encroached by agricultural expansion, it occurs in small clusters at the upper elevational limits of montane forests of the sub-Páramo in the eastern margins of the Cordillera de los Llanganates. Currently, there is no visual evidence of direct human disturbance in the VFL, which may have favoured the longevity of particularly tall specimens. A monitoring programme for this population is recommended to ensure that disturbances threatening its survival and the composition of co-occurring flora, which is more diverse than that associated with *E. pycnophylla* subsp. *angelensis* are detected early. Local recruitment of *E. pycnophylla* subsp. *llanganatensis* appeared healthy, but the overall dispersal capability of the subspecies remains unknown. Furthermore, it is not yet clear whether the observed occurrence in the sub-Páramo, within transitional areas between forest margins and waterlogged terrains is an indication of a subspecies trait and whether the VFL represents a refuge for *E. pycnophylla* subsp. *llanganatensis* or remnant of a previously broader habitat range and distribution. Habitat attributes observed in the VFL population resemble accounts of the environment surrounding *Espeletia* clusters east of Cerro Negro described by Andrade Marín (1936). From a conservation standpoint, these populations deserve further examination and a search for other populations should be initiated. Ultimately, the level of threat to the survival of this Ecuadorian endemic should be gauged more accurately and possible

connectivity corridors may be detected between the populations of the subsp. *angelensis* from the Northern Hemisphere and disjunct populations of subsp. *llanganatensis* from the Southern Hemisphere.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

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