

A developmental classification system for the comparison of *Puya raimondii* giant Andean rosettes

Mery Suni

Universidad Nacional Mayor de San Marcos

Giovana Vadillo

Universidad Nacional Mayor de San Marcos

Gerson Prado

Universidad Nacional Mayor de San Marcos

Liscely Tumi

Universidad Nacional Mayor de San Marcos

Paul Michael Ramsay

`paul.ramsay@udlap.mx`

Universidad de las Américas Puebla: Universidad de las Americas Puebla <https://orcid.org/0000-0001-7631-6480>

Research Article

Keywords: developmental stages, life stages, size structure, allometry, monocarpic, semelparous

Posted Date: September 23rd, 2024

DOI: <https://doi.org/10.21203/rs.3.rs-4954102/v1>

License:  This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Version of Record: A version of this preprint was published at Alpine Botany on January 11th, 2025. See the published version at <https://doi.org/10.1007/s00035-024-00326-8>.

Abstract

Puya raimondii Harms, an endangered giant bromeliad, has great ecological and cultural significance in the Central Andes. To help studies of population size structure in this species, this study aims to develop a rapid classification system based on plant developmental stages instead of using absolute size measurements, and applies it to three areas in or near Huascarán National Park, Peru. Plant height, stem height, total and photosynthetically-active rosette diameter and height to the base of the rosette were measured, to illustrate how the developmental stages compare, along with estimates of vegetation, rocks, and bare ground. Five plant developmental stages were identified in the study: juvenile, subadult, adult, reproductive adult, and senescent reproductive adult. The juvenile stage could, in future, be further divided into smaller, vulnerable plants and more established juveniles, but this requires more detailed study to determine appropriate distinguishing developmental criteria. Comparing locations, *Puya* plants in Queshque, were smaller than in the other locations, across all developmental stages. However, the environmental variables recorded in this study could not explain this difference, indicating the importance of other, unknown factors. This study provides an efficient and informative classification system for *P. raimondii* giant rosettes, using well-defined developmental stages, that can reveal important differences between populations and prompt the generation of new hypotheses about the ecology of these important plants. The classification system could be applied in populations across the species' distributional range in the Central Andes to explore how age, size and environmental factors affect growth and development in this species.

Introduction

The spectacular *Puya raimondii* Harms is the largest bromeliad in the world, and an endangered species which is emblematic of the puna in Peru and Bolivia (Raimondi 1874; Rees and Roe 1980; Lambe 2009; Salazar Castillo et al. 2011; Fortier 2024). Ecologically, *P. raimondii* is a keystone species, providing structure for climbing plants and foraging and nesting resources for birds (Dorst 1957; Salinas et al. 2007; Hornung-Leoni et al. 2013; Rocha 2023). Tourists are attracted to high mountain ecosystems by this charismatic megafauna, and the plants also hold significant cultural value to local people (Waite 1978; Venero Gonzales and Hostning 1986; Venero Gonzales 2001; Hornung-Leoni and Sosa 2004), who use *P. raimondii* for construction materials, fuel, animal forage and field boundaries (Villiger 1981; Venero Gonzales 1984; Rivera C. 1985; Leiva G. et al. 1991; Dávila 2004; Lounibos and Frank 2009).

The size structures of plant populations provide an insight into present and future demography of the species (Hara 1988; Holderegger 1997; Fortier 2024), which can be incorporated into conservation plans (Franco and Silvertown 2004; List et al. 2017). If repeated measures of plant sizes are taken through time, as part of a longer-term monitoring programme, it can provide information about growth rates and ages of plants of different sizes (Bierzychudek 2014).

P. raimondii, given its widespread distribution in the Central Andes and its endangered status, requires a better understanding of its population structure in different locations and over time. However, there are a

limited number of studies which have reported information linked to the size structure of *P. raimondii* populations in the puna (Venero Gonzales 1984; Salazar Castillo and Villasante Benavides 2012; Montesinos 2014; Aquino et al. 2018; Prado-Aliaga et al. 2021; Veldhuisen et al. 2022), other *Puya* species in the páramos of the Northern Andes (Miller and Silander 1991; Mora et al. 2005; Mora et al. 2007; Garcia-Meneses and Ramsay 2014; Veldhuisen et al. 2022), and even one species from the páramo of Costa Rica (Augspurger 1985). However, collecting comprehensive and detailed information about rosette size and plant height in remote and rugged terrain presents practical difficulties, and a simpler system of developmental phases could provide a more effective way to collect valuable demographic information about population size structure. For example, Suni et al. (2024) assigned *P. raimondii* plants to developmental phases according to rosette height, corresponding to broad developmental phases of the plant: juveniles < 0.5 m height; hemispherical juveniles 0.50–1.49 m height; spherical adults 1.50–2.99 m height; and mature adults ≥ 3.0 m. An alternative classification, using developmental morphology rather than fixed size thresholds could be more suitable, especially for making comparisons between populations where there could be differences in the size of plants within the developmental phases.

Using detailed measurements of representative plants, we aim to develop a rapid evaluation system for *P. raimondii* plants to assign them to biologically meaningful developmental categories. To illustrate how such a system could be applied to different populations of *P. raimondii* throughout the Central Andes, we compare three different locations with important stands of this giant rosette plant in and around Huascarán National Park, Peru.

Methods

Study areas

The locations of two large populations of *P. raimondii* plants in Huascarán National Park has been reported by Shoobridge (2005) and Vadillo Gálvez (2011): Pumapampa and Queshque. A third large population of plants is located mostly outside the national park, near the village of Pachapaqui. All three areas were included in our study (Fig. 1).

Size structure of *P. raimondii* in the field

In August and September 2017, *P. raimondii* plants were measured in the three study areas within rectangular plots of 50 m x 6 m, established at random within the *Puya* stands. Four plots each were employed in Queshque and Pachapaqui, and ten plots in Pumapampa (Fig. 1, Online Resource 1). The reduced number of plots in Queshque and Pachapaqui reflected difficulties in accessing the populations in those places.

All *P. raimondii* plants with rosette centres within the limits of the plots were located and four allometric variables measured: total rosette diameter, live rosette diameter, total plant height, and stem height. Total rosette diameter represented the greatest distance across the rosette from one leaf point to

another. Live rosette diameter represented the greatest distance across the rosette of green, photosynthetically-active leaf tissue. Total plant height was measured from ground level to the highest point of the plant (vertical leaf points for immature plants, and the top of the inflorescence for mature, reproductively-active plants). Stem height was measured from ground level to the apical meristem in the rosette, the height at which leaves are held horizontally from the centre of the rosette—see Fig. 4 of Tomita et al. (2011). Inflorescence length was calculated as the difference between total plant height and stem height (in vegetative plants, total plant height = stem height). For all height measurements made on sloping terrain, ground level was measured at the sides of the plants, perpendicular to the slope.

Senescent reproductive rosettes, with all rosette leaves below the horizontal plane, were recorded with zero rosette diameter and, in these plants, the reproductive axis was entirely in fruit. Dead plants often remain standing for several years after reproduction has been completed. Such plants were not measured in this study.

Environmental variables in each area

Percentage covers of vegetation, parent rock, and stones greater than 20 cm across (averaging perpendicular dimensions) were estimated within ten 2 m² areas, arranged in pairs at 5.5, 15.5, 25.5, 35.5 and 45.5 m along the length of each plot. The percentage cover of bare ground with smaller stones (less than 20 cm across, averaging perpendicular dimensions) was calculated, in each case, by subtraction of the other percentage covers from 100%. In the centre of each 2 m² area, vegetation height was estimated using the drop disc technique (disc 30 cm diameter and 40 g).

Data analysis

For our statistical analysis, we used R (R Core Team 2023). Comparisons of *P. raimondii* dimensions between locations were carried out using the gstatsplot package (Patil 2021). We used Welch's ANOVA and the Games-Howell multiple comparisons test, since the data were heteroscedastic (different standard deviations across the range of dimensions). For some developmental stages, the measurements were not normally distributed and for the statistical comparisons we use natural logarithm transformations to satisfy the assumptions of Welch's ANOVA.

Principal Components Analysis (PCA, using R) was used to explore the potential differences between study areas in terms of soil depth, vegetation height and cover of parent rock, large rocks, vegetation, and soil with small stones.

Results

Classification of *P. raimondii* plants into developmental stage categories

Within the sampled plots, 246 *P. raimondii* plants (of which 23 were mature plants) were found at Pumapampa, 248 plants (5 mature) at Queshque, and 73 plants (11 mature) at Pachapaqui.

P. raimondii plants change shape over the course of their lives. We characterized four phases of *Puya* development (developmental stages), using key morphological features rather than absolute measurements (Fig. 2). “Juvenile” plants have the apical meristem, at the centre of the rosette, located at more or less ground level. The younger plants in this developmental stage have fewer, smaller leaves and older plants have many more leaves and a distinct hemispherical rosette shape. The “subadult” developmental stage is characterized by the formation of a stem, which lifts the apical meristem above the ground and, eventually, once the stem is tall enough, allows the rosette to develop a spherical shape. In the “adult” developmental stage, senescent and dead leaves begin to accumulate below the base of the spherical rosette, forming a skirt. At the end of its life, the *Puya* plant produces an inflorescence while still supporting a living rosette of leaves (the “reproductive adult” developmental stage). Finally, the rosette leaves senesce and fall below the horizontal plane, as resources are diverted into fruit and seed production (the “senescent reproductive adult” developmental stage). Completely dead plants (all plant parts very dark, almost black) were not included in the developmental stage categories, though they can remain standing for several years after death.

These five developmental stages (juvenile, subadult, adult, reproductive adult, and senescent reproductive adult) were used in subsequent analyses to determine relationships between plant dimensions and to identify potential differences in plant dimensions between the three study areas.

Relationships between allometric variables of *P. raimondii* plants

For subadult and adult plants (with stems and with no inflorescences), there was a clear positive relationship between stem height and total height (Fig. 3a; combined study areas regression $p < 0.001$, $R^2 = 0.90$; fitted line: total height = $-0.295 \times \text{stem-height}^2 + 2.048 \times \text{stem-height} + 0.43$). Similar relationships were found for each of the three study areas separately: Pachapaqui ($p < 0.001$, $R^2 = 0.92$, fitted line: total height = $-0.277 \times \text{stem-height}^2 + 1.943 \times \text{stem-height} + 0.60$), Pumapampa ($p < 0.001$, $R^2 = 0.85$, fitted line: total height = $-0.242 \times \text{stem-height}^2 + 1.871 \times \text{stem-height} + 0.54$) and Queshque ($p < 0.001$, $R^2 = 0.90$, fitted line: total height = $-0.161 \times \text{stem-height}^2 + 1.897 \times \text{stem-height} + 0.37$). For all three study areas combined, the stem first appeared when the total plant height was 0.43 m (where stem height = 0 in Fig. 3a, 95% confidence interval = 0.33–0.53 m), but there was some variation between study areas. For Pachapaqui, the stem first appeared in plants, on average, 0.60 m tall (95% confidence interval = 0.33–0.86 m), compared with 0.54 m (0.35–0.72 m) for Pumapampa, and 0.36 m (0.24–0.49 m) for Queshque.

A clear positive relationship was found for juveniles, subadult and adult plants (no plants with inflorescences) between total rosette diameter and total plant height (Fig. 3b; combined study areas regression $p < 0.001$, $R^2 = 0.89$; fitted line: total height = $0.760 \times \text{diameter} + 0.003$). This relationship was very similar in each study area separately: Pachapaqui ($p < 0.001$, $R^2 = 0.86$, fitted line: total height = $0.904 \times \text{diameter} - 0.10$), Pumapampa ($p < 0.001$, $R^2 = 0.87$, fitted line: total height = $0.712 \times \text{diameter} + 0.02$) and Queshque ($p < 0.001$, $R^2 = 0.93$, fitted line: total height = $0.751 \times \text{diameter} + 0.02$).

Combining juveniles, subadult and adult plants from all three study areas, a positive relationship was also found between live rosette diameter—just the photosynthetically-active green parts of the leaves—and total plant height (Fig. 3c; regression $p < 0.001$, $R^2 = 0.90$; fitted line: total height = $0.876 \times \text{diameter} + 0.09$). Similar patterns were derived from each of the study areas independently: Pachapaqui ($p < 0.001$, $R^2 = 0.89$, fitted line: total height = $0.966 \times \text{diameter} + 0.05$), Pumapampa ($p < 0.001$, $R^2 = 0.87$, fitted line: total height = $0.822 \times \text{diameter} + 0.11$) and Queshque ($p < 0.001$, $R^2 = 0.89$, fitted line: total height = $0.918 \times \text{diameter} + 0.08$).

Another clear positive relationship was found for juveniles, subadult and adult plants from all three study areas combined between live and total rosette diameters (Fig. 3d; regression $p < 0.001$, $R^2 = 0.97$; fitted line: total rosette diameter = $1.131 \times \text{live rosette diameter} + 0.13$). Similar patterns were derived from each of the study areas independently: Pachapaqui ($p < 0.001$, $R^2 = 0.97$, fitted line: total rosette diameter = $1.037 \times \text{live rosette diameter} + 0.21$), Pumapampa ($p < 0.001$, $R^2 = 0.97$, fitted line: total rosette diameter = $1.138 \times \text{live rosette diameter} + 0.15$) and Queshque ($p < 0.001$, $R^2 = 0.95$, fitted line: total rosette diameter = $1.218 \times \text{live rosette diameter} + 0.09$).

For adult plants, the relationship between total height and height to the base of the spherical rosette was significant, but showed considerable variability (Fig. 3e; regression $p < 0.001$, $R^2 = 0.27$; fitted line: total height = $2.487 \times \text{height to the base of the spherical rosette} + 2.98$). For all three study areas combined, the spherical rosette lifted off the ground, on average, when the total plant height was 2.49 m (where height to the base of the spherical rosette = 0 in Fig. 3e, 95% confidence interval = 1.51–3.47 m).

Differences in *P. raimondii* allometric variables between study areas

The numbers of plants in each developmental stage varied considerably between study areas, so equal numbers of plants were selected at random for the statistical analyses reported here. Graphical comparisons of all the plants measured in each study area are provided in Online Resources 2–6.

Juvenile plants in Queshque were smaller than those in Pachapaqui and Pumapampa in all three dimensions compared. For total plant height, Queshque plants were shorter than those of Pachapaqui (Fig. 4a; Welch's ANOVA: $F_{2,49.7} = 10.28$, $p < 0.001$; Games-Howell pairwise test $p = 0.04$) and Pumapampa (Games-Howell pairwise test $p < 0.001$). Queshque plants were also smaller in total rosette diameter compared with Pachapaqui (Fig. 4b; Welch's ANOVA: $F_{2,49.8} = 12.38$, $p < 0.001$; Games-Howell pairwise test $p = 0.03$) and Pumapampa (Games-Howell pairwise test $p < 0.001$). Queshque plants were also smaller in live diameter than Pachapaqui (Fig. 4c; Welch's ANOVA: $F_{2,49.7} = 12.16$, $p < 0.001$; Games-Howell pairwise test $p = 0.04$) and Pumapampa (Games-Howell pairwise test $p < 0.001$).

Subadult plant dimensions were significantly smaller in Queshque compared with Pumapampa for total height (Fig. 5a; Welch's ANOVA: $F_{2,43.9} = 9.33$, $p < 0.001$; Games-Howell pairwise test $p < 0.001$) and stem height (Fig. 5b; Welch's ANOVA: $F_{2,45.5} = 6.40$, $p = 0.003$; Games-Howell pairwise test $p < 0.001$).

Queshque rosettes were smaller in total diameter than those from Pachapaqui (Fig. 5c; Welch's ANOVA:

$F_{2,42.3} = 11.93$, $p < 0.001$; Games-Howell pairwise test $p < 0.001$) and Pumapampa (Games-Howell pairwise test $p = 0.010$). The same pattern was found for live rosette diameter between Queshque and Pachapaqui (Fig. 5d; Welch's ANOVA: $F_{2,43.3} = 18.08$, $p < 0.001$; Games-Howell pairwise test $p < 0.001$) and Pumapampa (Games-Howell pairwise test $p = 0.002$).

There were only three adult plants in Queshque and they were not included in formal statistical comparisons with the other study areas. However, the three adult plants in Queshque were smaller than most adult plants in Pumapampa and Pachapaqui in terms of total height, stem height, total diameter and live diameter—a similar pattern to those found for juvenile and subadult plants (Fig. 6). Adult plants in Pumapampa and Pachapaqui were not statistically different for any of the measured dimensions ($n = 10$ for both areas; Fig. 6a, total height, Welch's $t_{17.9} = -0.02$, $p = 0.99$; Fig. 6b, stem height, Welch's $t_{18.0} = -0.38$, $p = 0.70$; Fig. 6c, height to base of spherical rosette, Welch's $t_{15.2} = -0.61$, $p = 0.55$; Fig. 6d, total rosette diameter, Welch's $t_{16.4} = -0.53$, $p = 0.60$; Fig. 6e, live rosette diameter, Welch's $t_{15.9} = -0.33$, $p = 0.75$).

Very few reproductive adult plants were present in the study area plots: twelve in Pumapampa, two in Queshque, and none in Pachapaqui. There were insufficient plants for meaningful statistical analyses. Reproductive adults from Pumapampa tended to be larger than those from Queshque in total plant height (mean $7.28 \pm$ standard deviation 1.60 m compared with 6.25 ± 0.68 m), inflorescence height (4.87 ± 1.67 m vs. 3.55 ± 0.13 m), rosette diameter (3.10 ± 0.60 m vs. 2.47 ± 0.37 m) and live rosette diameter (3.35 ± 0.75 m vs. 1.58 ± 0.32 m). However, the Pumapampa plants had comparatively shorter stems (2.41 ± 0.40 m vs. 2.71 ± 0.64) and less distance from the ground to the base of the spherical rosette (1.22 ± 0.47 m vs. 1.99 ± 0.55 m).

Senescent reproductive adult plants are compared in Fig. 7. No statistical comparisons were possible for Queshque ($n = 3$). Pumapampa plants, compared with ones from Pachapaqui, had longer inflorescences (Welch's $t_{141.0} = -2.46$, $p = 0.02$) and were taller overall (Welch's $t_{149.2} = -1.98$, $p = 0.05$), but there were no differences in stem height (Welch's $t_{153.4} = -1.07$, $p = 0.29$) or height to base of spherical rosette (Welch's $t_{143.9} = -0.55$, $p = 0.58$).

Environmental variables in each area

Approximately 55.4% of the variability in these variables was represented in the first two axes of the PCA (Fig. 8). The first axis was most strongly related to vegetation cover, the second to parent rock, large rocks and soil cover. Pumapampa tended to have taller vegetation with lower cover of large rocks while Queshque showed the opposite tendency. In general, however, all three study areas shared similar conditions, in terms of the variables estimated.

Discussion

The main contribution of this study is to provide the basis for a relatively easy-to-use developmental stage classification of *P. raimondii* plants in the field. Previous attempts to classify *P. raimondii* have used absolute measurements of plant parts (Miller and Silander 1991; Salazar Castillo and Villasante Benavides 2012; Zavaleta Zavaleta 2017; Prado-Aliaga et al. 2021; Suni et al. 2024), or overall plant size with reproductive status (Venero Gonzales 1984; Montesinos 2014; Aquino et al. 2018). To date, no classification system for *P. raimondii* has been based on morphological characteristics of developmental stages (except to distinguish reproductive plants from immature, vegetative ones). Our system does not depend on specific measurements of plant parts but is based entirely on developmental stages related to the development of the rosette, stem, and reproductive axis.

Classifying *P. raimondii* using developmental stages rather than specific size thresholds has several advantages. First, it is faster. Reducing time in the field is important in remote, rugged and high-altitude terrain with cold temperatures. Faster processing of individual plants increases the number of plants that can be classified in a given amount of time, providing richer data for plant abundance and density studies. In protected areas, where the impact of conservation management plans needs to be evaluated from time to time, it would be useful to know how many juveniles, subadults, adults and reproductive adults were present in population censuses, offering a more detailed view of population demography.

Secondly, for a monocarpic plant like *P. raimondii*, where investment of resources over the lifetime is vital, our developmental stage classification allows for comparisons of plant development in different contexts. For example, plants could be compared in different locations (similar to the current study, or across the species' geographical range of more than 11° of latitude). Plants could also be compared from different microsite contexts within the same location, linking landscape-scale and fine-scale environmental conditions to plant development. Such studies could consider plants of all developmental stages or focus on one particular stage. For example, our personal observations have suggested that juvenile plants survive and develop at different rates according to local microsite conditions, representing an important demographic filter that could have conservation applications.

Thirdly, our relatively quick classification would allow researchers to control more easily the numbers of plants in each developmental stage category to provide more powerful and robust statistical analysis.

An improvement to our current developmental stage system would be to subdivide the current juvenile category into two. At present, it covers a wide range of plants, some of which are newly germinated seedlings and very young plants that are most likely to die and others are well established plants growing towards the next developmental stage with a low probability of mortality. Distinguishing between vulnerable seedlings and very young plants, likely to die, and established juveniles that are likely to survive would improve the utility of our scheme.

Puya species are well known for producing large numbers of seedlings around parent plants soon after germination (Moscol Olivera and Cleef 2009; Garcia-Meneses and Ramsay 2014), but almost all of these do not survive long. In our study of *P. raimondii*, Queshque had many very young plants, skewing the comparisons at the juvenile stage. Most of the smaller juvenile plants were close to the remains of a

single mother plant, reflecting the large numbers of seeds produced by mother plants, estimated at several million (Zavaleta Zavaleta 2017). This is likely to be a common problem unless the classification system is modified. Unfortunately, in this study, we did not collect data that allowed us to distinguish between these two juvenile categories. From our personal observations, rosette diameter and plant height are unsuitable as distinguishing characteristics for distinguishing younger and more-established juvenile plants, because some recently-germinated rosettes have fewer, horizontal leaves and others have more numerous, vertical leaves. Thus, leaf density and leaf arrangement offer promising ways of distinguishing them, perhaps related to physical protection of the plant meristem, but it requires further investigation.

A classic problem when working with monocarpic plants, like *P. raimondii*, is whether plants develop according to a broadly similar temporal schedule aligned with absolute age or, instead, do they develop in accordance with the size of the plant independent of age (Burd et al. 2006). In the current study, we report wide ranges of sizes associated with each developmental stage, but we do not have information about the age of our plants. In future, studies could be specifically designed to track developmental stages of the same plants through time, with allometric measurement, to determine what drives developmental stage progression in these plants. This has been done in some monocarpic plants with useful insights into the ecology and conservation of those species (Holderegger 1997; Burd et al. 2006; Veldhuisen et al. 2022).

The total height of *P. raimondii* immature plants (juveniles, subadults and adults) is driven by increases in both rosette size (closely linked to leaf length) and stem height. Total rosette diameter and total height of *Puya* plants shows a linear relationship across the range of plant sizes. However, the relationship between stem and total height is non-linear, with a greater contribution of stem height to overall height growth in the majority of the subadult stage, between the appearance of the stem (on average when plants were 0.43 m tall in total) and reaching 2 m in total height. Within this size range, it is important to raise the apical meristem above the ground quickly to accommodate longer rosette leaves (and greater photosynthetic area). Another possibility is the increased water storage capacity afforded by additional stem height as protection against temporary or prolonged water stress (Males 2016; Chondol et al. 2024), as established for *Espeletia*, the other prominent group of Andean giant rosette plants (Goldstein et al. 1984).

Approximately 90% of total rosette diameter (or 95% of leaf length) was photosynthetically active (the live rosette diameter). This relationship held well across all rosette sizes. For a rosette of 0.5 m total diameter, this represents a loss of 0.04 m² of potential photosynthetic area, but represents a loss of 1.83 m² for a rosette with a total diameter of 3.5 m. Interestingly, Suni et al. (2024) observed significant decreases in photosynthetically active rosette area in drier-than-usual years, in ways that differed between young and older plants. Therefore, the relationship reported in the current study might differ from that found in other places, or even in the same places in years with different levels of precipitation. Indeed, this relationship could be a good indicator of local precipitation levels and water stress in *P. raimondii* plants, and merits further investigation.

The relationship between total plant height and the height to the base of the spherical rosette was relatively loose. This relationship depends on several different dimensions of plant size, each with their own inherent variability: total plant height, leaf lengths (reflected in rosette diameter), and stem height. Nevertheless, this relationship differed between the three locations in our study, with a clear contrast between the taller plants in Pumpampa and the shorter plants in Queshque. Combining the observations from all three locations, exposed stem or skirt first appeared in plants from 1.51–3.47 m (95% confidence interval), highlighting the variability in this feature of *P. raimondii* plants. Furthermore, periodic fires can burn away marcescent leaves (which form the base of the rosette as well as the hanging “skirt”). Burned plants will have a greater height to the base of the rosette for this reason.

In our comparison of the three locations with *P. raimondii* in Huascarán National Park, plants from Queshque tended to be smaller than ones from the other sites, across all developmental stages. In other words, plants from Queshque generally reached the developmental thresholds in our classification system at smaller sizes. Soil, vegetation and rock variables in the three locations did not explain this difference. Elevation, slope and aspect were also similar in the three locations. Mountainous terrain typically produces climatic differences over relatively short distances (Hoorn et al. 2018). Detailed climate data for the three locations does not exist, and it is not possible to rule out differences in water availability during the wet season, leading to different growth patterns for *Puya*. The Queshque population could differ genetically from the other populations, perhaps in response to local selection pressures there, or merely as a result of genetic drift associated with the founding plants in this location. This illustrates how our *P. raimondii* classification system can generate results that highlight patterns requiring further research. Comparisons with more *P. raimondii* populations across its range will show how variable size is in life stages and allow us to put the plants from Queshque into a wider context.

One problem we experienced in this study is the annual variability in *P. raimondii* flowering. In most years, very few or no plants reproduce, while in others many do (Hartmann 1981). There are clear evolutionary advantages to mass flowering events (Beck et al. 2024). Hartmann (1981) suggested that mass flowering was associated with drier years though Venero Gonzales (1984) did not observe more flowering in a dry year in the south of Peru. Regardless, our field visits during this study coincided with a year with very few reproductive plants to include in our analysis. If reproduction is triggered by somewhat periodic variations in climate, perhaps linked to the El Niño Southern Oscillation, we would expect to find a wide range of sizes associated with the reproductive adult stage in those years. Since we did not find many reproductive plants during our field visits, we were not able to test this hypothesis. Future studies could focus on this aspect of life history, however.

Conclusions

It was possible to classify *P. raimondii* plants into meaningful developmental stages without needing to make detailed measurements, using the form of the rosette, stem development, the growth of reproductive structures and the senescence of leaves. Our system can be used in a variety of different kinds of studies of this species to provide richer datasets without significant extra cost. However, a

modification to the juvenile category presented here would be useful in future, to separate vulnerable plants from more-established juveniles.

The Queshque population was clearly smaller than the other populations, across all the developmental phases. It is not clear what is responsible for this difference, but this illustrates the value of comparing developmental stages in different places to develop hypotheses and further studies, to expand our understanding of the ecology of this endangered plant and improve our plans to conserve it. We hope that our classification system (or modifications of it) will be employed across the geographical and ecological ranges of *P. raimondii* in future to gain further insights into the ecology of this important plant.

Declarations

Conflicts of interest/Competing interests

The authors have declared that no conflicts of interest or competing interests exist.

Acknowledgements

The authors would like to thank Karen Santisteban, Jean Salcedo, Mónica Arakaki, Susy Castillo and Kelly Huerta for their help in the field work, and Huascarán National Park for the use of their facilities in Pumapampa. This research was supported by the Universidad Nacional Mayor de San Marcos RR N°04274-R-17 and Project number B17100111. Huascarán National Park authorized the study (Resolución Jefatural de Parque Nacional Huascarán N°14-2017-SERNANP-JEF).

Availability of data and material

The datasets used in this study are available on Zenodo (DOI: 10.5281/zenodo.13357075).

References

1. Aquino W, Condo F, Romero J, Yllaconza R (2018) Distribución geográfica y poblacional de *Puya raimondii* Harms en el distrito de Huarochirí, Provincia de Huarochirí, Lima, Perú. *The Biologist* (Lima) 16: 25–33
2. Augspurger CK (1985) Demography and life history variation of *Puya dasylirioides*, a long-lived rosette in tropical subalpine bogs. *Oikos* 45:341–352. <https://doi.org/10.2307/3565569>
3. Beck JJ, McKone MJ, Wagenius S (2024) Masting, fire-stimulated flowering, and the evolutionary ecology of synchronized reproduction. *Ecology* 105:e4261. <https://doi.org/https://doi.org/10.1002/ecy.4261>
4. Bierzychudek P (2014) Plant biodiversity and population dynamics. In: Monson RK (ed) *Ecology and the Environment*. Springer New York, New York, NY, pp 29–65. doi: <https://doi.org/10.1007/978-1->

5. Burd M, Read J, Sanson GD, Jaffré T (2006) Age-size plasticity for reproduction in monocarpic plants. *Ecology* 87:2755–2764. [https://doi.org/10.1890/0012-9658\(2006\)87\[2755:APFRIM\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2755:APFRIM]2.0.CO;2)
6. Chondol T, Korznikov KA, Doležal J (2024) Ecological significance of marcescence in Himalayan plants: Why is standing dead phytomass more important in demanding, resource-limited environments? *Funct Ecol* 38:942–954. [https://doi.org/https://doi.org/10.1111/1365-2435.14513](https://doi.org/10.1111/1365-2435.14513)
7. Dávila B (2004) Evaluación ecológica y de conservación en los rodales de *Puya raimondii*. Huinipampa (Espinar-Cusco); y una propuesta para forjar valores y bienestar humano común. Universidad Nacional de San Agustín, Arequipa, Perú
8. Dorst J (1957) The *Puya* stands of the Peruvian high plateaux as a bird habitat. *Ibis* 99:594–599. <https://doi.org/10.1111/j.1474-919X.1957.tb03051.x>
9. Fortier RP (2024) Queen of the Andes: the ecology and conservation of *Puya raimondii*. *Front Conserv Sci* 5:6. <https://doi.org/10.3389/fcosc.2024.1349553>
10. Franco M, Silvertown J (2004) A comparative demography of plants based upon elasticities of vital rates. *Ecology* 85:531–538. [https://doi.org/https://doi.org/10.1890/02-0651](https://doi.org/10.1890/02-0651)
11. Garcia-Meneses PM, Ramsay PM (2014) *Puya hamata* demography as an indicator of recent fire history in the páramo of El Ángel and Volcán. *Ecuador-Colombia Caldasia* 36:53–69. <https://doi.org/10.15446/caldas.v36n1.43891>. Chiles
12. Goldstein G, Meinzer FC, Monasterio M (1984) The role of capacitance in the water balance of Andean giant rosette species. *Plant Cell Environ* 7:179–186. <https://doi.org/10.1111/1365-3040.ep11614612>
13. Hara T (1988) Dynamics of size structure in plant populations. *Trends Ecol Evol* 3:129–133. [https://doi.org/10.1016/0169-5347\(88\)90175-9](https://doi.org/10.1016/0169-5347(88)90175-9)
14. Hartmann O (1981) *Puya raimondii* Harms cada vez son menos. *Bol Lima* 10:79–83
15. Holderegger R (1997) Intrapopulation size structure of the monocarpic species *Saxifraga mutata* and its relationship to succession. *Flora* 192:151–156. [https://doi.org/https://doi.org/10.1016/S0367-2530\(17\)30770-3](https://doi.org/10.1016/S0367-2530(17)30770-3)
16. Hoorn C, Perrigo A, Antonelli A (eds) (2018) *Mountains, Climate and Biodiversity*. Wiley, Hoboken (NJ), USA
17. Hornung-Leoni C, Sosa V (2004) Uses of the giant bromeliad, *Puya raimondii*. *J Bromeliad Soc* 54:3–8
18. Hornung-Leoni CT, Gonzalez-Gomez PL, Troncoso AJ (2013) Morphology, nectar characteristics and avian pollinators in five Andean *Puya* species (Bromeliaceae). *Acta Oecol-Int J Ecol* 51:54–61. <https://doi.org/10.1016/j.actao.2013.05.010>
19. Lambe E (2009) *Puya raimondii*. The IUCN Red List of Threatened Species 2009: e.T168358A6482345. <https://doi.org/10.2305/IUCN.UK.2009-2.RLTS.T168358A6482345.en>

20. Leiva GS, Tellez AC, Lezama AP (1991) *Puya raimondii*: una espectacular forma vegetal. *Arnaldoa* 1:93–100
21. List R, Rodríguez P, Pelz-Serrano K, Benítez-Malvido J, Lobato JM (2017) La conservación en México: exploración de logros, retos y perspectivas desde la ecología terrestre. *Rev Mex Biodivers* 88:65–75. <https://doi.org/https://doi.org/10.1016/j.rmb.2017.10.007>
22. Lounibos F (2009) Insects and allies associated with bromeliads: a review. *Terr Arthropod Rev* 1:125–153. <https://doi.org/10.1163/187498308X414742>
23. Males J (2016) Think tank: water relations of Bromeliaceae in their evolutionary context. *Bot J Linn Soc* 181:415–440. <https://doi.org/https://doi.org/10.1111/boj.12423>
24. Miller GA, Silander JA Jr (1991) Control of the distribution of giant rosette species of *Puya* (Bromeliaceae) in the Ecuadorian páramos. *Biotropica* 23:124–133. <https://doi.org/10.2307/2388297>
25. Montesinos D (2014) Inventario y estado de conservación de *Puya raimondii* (Bromeliaceae) en el departamento de Moquegua, Perú. *Chloris Chilensis* 17:1–9
26. Mora F, Chaparro HA, Bonilla MA, Vargas O (2005) Rasgos de la historia de la vida de *Puya cryptantha*, una bromelia monocárpica perenne. In: Bonilla MA (ed) Estrategias adaptativas de plantas del páramo y del bosque altoandino en la Cordillera Oriental de Colombia. Universidad Nacional de Colombia, Bogotá, pp 289–306
27. Mora F, Chaparro HA, Vargas O, Bonilla MA (2007) Dinámica de la germinación, latencia de semillas y reclutamiento de plántulas en *Puya cryptantha* and *P. trianae*, dos rosetas gigantes de los páramos colombianos. *Ecotropicos* 20:31–40
28. Moscol Olivera MC, Cleef AM (2009) A phytosociological study of the paramo along two altitudinal transects in El Carchi province, northern Ecuador. *Phytocoenologia* 39:79–107. <https://doi.org/10.1127/0340-269x/2009/0039-0079>
29. Patil I (2021) Visualizations with statistical details: The 'ggstatsplot' approach. *J Open Source Softw* 6. <https://doi.org/10.21105/joss.03167>
30. Prado-Aliaga GE, Salcedo-Aliaga JC, Vicuña-Zevallos WW, Mery L, Suni-Ninataype ML (2021) Las poblaciones de *Puya raimondii* de la provincia de Chupaca, Junín, Perú: propuesta de un método de delimitación espacial y evaluación del estado actual. *Chloris Chilensis* 24:94–118
31. R Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, URL. <https://www.r-project.org/>
32. Raimondi A (1874) El Perú, Tomo I. Imprenta del Estado, Lima
33. Rees WE, Roe NA (1980) *Puya raimondii* (Pitcairnioideae, Bromeliaceae) and birds: an hypothesis on nutrient relationships. *Can J Bot* 58:1262–1268. <https://doi.org/10.1139/b80-157>
34. Rivera CCA (1985) *Puya raimondii* Harms. *Bol Lima* 7:85–91
35. Rocha J (2023) Neotropical bromeliads as food sources for birds: a systematic review and perspectives on the management of ecological interactions. *Ibis* 165:17–33.

<https://doi.org/10.1111/ibi.13138>

36. Salazar Castillo J, Cáceres de Baldarrago F, Poma I (2011) *Puya raimondii*, The Queen of the Andes. Cactus Co 15:28–51
37. Salazar Castillo J, Villasante Benavides F (2012) Distribución geográfica y situación actual de *Puya raimondii* Harms en la región de Arequipa, Perú, Octubre 2009 – Marzo 2011. Quad Bot Amb Appl 23: 31–39
38. Salinas L, Arana C, Suni M (2007) El néctar de especies de *Puya* como recurso para picaflores Altoandinos de Ancash, Perú. Rev Peru Biol 14:129–134
39. Shoobridge D (2005) Parque Nacional Huascarán. ParksWatch – Perú, Lima
40. Suni ML, Vadillo GP, Arana C, Jara-Peña E, Salinas L, Ponce ME, Ramsay PM (2024) Post-fire recovery of *Puya raimondii*, vegetation and birds in the puna of Huascarán National Park, Perú. J Mt Sci 21:20–32. <https://doi.org/10.1007/s11629-023-8263-7>
41. Tomita M, Okuda K, Wada H, Masuzawa T, Ohta T, Nakamura T (2011) Examination of method for estimating growth age of herbaceous plants, using the century plant *Puya raimondii* [Original in Japanese]. Nagoya Univ Accelerator Mass Spectrometer Perform Rep 22:187–189
42. Vadillo Gálvez GP (2011) Bases para la conservación de *Puya raimondii* Harms (Bromeliaceae). MSc. Universidad Nacional Mayor de San Marcos, Lima
43. Veldhuisen L, Garcia Lino MC, Bodine E, Aguirre-Santoro J, Jabaily R (2022) Description of life history and reproductive size thresholds in three high elevation *Puya* (Bromeliaceae). bioRxiv: 2022.2002.2018.480924. <https://doi.org/10.1101/2022.02.18.480924>
44. Venero Gonzales JL, Hostning R (1986) Las Titancas de Aymaraes (Apurímac). Bol Lima 48:83–88
45. Venero Gonzales L (1984) El rodal de *Puya raimondii* en Lares- Calca. Bol Lima 31:84–91
46. Venero Gonzales L (2001) *Puya raimondii* en ESPINAR-CUSCO. Biota 18:37–42
47. Villiger F (1981) Rodales de *Puya raimondii* y su protección. Bol Lima 2:84–91
48. Waite BH (1978) *Puya raimondii*. wonder of the Bolivian Andes. J Bromeliad Soc 28:200–208
49. Zavaleta Zavaleta EH (2017) *Puya raimondii* Harms del Santuario Nacional Calipuy, La Libertad. Revista de Glaciares y Ecosistemas de Montaña 3:113–119

Figures

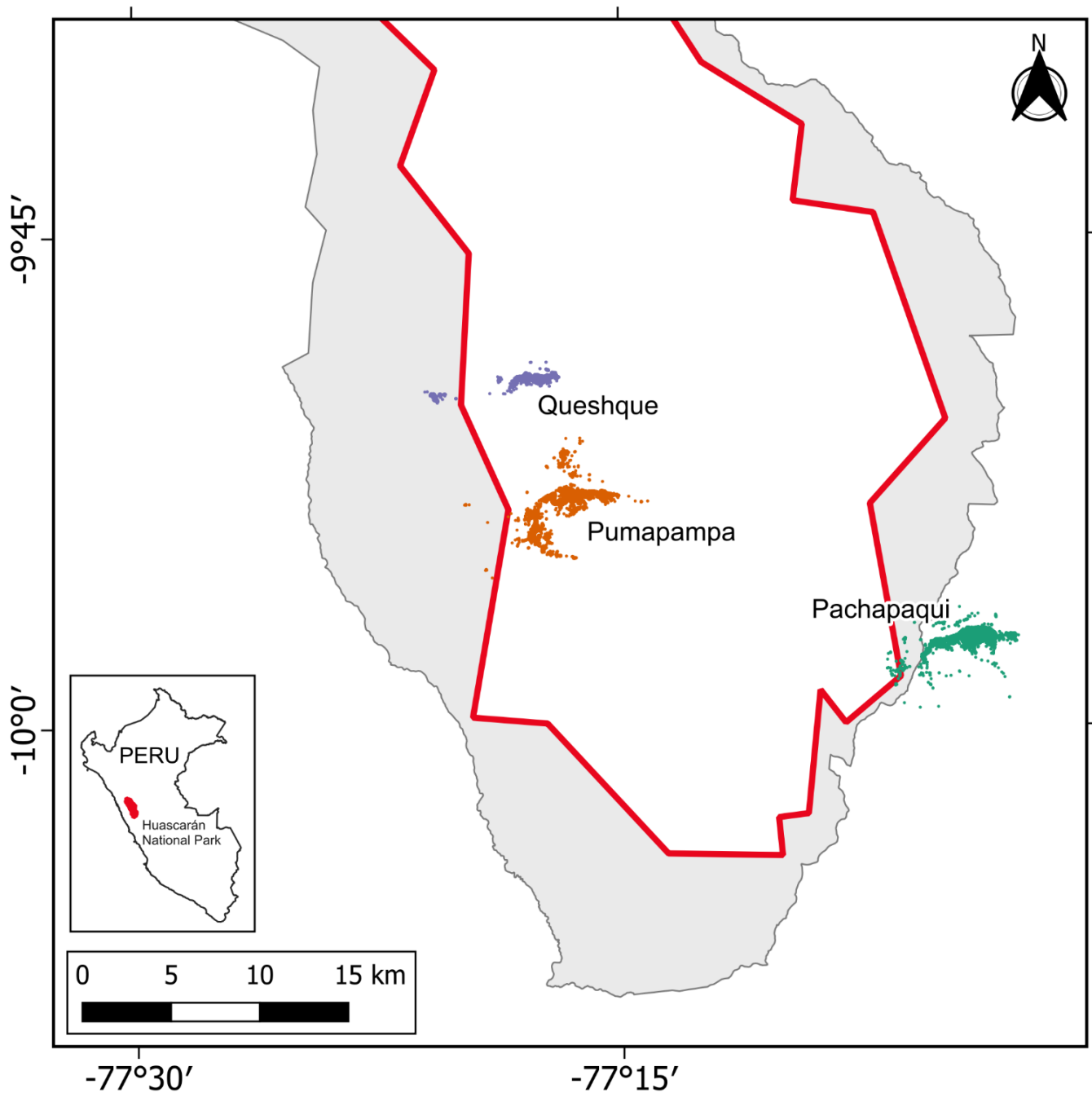


Figure 1

Location of the three study locations of *Puya raimondii* plants within Huascarán National Park, Perú. The colours of the study locations correspond to the colours used in later figures. The southern part of the national park's boundary is shown in red, with the grey buffer zone surrounding it. The inset map shows the location of the park within Perú.

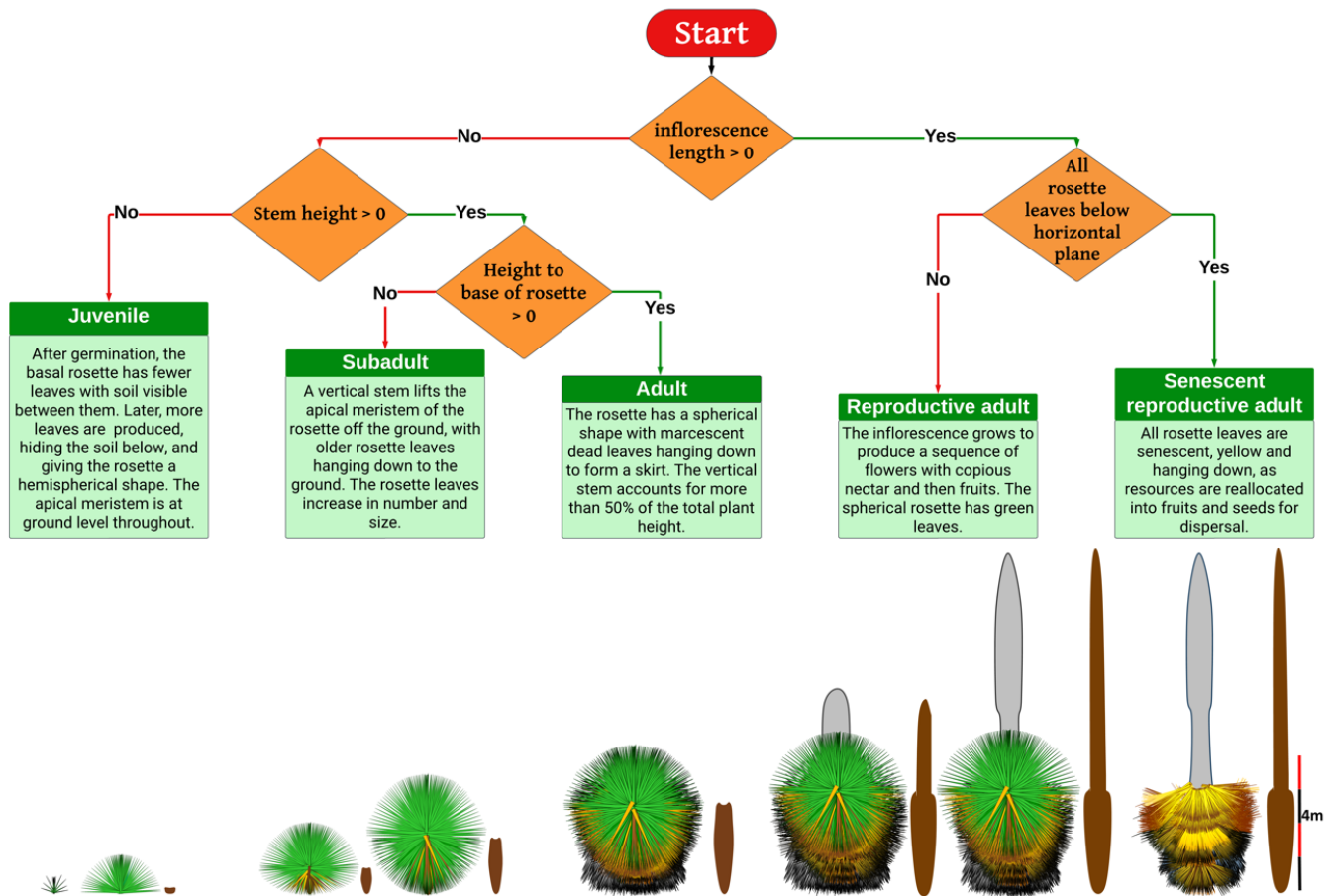


Figure 2

Key to *P. raimondii* developmental stage categories. Transitions between stages are marked by the form of the rosette (hemispherical or spherical, the presence of a skirt of marcescent leaves, orientation of leaves) and the growth of the stem and inflorescence. Completely dead plants (all plant parts very dark, almost black) were not included in the developmental stage categories, though they can remain standing for several years after death.

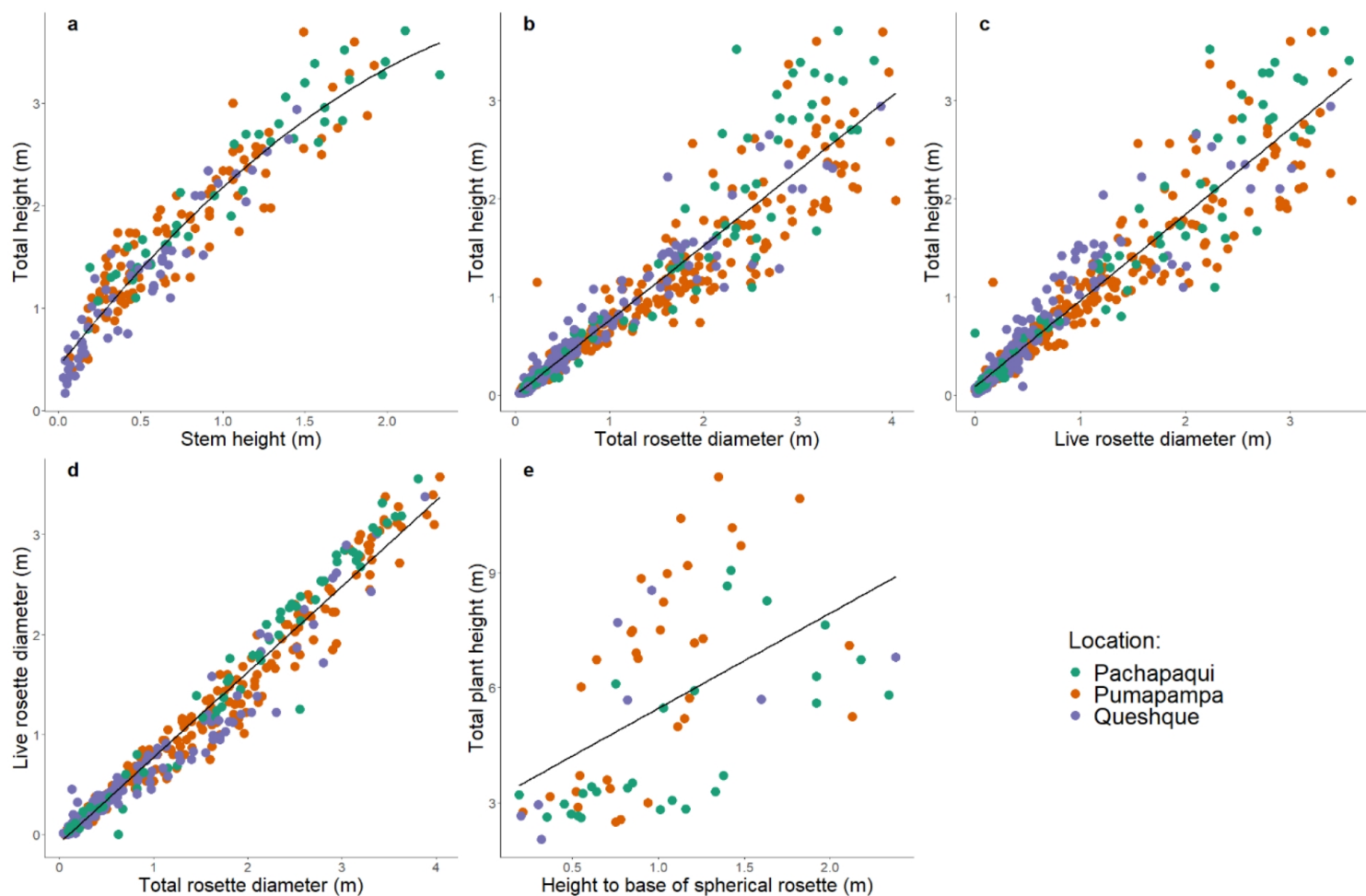


Figure 3

Relationships between dimensions of *P. raimondii* plants in three locations. **a.** Stem height and total plant height. **b.** Total rosette diameter and total plant height. **c.** Live rosette diameter and total plant height. **d.** Total rosette diameter and live rosette diameter. **e.** Height to base of spherical rosette and total plant height. Plants with inflorescences and infrutescences were excluded from these analyses.

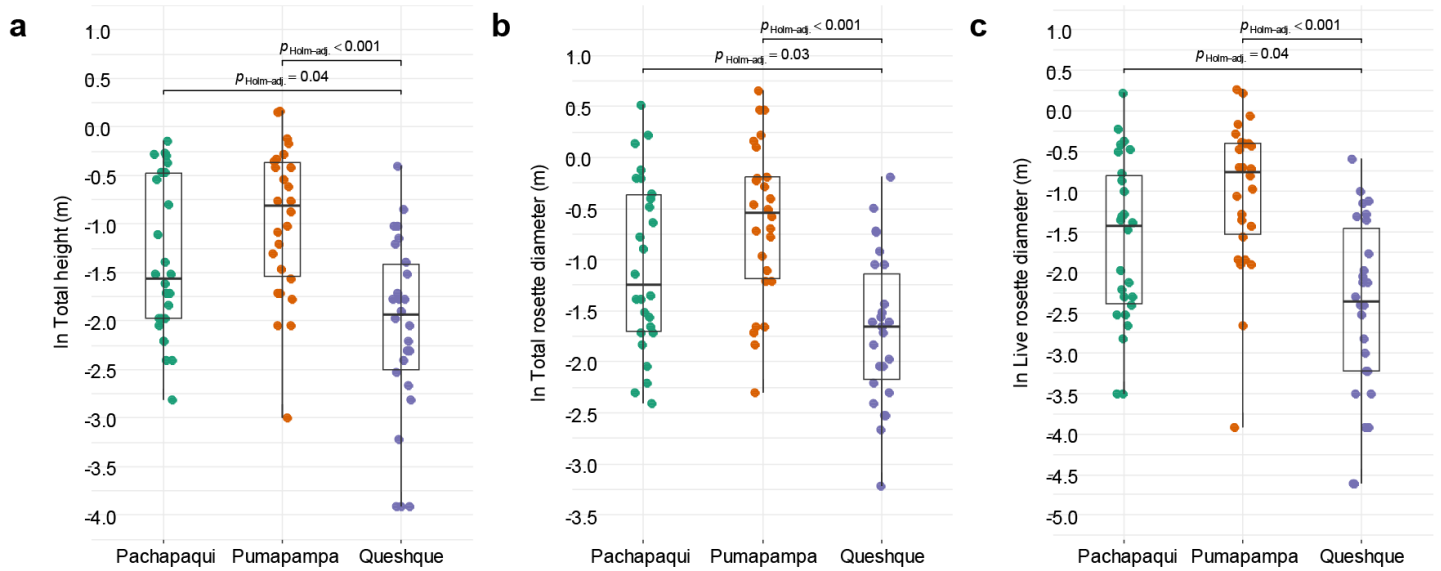


Figure 4

Comparisons of the juvenile developmental stage of *P. raimondii* plants between the three study areas. **a.** Total plant height. **b.** Total rosette diameter. **c.** Live rosette diameter. $n = 26$ in all study areas. All the datasets were transformed to natural logarithms (ln). Significant differences are shown, and all other pairwise comparisons were not significant. The whiskers show 95% confidence ranges.

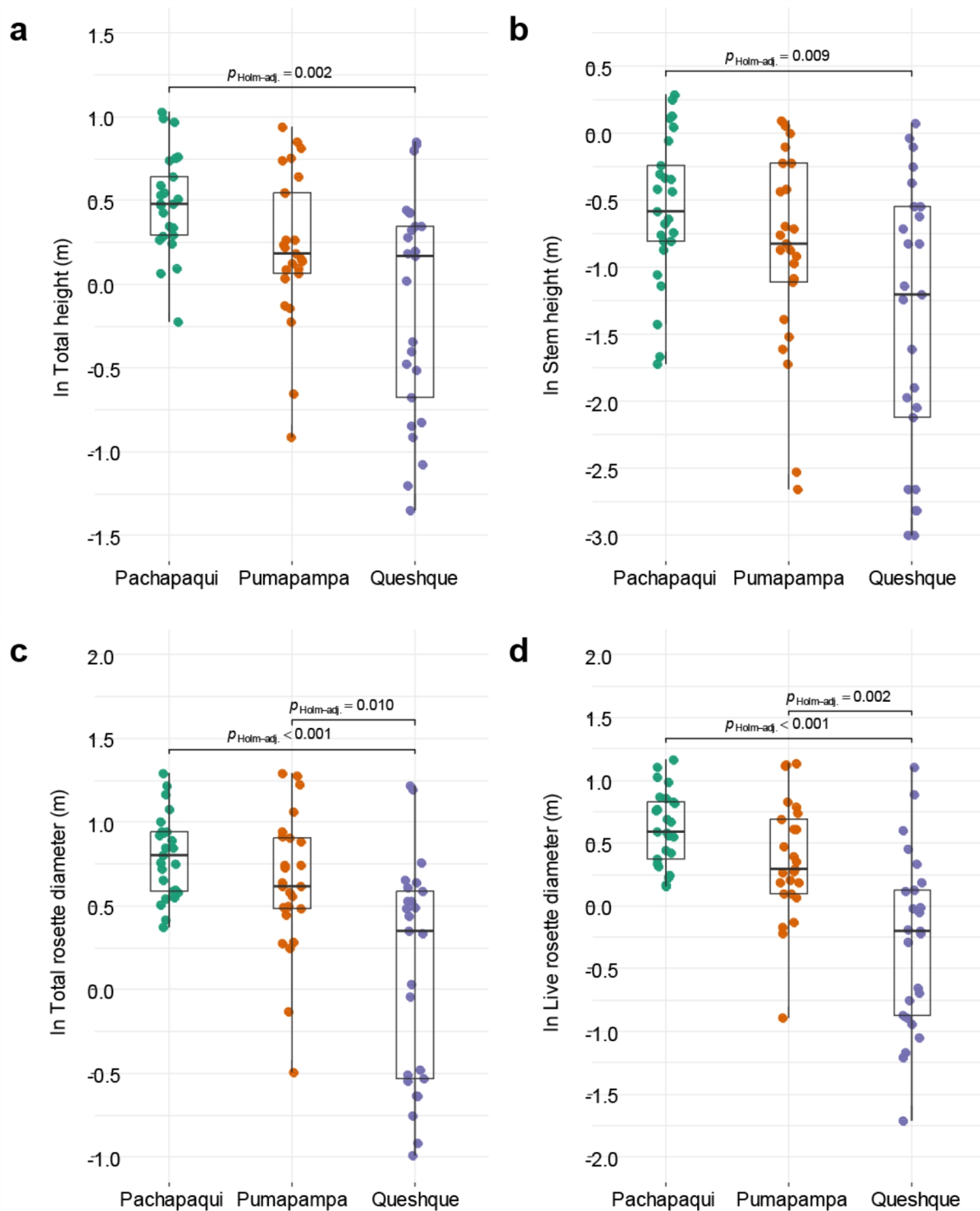


Figure 5

Comparisons of the subadult developmental stage of *P. raimondii* plants between the three study areas. **a.** Total plant height. **b.** Stem height. **c.** Total rosette diameter. **d.** Live rosette diameter. $n = 25$ in all study areas. All the datasets were transformed to natural logarithms (ln). Significant differences are shown, and all other pairwise comparisons were not significant. The whiskers show 95% confidence ranges.

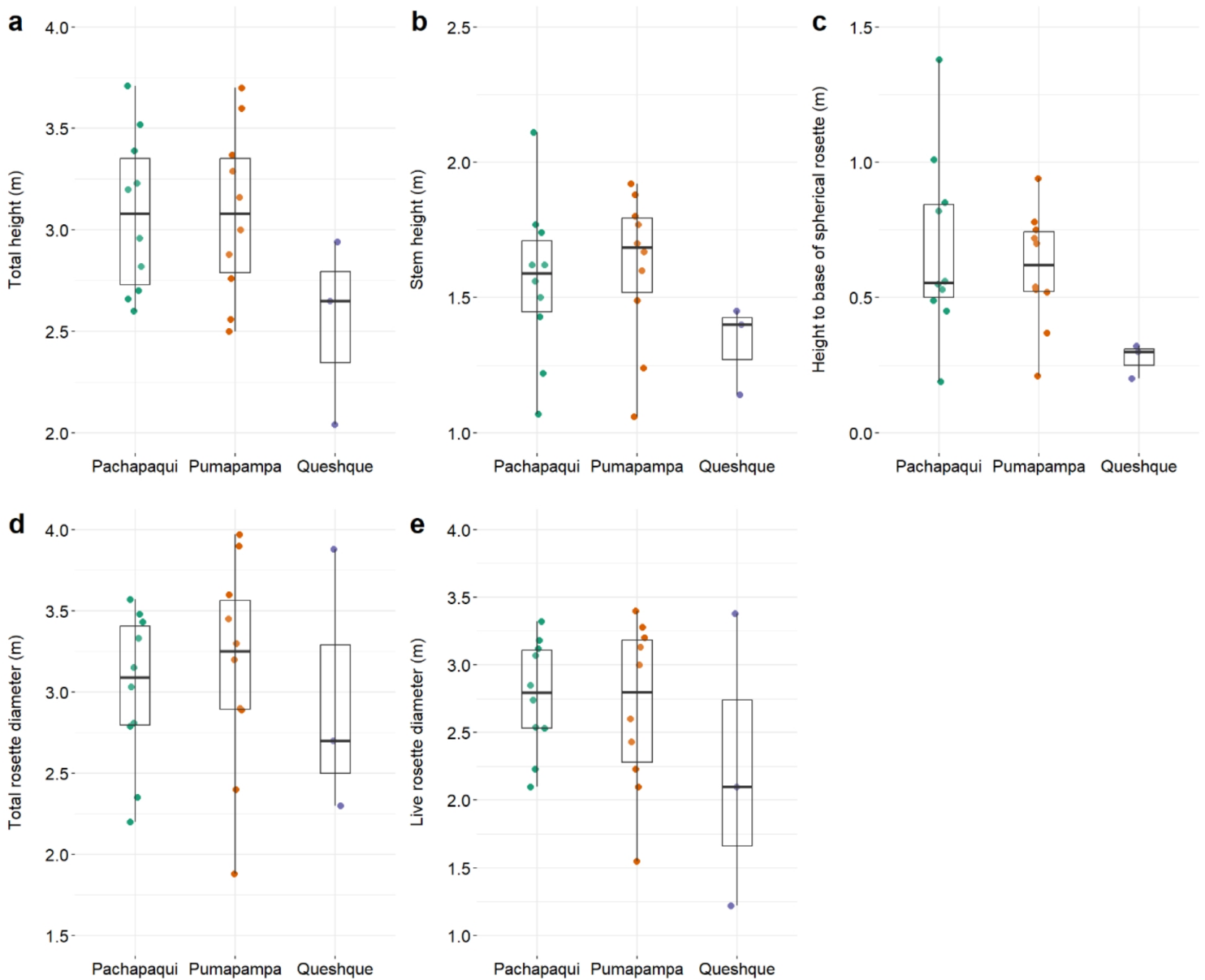


Figure 6

Comparisons of the adult developmental stage of *P. raimondii* plants between the three study areas. **a.** Total plant height. **b.** Stem height. **c.** Height to base of spherical rosette. **d.** Total rosette diameter. **e.** Live rosette diameter. $n = 10$ for Pumapampa and Pachapaqui; Queshque is included for qualitative comparison, but was not included in statistical tests because only three adults were measured there. No significant differences between Pumapampa and Pachapaqui were found in any of the plant measurements. The whiskers show 95% confidence ranges.

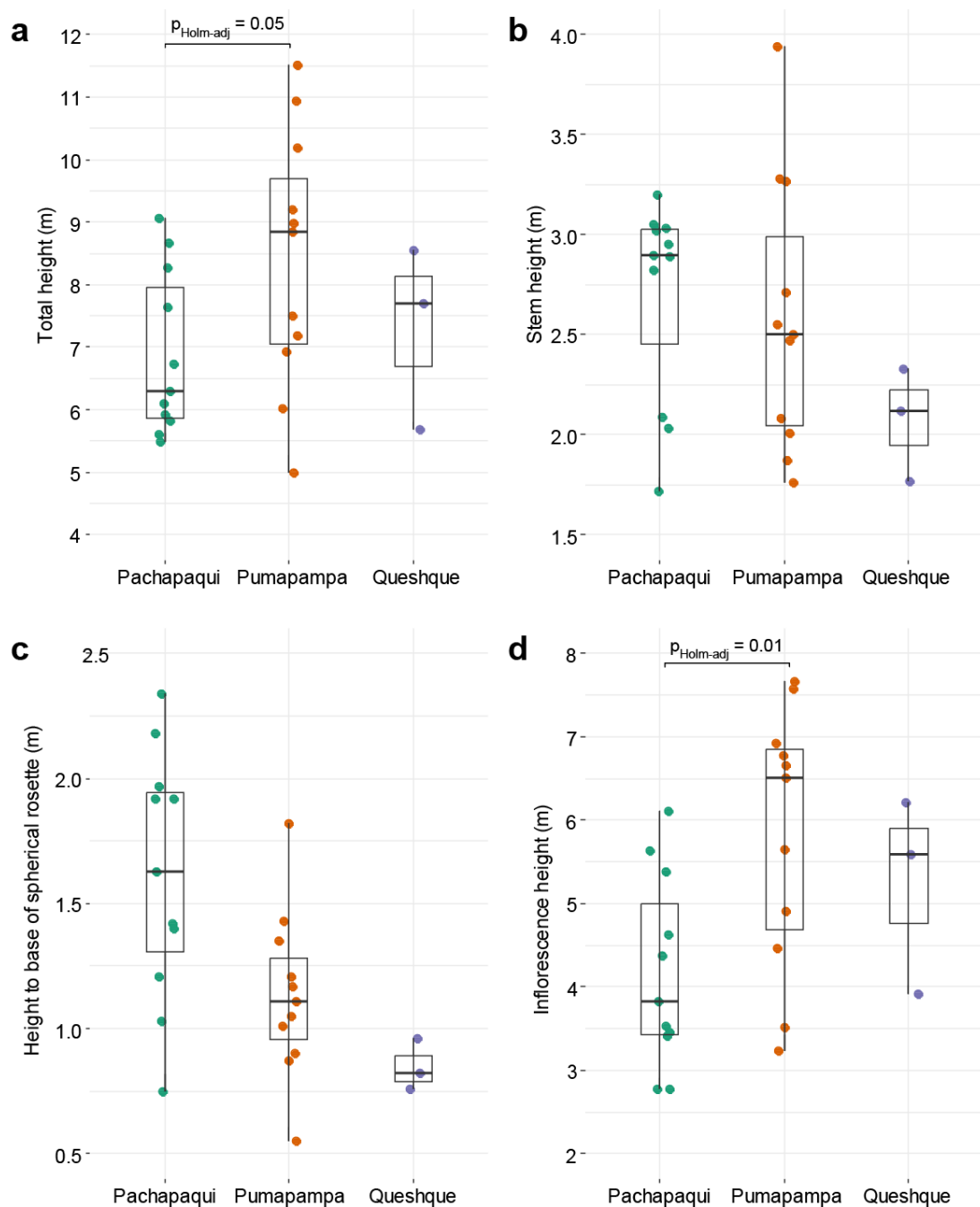


Figure 7

Comparisons of the senescent reproductive adult developmental stage of *P. raimondii* plants between the three study areas. **a.** Total plant height. **b.** Stem height. **c.** Height to base of spherical rosette. **d.** Inflorescence height. $n = 11$ for Pumapampa and Pachapaqui; Queshque is included for qualitative comparison, but was not included in statistical tests because only three adults were measured there. The whiskers show 95% confidence ranges.

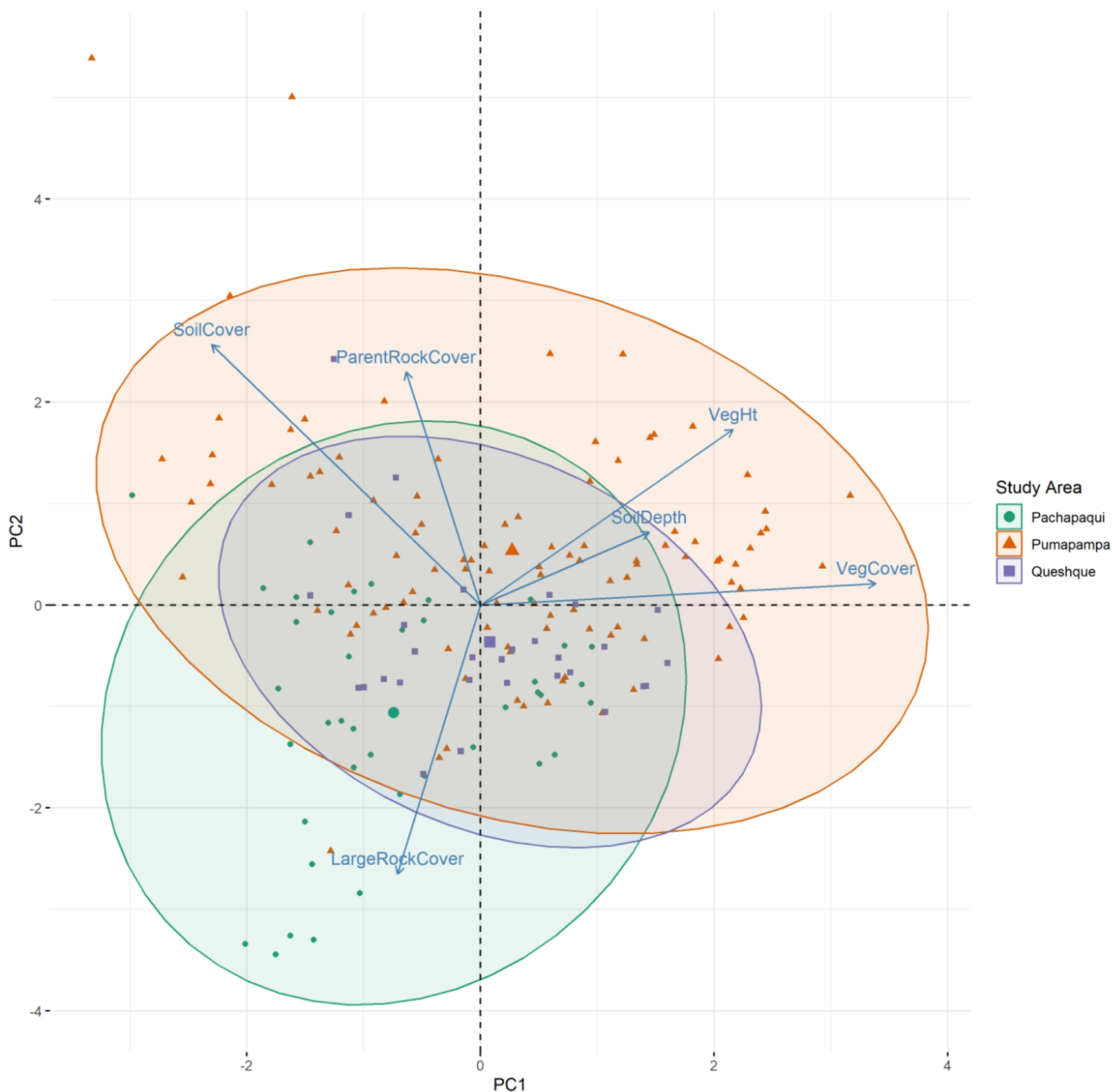


Figure 8

Principal Components Analysis of cover, soil depth and vegetation height estimates in plots from the three study areas. Arrows represent the variables and the points represent samples. Longer arrows explain more of the variance, and points closer together are more similar in the values of the variables found there. For each study area, the single larger symbol represents the centroid of all the samples found there. Variable labels: ParentRockCover = Percentage cover of parent rock; LargeRockCover = Percentage cover of rocks greater than 20 cm across; SoilCover = Percentage cover of soil and stones <

20 cm across; VegCover = Percentage cover of vegetation; SoilDepth = Depth of soil to rock below; VegHt = Height of vegetation.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryInformationAlpineBotany.docx](#)