

Vegetation of Andean wetlands (*bofedales*) in Huascarán National Park, Peru

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SUMMARY

Hybrid terrestrial-aquatic ecosystems in the Andes, commonly known as *bofedales*, consist of both peatlands and wet meadows and line valley floors at elevations > 3800 m. Compared with similar ecosystems at lower altitudes and higher latitudes, the ecosystem processes and spatial patterns of *bofedales* are only just beginning to be understood. The research presented here provides the first exploratory and descriptive analysis of the biodiversity and place-to-place variation of vegetation in *bofedales* in three valleys inside Peru's Huascarán National Park. Through vegetation surveys, we recorded 112 plant species in 29 families. Over a short geographical distance, a valley-to-valley comparison showed high dissimilarity in terms of species composition. Based on dominant life form and species composition, vegetation in *bofedales* can be grouped into five assemblages. Our preliminary analysis suggests that several abiotic factors could influence the floristic composition of *bofedales*: elevation, bulk density, percent organic matter, and cation exchange capacity. The findings of high valley-to-valley variation in species, soil and elevation influences may be useful to land managers of high mountain landscapes that are undergoing transformation related to glacier recession. While our findings advance research on tropical Andean *bofedales*, they also highlight the need for additional comprehensive investigations to fill gaps in knowledge about the tropical mountains of Latin America.

KEY WORDS: mountain peatlands, plant diversity, puna, tropical Andes

INTRODUCTION

Tropical high-altitude wetlands, consisting of peatlands and wet meadows, occur in the mountains of East Africa, New Guinea, Hawaii, and in the Andes from Venezuela to Peru. Known in the Andes as *bofedales*, *oconales*, *humedales*, or *turberas* (and hereafter referred to as *bofedales*, singular *bofedal*), these ecosystems can form peat deposits up to 10 m thick (Hribljan *et al.* 2015). Mountain wetlands can function as carbon sinks or sources and they transport and filter nutrients (Charman 2002, Chimner & Karberg 2008, Cooper *et al.* 2015, Hribljan *et al.* 2015, Hribljan *et al.* 2016). Soil carbon content in *bofedales* may be low, and in these cases, they are referred to as wet meadows because the soil is more mineral-rich (Cooper *et al.* 2010). A series of recent publications highlight the ecosystem services provided by tropical high-altitude wetlands (Buytaert *et al.* 2011, Valencia *et al.* 2013, Benavides 2014, Maldonado Fonkén 2014, Salvador *et al.* 2014, Cooper *et al.* 2015, Izquierdo *et al.* 2015, Cochi Machaca *et al.* 2018). The ecosystems store precipitation and groundwater in the soil (Harden 2006, Gordon *et al.* 2015) and regulate the release of

stored water seasonally (Buytaert *et al.* 2006), thus buffering against low stream discharge during the dry season. For example, dry-season baseflow in the upper Marañon river, a major tributary of the Amazon, consists of groundwater released by *bofedales* (Hill *et al.* 2018). In the high Andes, plant species endemism is common and diverse communities of plants, invertebrates and birds are characteristic (Coronel *et al.* 2007, Zinck 2011, Gibbons 2012, Scheibler *et al.* 2016). The research we present is relevant to peatland and wetland scientists working in pan-tropical high-altitude ecosystems because it provides the first exploratory and descriptive analysis of the biodiversity and place-to-place variation of vegetation in *bofedales* at the scale of Peru's Huascarán National Park.

Huascarán National Park (HNP) encompasses much of the Cordillera Blanca, a mountain range with the highest density of tropical glaciers globally (Kaser *et al.* 1990). Glacier retreat is well-documented in the area (Silverio & Jaquet 2005, Racoviteanu *et al.* 2008, Autoridad Nacional del Agua, Unidad de Glaciología 2013, Burns & Nolin 2014). In 1970, total glacier area in the Cordillera Blanca was 721 km². By 2016, total glacier area was

449 km² (Silverio & Jaquet 2017). Changes in the cryosphere are cascading downslope, affecting hydrology, ecology and social systems (Carey *et al.* 2014, Gordon *et al.*, 2015, Mark *et al.* 2017). Spatio-temporal changes of *bofedales* have been documented: in HNP they are experiencing shrinkage, fragmentation and perforation, three transformations that could have negative ecological consequences (Young *et al.* 2011, Polk *et al.* 2017). Glacier recession has also been linked to ecological succession: as ice melts, plants colonise newly open substrates (Young *et al.* 2017). Predictions suggest that decreased annual rainfall associated with climate change could result in loss of *bofedales* (Otto & Gibbons 2017).

Given these spatio-temporal changes and the effects of glacier retreat, our aim was to complete an exploratory evaluation of vegetation in *bofedales* in HNP. Before our work, David N. Smith studied all flora in HNP in coordination with a 1984 Missouri Botanical Garden project. According to Smith (1988), previous taxonomic work had occurred north of the equatorial Andes, but HNP was representative of a variety of high mountain vegetation in Peru that had not yet been inventoried. In addition to Smith's work, there is only one field guide for the region's flora and it is specific to the Conchucos valley on the east side of the park (Cano *et al.* 2006). The work by Ramírez Huaroto (2011) is for the *bofedales* adjacent to Conococha, a lake south of the HNP boundary. Prior to this study, there was no detailed inventory of flora for *bofedales* in the park.

In addition to the lack of an inventory, there are no published data on plant assemblages in *bofedales* in HNP, or plant species that tend to occur in association. Smith (1988) observed that cushion plants in HNP are in the Cyperaceae, Asteraceae, and Poaceae families, but he did not complete quantitative characterisations of wetland plant groups in HNP. Building on the work of Weberbauer (1945), Maldonado Fonkén (2014) proposed that plant species in Peruvian *bofedales* can be categorised into four groups: *Distichia*-dominated peatlands, peatlands with mosses and shrubs, peaty meadows, and grass-dominated streamside wetlands. Maldonado Fonkén (2014) incorporated observations from across Peru with the exception of the department of Ancash, where HNP is located. Therefore, we wanted to examine whether or not these same assemblages exist in HNP. Furthermore, we expected that there would be more similarities than dissimilarities in *bofedal* vegetation from valley to valley because the geographical distances between park valleys are short.

While plant inventories, plant assemblages and

valley-to-valley comparisons are lacking, there is a body of work on the associations between *bofedal* vegetation composition and environmental gradients. Broadly, variation in wetland vegetation composition can be explained by two environmental gradients: a) variation in wetness and soil aeration, and b) variation in pH, base richness and nutrient availability (Rydin & Jeglum 2013). However, in mountains, elevation (altitude) is also a factor. A review of the literature on factors influencing vegetation variation in *bofedales* illustrates that there is no consensus on which factors predominate. Instead, complex combinations of gradients are at work and vary across the Andes. In the Colombian páramo, Bosman *et al.* (1993) found that peat thickness, nitrogen and iron concentrations, electrical conductivity and pH explained vegetation composition. Another study from the Colombian páramo pointed to elevation, precipitation, and pH gradients (Benavides & Vitt 2014). Biotic variables such as grazing, animal seed dispersal and human impacts (drainage channels, agricultural activity) have also played a role in shaping vegetation composition (Benavides 2014, Squeo *et al.* 2006, Tovar *et al.* 2012). Two studies from Peru north of HNP in the *jalca* (tropical high-altitude grasslands dominated by tussock-forming species) found different factors controlling vegetation. For example, Cooper *et al.* (2010) reported that floristic composition is driven by groundwater chemistry (HCO₃ and pH) and a complex gradient of hydrological factors, soil temperature and peat thickness. Tovar *et al.* (2012) identified pH, elevation and wetland patch size to be the controlling factors. High acidity has been documented in HNP: > 70 % of stream samples collected in one valley were pH < 4; receding glaciers exposed sulphide-rich rocks that change stream biochemistry (Fortner *et al.* 2011). Given these previous findings, our intent was to explore which abiotic factors might be associated with *bofedal* vegetation composition variability in the study area. Based on the work by Tovar *et al.* (2012) and Cooper *et al.* (2010), we hypothesised that elevation and pH would be relevant to *bofedal* vegetation composition variability.

Our research had four objectives that were intended to provide an initial, exploratory understanding of *bofedal* vegetation in HNP: 1) compile a floristic inventory for HNP *bofedales* in three valleys; 2) determine similarities and dissimilarities among the *bofedales* in the three valleys based on diversity, elevation and vegetation height; 3) distinguish plant assemblages; and 4) identify possible abiotic factors associated with *bofedal* vegetation composition.

METHODS

Study area

The study area is within the boundaries of Peru's Huascarán National Park in three valleys: Llanganuco, Quilcayhuanca and Carhuascancha (Figures 1, 2). The park is a UNESCO Biosphere Reserve measuring 3400 km² and the altitude range is ~3500–6768 m a.s.l. Oriented on a northwest-southeast axis, the park is transected by valleys that are perpendicular to the axis. These valleys were formed by uplift, glacial scouring and fluvial erosion; processes that continue to be active today. The climate is dominated by tropical wet-dry seasonality. Approximately 90 % of precipitation occurs during the wet season (between October and April), when the Intertropical Convergence Zone (ITCZ) is in its southerly position. The remainder occurs during the dry season (from May to September), when the ITCZ is in its northerly position (Kaser *et al.* 2003). There is a north-south precipitation gradient across the study area; the northern section of HNP receives 770 mm year⁻¹, whereas the southern section receives

470 mm year⁻¹ (Vuille *et al.* 2008). The annual temperature range is 0–14° C at 3955 m.a.s.l. and, as is typical for the tropics, the daily temperature variation is greater than annual variation (Kaser *et al.* 1990).

The park is in the northernmost humid puna (*puna húmeda*), a high Andean ecosystem located between the wetter *páramo* to the north and the drier puna to the south (Young *et al.* 1997, Troll 1968). Vegetation cover is heterogeneous and is composed of bunch grasses, forest patches of *Polylepis*, *Buddleia* and *Gynoxis*, and 1–2 m tall shrublands. Ground cover above 5000 m a.s.l. consists of scree, barren rock, snow and ice. *Bofedales* line the valley floors, occurring primarily on flat areas and gentle slopes, but some smaller *bofedales* were observed on slopes of 20–26°. HNP is a protected area, yet land use inside the park boundaries includes pastoralism, ecotourism and other recreational uses (Gilbert 2015). Livestock grazing occurs throughout the park and is a permitted use; local residents have historically used the park as pasture for their cattle, sheep and horses (Lipton 2014).

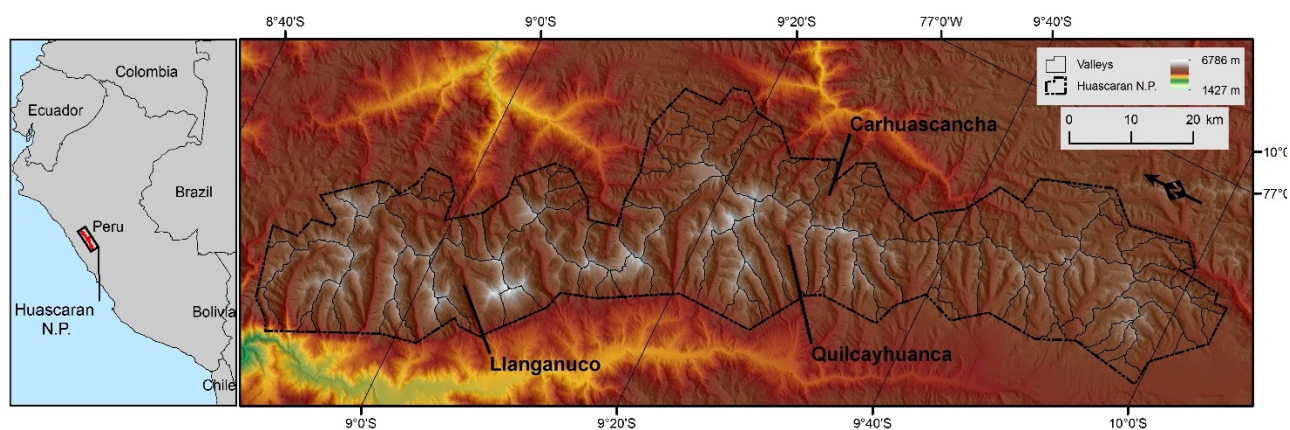


Figure 1. Location of Huascarán National Park in Peru and the three valleys where fieldwork occurred within the park: Llanganuco, Quilcayhuanca, and Carhuascancha.



Figure 2. Images of the three valleys where fieldwork occurred: Llanganuco (left), Quilcayhuanca (centre), and Carhuascancha (right).

Data collection

Data collection occurred in three valleys, Llanganuco, Quilcayhuanca, and Carhuascancha (Figures 1, 2). We strategically selected these valleys because they represent a range of relevant environmental variables at the scale of the park, namely: size, elevation, percent glaciated, location and drainage basin (Table 1). The distances from valley centre to valley centre are: Llanganuco to Quilcayhuanca 52 km, Llanganuco to Carhuascancha 55 km, and Carhuascancha to Quilcayhuanca 11 km. Fieldwork was conducted during the dry season (June and July in 2012, 2013 and 2014) when the study area is physically accessible. Intra-annual changes in vegetation composition are minimal and unlikely to complicate the analyses. A total of 65 sample sites were randomly selected and stratified by elevation; the number of quadrats varied by valley (Table 1). Pairs of 2 m × 2 m quadrats were placed in a homogeneous *bofedal* patch. *Sphagnum* is rare in HNP and uncommon in the tropical Andes (Earle *et al.* 2003, Maldonado Fonkén 2014); therefore, we focused on vascular plants (during fieldwork we observed *Sphagnum* only once in a <1 m² patch). Species data for plants were collected in every quadrat and included botanical name, height and name of tallest species. Percent cover using the Domin scale (Kent 2012) was estimated by consensus of the four researchers. Unknown specimens were verified against voucher specimens at the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos in Lima, Peru. In each quadrat pair, we collected the following environmental variables: location, elevation, slope, aspect, peat depth and wetness index. The wetness

index was adapted from Lemly & Cooper (2011) and ranged from 1 to 4 where 1 = saturated soil, hummocks, and no standing water; 2 = saturated soil, no standing water; 3 = <25 cm standing water depth; 4 = dry soil. Peat depth was measured with a 1 cm (3/8 inches) diameter steel tile probe (in 1 m rod lengths with 1 m attachable extensions) that was pushed into the peat soil until an impenetrable gravel or rock layer was encountered.

Soil analysis

A one-kilogram soil sample was collected in each quadrat pair at 10 cm depth. Soil analysis occurred at the Laboratorio de Suelos at the Universidad Nacional Agraria La Molina in Lima. The following chemical and physical factors were analysed: pH, percent organic matter (OM), phosphorus (dissolved), potassium (dissolved), textural class, cation exchange capacity (CEC) and bulk density (Table 2). Bulk density is commonly measured by dividing dry soil mass by total volume of the original sample, but the paraffin clod method was used by La Molina; the results from these two methods are generally similar (Campbell & Henshall 2000).

Vegetation analyses

Following fieldwork and soil analysis, we prepared the data for the vegetation analyses (summary statistics in Tables 3, 4, 5, 6). The species area curve reached an asymptote indicating that the sample size adequately captures the species present in the community. All analyses were performed in PC-ORD v. 6.08 (McCune & Mefford 2011) except for the Steinhaus (Sørensen/Czekanowski) coefficient, which was calculated in Microsoft Excel.

Table 1. Characteristics of the three valleys where fieldwork occurred.

	Llanganuco	Quilcayhuanca	Carhuascancha
Valley size (km ²)	144	98	96
Number of quadrats	22	26	17
Elevation range (m.a.s.l.)	2428–6685	3675–6158	2875–6265
Extent of <i>bofedales</i> (km ²)	0.3	2.0	1.6
% glaciated	20	16	8
Side of Cordillera Blanca	west	west	east
Drainage	Santa River to Pacific Ocean	Santa River to Pacific Ocean	Mosna River to Amazon River to Atlantic Ocean
Latitude	9° 02' S	9° 29' S	9° 28' S
Longitude	77° 36' W	77° 24' W	77° 14' W

After compiling the floristic inventory, we calculated six floristic diversity measures. Alpha (α) diversity expresses the mean number of species per quadrat for each valley and for all three valleys combined. Beta (β) is Whittaker's (1972) measure where Gamma (γ) represents the sum of all species present in each valley and for the entire dataset:

$$\beta = \gamma / \alpha - 1 \quad [1]$$

The Shannon index (Shannon & Weaver 1949) accounts for evenness and abundance where s is the number of species and p_i is the proportion of individuals of a given species i (McCune & Grace 2002):

$$H' = -\sum_i^s p_i \log p_i \quad [2]$$

The Simpson index (D) is the likelihood that two randomly chosen individual plants will be from different species (McCune & Grace 2002):

$$D = 1 - \sum_i^s p_i^2 \quad [3]$$

Next, we estimated similarity and dissimilarity among valleys. The Steinhaus coefficient of similarity is given as:

$$S_s = \frac{2a}{2a+b+c} \quad [4]$$

Dissimilarity is given as:

$$D_s = 1.0 - S_s \quad [5]$$

Table 2. Methods used by the Laboratorio de Suelos, Universidad Nacional Agraria La Molina for soil samples.

Factor	Method
pH	Soil to water 1:1 ratio
% organic matter	Oxidation of organic carbon with potassium dichromate (Walkley & Black 1934)
Phosphorus	Extraction of with NaHCO ₃ 0.5N, pH 8.5 (modified Olsen method)
Potassium	Extraction with ammonium acetate, spectrophotometry of atomic absorption
Textural class	Quantification of sand, loam, clay using hydrometer
Cation Exchange Capacity	Saturation of the clay-humic complex with ammonium acetate and posterior distillation with nitrogen (Kjeldahl in Busenberg & Clemency 1973)
Bulk density	Soil clod in paraffin

Table 3. Summary statistics for environmental variables and soils for all valleys.

	Min.	Max.	Mean	Median	Std. Dev.
Elevation (m.a.s.l.)	3827	4629	4148	4166	221.7
Slope (°)	0	26	5	4	4.2
Peat depth (cm)	0	8320	321	95	1230.2
pH	3.6	5.4	4.4	4.5	0.4
Organic matter (%)	1.8	81.5	46.3	55.3	24.1
P (ppm)	0.1	260.0	41.6	13.8	56.9
K (ppm)	26.0	1053.0	348.8	289.0	280.6
Cation Exchange Capacity (meq 100g ⁻¹)	3.2	80.0	45.5	51.2	24.4
Bulk density (g cm ⁻³)	0.1	1.2	0.3	0.1	0.4

Table 4. Summary statistics for environmental variables and soils for Llanganuco.

	Min.	Max.	Mean	Median	Std. Dev.
Elevation (m.a.s.l.)	3845	4629	4227	4380	280.3
Slope (°)	1	8	4	4	2.2
Peat depth (cm)	0	150	79	100	68.9
pH	4.1	5.2	4.5	4.5	0.3
Organic matter (%)	1.8	67.7	27.6	10.0	27.3
P (ppm)	0.1	168.5	36.7	4.8	53.9
K (ppm)	30.0	1053.0	322.0	134.0	346.9
Cation Exchange Capacity (meq 100g ⁻¹)	3.2	60.8	24.8	11.7	21.6
Bulk density (g cm ⁻³)	0.1	1.2	0.5	0.5	0.4

Table 5. Summary statistics for environmental variables and soils for Quilcayhuanca.

	Min.	Max.	Mean	Median	Std. Dev.
Elevation (m.a.s.l.)	3827	4176	4018	4002	118.0
Slope (°)	1	17	5	5	3.2
Peat depth (cm)	0	8320	669	113	1910.1
pH	3.6	5.6	4.1	4.0	0.4
Organic matter (%)	36.6	68.3	53.0	54.7	9.9
P (ppm)	8.0	260.0	34.4	13.6	66.5
K (ppm)	55.0	880.0	300.5	261.5	210.7
Cation Exchange Capacity (meq 100g ⁻¹)	11.2	76.0	61.0	66.0	16.7
Bulk density (g cm ⁻³)	0.1	1.1	0.2	0.1	0.2

Table 6. Summary statistics for environmental variables and soils for Carhuascancha.

	Min.	Max.	Mean	Median	Std. Dev.
Elevation (m.a.s.l.)	3943	4455	4246	4193	158.4
Slope (°)	0	26	7	5	6.5
Peat depth (cm)	0	489	100	75	131.4
pH	0	5.2	4.1	4.6	1.4
Organic matter (%)	2.4	81.5	58.7	64.7	23.7
P (ppm)	3.6	119.1	58.6	58.3	45.8
K (ppm)	26	1045	456.7	416.0	289.9
Cation Exchange Capacity (meq/100g ⁻¹)	9.1	80.0	48.3	51.2	19.5
Bulk density (g cm ⁻³)	0.1	1.2	0.3	0.2	0.3

where a is the number of species common to both valleys, b is the number of species in one valley, and c is the number of species in another valley (Kent 2012). To test the hypothesis of no difference among valleys, Multi-Response Permutation Procedures (MRPP) were applied using Sørensen (Bray-Curtis) distance and groups were defined by valleys. No transformations or relativisations were applied. To further compare valleys, we calculated two correlations: richness and elevation, and height and elevation. This was done using Spearman's rank correlation coefficient that measures the strength and association between two continuous variables.

To evaluate plant assemblages, we used cluster analysis (Euclidean distance and Ward's measure of linkage) using abundance. A strict criterion for species inclusion was used in the cluster analysis because species with few occurrences do not provide enough information to form groups (McCune & Grace 2002). To be included, a species had to have occurred in ≥ 5 quadrats; consequently, 38 species were used in the cluster analysis and 74 were omitted. Abundance data for the cluster analysis were relativised by species sums of squares to remove the influence of absolute abundance (McCune & Grace 2002).

Finally, to identify the abiotic factors that might influence vegetation composition variation, Non-Metric Multidimensional Scaling (NMS) was used (Kruskal (1964) and Mather (1976) algorithms). In this case, where the goal was exploratory and to identify possible abiotic factors associated with *bofedal* vegetation composition, the ordination was performed on a subset of the data, or 34 quadrats where soil samples were collected in the paired design. The same strict criterion for species inclusion was employed (occurrence in ≥ 5 quadrats, 38 species). Ten continuous variables were included: elevation, slope, pH, % organic matter, phosphorus, potassium, cation exchange capacity, bulk density, peat depth and species richness. Categorical variables were aspect and wetness index. Transformation and relativisation of the NMS data was deemed unnecessary because there was a small range in percent cover (42–97 %) and the goal was to allow differences among quadrats to be expressed in the analysis, which would have been muted by relativisation and transformation (McCune *et al.* 2000). The distance measure was Sørensen (Bray-Curtis). Three preliminary NMS runs using the Autopilot feature were completed to determine the optimum number of axes (3). The three subsequent manual runs demonstrated consistency in final stress levels between 10.856 and 10.876. The ordination graphs were also qualitatively consistent indicating a

stable solution. The lowest final stress results, 10.856, are reported herein, which completed in 107 iterations and are deemed fair per Kruskal (1964) and acceptable but cautionary by Clarke (1993).

RESULTS

Floristic inventory

There were 112 vascular plant species in the *bofedales* (see Table A1 in Appendix for complete list with full names). Llanganuco had the highest species richness with 78 species, followed by Quilcayhuanca with 58 species and Carhuascancha with 49 species. The 112 species are in 29 families and 11 families contain only one species. The most species-rich families are Poaceae (20 spp.), Asteraceae (19 spp.) and Cyperaceae (11 spp.) (Table 7). The most frequent species were *Plantago tubulosa* (66 % of all quadrats), *Eleocharis albibracteata* (65 %), *Juncus ebracteatus* (60 %), *Gentiana sedifolia* (57 %) and *Calamagrostis rigescens* (55 %). There were many rare species: 42 species occurred in only one quadrat (37.5 % of all species) and 17 species occurred in only two quadrats (15.1 % of all species). Seven species were endemic to Peru, with the remainder having either Andean or global distributions. Of note is the presence of two non-native species, the invasive African grass *Pennisetum clandestinum* that reproduces vegetatively (Marais 2001) and a clover, *Trifolium amabile*. Dense homogeneous patches of *Pennisetum clandestinum* (≥ 100 m²) were observed in all three valleys. Species that indicate overgrazing were present: the non-native *Trifolium amabile* and the native species *Wernernia nubigena* and *Lachemilla orbiculata*. These three species can dominate vegetation cover in overgrazed areas in the Andes (Adler & Morales 1999, Young *et al.* 2007). No *Sphagnum* species were recorded in any of the quadrats; they are uncommon in *bofedales* (Earle *et al.* 2003).

Diversity and valley-to-valley comparisons

Mean Alpha diversity for all three valleys combined was 12.6, a relatively low value that would be expected for high mountain elevations (mean elevation = 4148 m). The quadrat with the highest species richness contained 28 species; the quadrat with the lowest species richness had five species. Beta diversity was 7.9 overall. Gamma diversity was 112. Shannon diversity was 1.16. Evenness for all valleys was 0.46. The Simpson index was 0.56 (Table 8).

Table 7. Plant families, number of species, and percent of all taxa for the full dataset.

Family	Number of species	% of taxa
Poaceae	20	17.9
Asteraceae	19	17.0
Cyperaceae	11	9.8
Gentianaceae	6	5.4
Rosaceae	5	4.5
Apiaceae	4	3.6
Caryophyllaceae	4	3.6
Juncaceae	4	3.6
Orobanchaceae	4	3.6
Fabaceae	3	2.7
Iridaceae	3	2.7
Onagraceae	3	2.7
Orchidaceae	3	2.7
Ranunculaceae	3	2.7
Rubiaceae	3	2.7
Hypericaceae	2	1.8
Plantaginaceae	2	1.8
Polygonaceae	2	1.8
Brassicaceae	1	0.9
Campanulaceae	1	0.9
Equisetaceae	1	0.9
Ericaceae	1	0.9
Lamiaceae	1	0.9
Lycopodiaceae	1	0.9
Montiaceae	1	0.9
Ophioglossaceae	1	0.9
Phrymaceae	1	0.9
Scrophulariaceae	1	0.9
Valerianaceae	1	0.9
Total	112	100

In terms of inter-valley similarities and differences in diversity, elevation and height we found two main results (Table 8, Figure 3). First, Llanganuco was the most species-rich and most diverse; whereas Carhuascancha, on the east side of the mountain range, was the valley with the lowest number of species. Secondly, the relationship between vegetation height (a proxy for vegetation structure) and elevation was positive and statistically significant ($p < 0.01$) for the full dataset from all three valleys; however, when the valleys were analysed individually, the only statistically significant relationship between vegetation height and elevation was in Carhuascancha. In Llanganuco and Quilcayhuanca, there appears to be no relationship or a negative relationship. We found no statistically significant relationship between species richness and elevation using the full dataset for all three valleys (p -value = 0.27).

The Steinhaus coefficient, which approximates (dis)similarity among valleys (Kent 2012), showed that the valleys are more dissimilar in their species composition than they are similar, sharing only 35 % of species on average (Table 9). The MRPP results report that A is close to zero in all three cases and this suggests that the valleys are highly dissimilar to one another. For two pairwise comparisons, Llanganuco vs. Carhuascancha and Quilcayhuanca vs. Carhuascancha, p -values were statistically significant and T values were strongly negative indicating strong separation. The Llanganuco vs. Quilcayhuanca pairwise comparison was not statistically significant (p -value = 0.14). For the entire dataset, the MRPP chance-corrected within-group agreement, A , equalled 0.083 (p -value $\ll 0.01$).

Plant assemblages

The cluster analysis, which we used to distinguish plant assemblages using relativised species abundance, suggests that plants of *bofedales* in HNP can be organised into five assemblages or groups: two cushion plants, rushes, grasses and asters (Figure 4). The distinction among these assemblages was determined by trimming the cluster dendrogram at 75 % information remaining, representing 25 % of the variation. At this level, an intuitive and interpretable affinity among species is observed. The assemblages are described below (see Figure A1 in Appendix for photographs of selected assemblages).

Group 1. Plantago tubulosa - Oreobolus obtusangulus. This group is dominated by two cushion plant species, *Plantago tubulosa* and *Oreobolus obtusangulus*, with associated species such as *Gentiana sedifolia*, *Phylloscirpus deserticola* and *Lobelia reniformis*. Together, species in this

Table 8. Diversity measures for each of the three valleys sampled and all valleys combined.

	Diversity measures					
	Alpha	Beta	Gamma	Shannon index	Evenness index	Simpson index
Llanganuco	14.1	4.5	78	1.44	0.56	0.66
Quilcayhuanca	11.8	3.9	58	0.95	0.39	0.46
Carhuascancha	11.9	3.1	49	1.14	0.46	0.56
All valleys	12.6	7.9	112	1.16	0.46	0.56

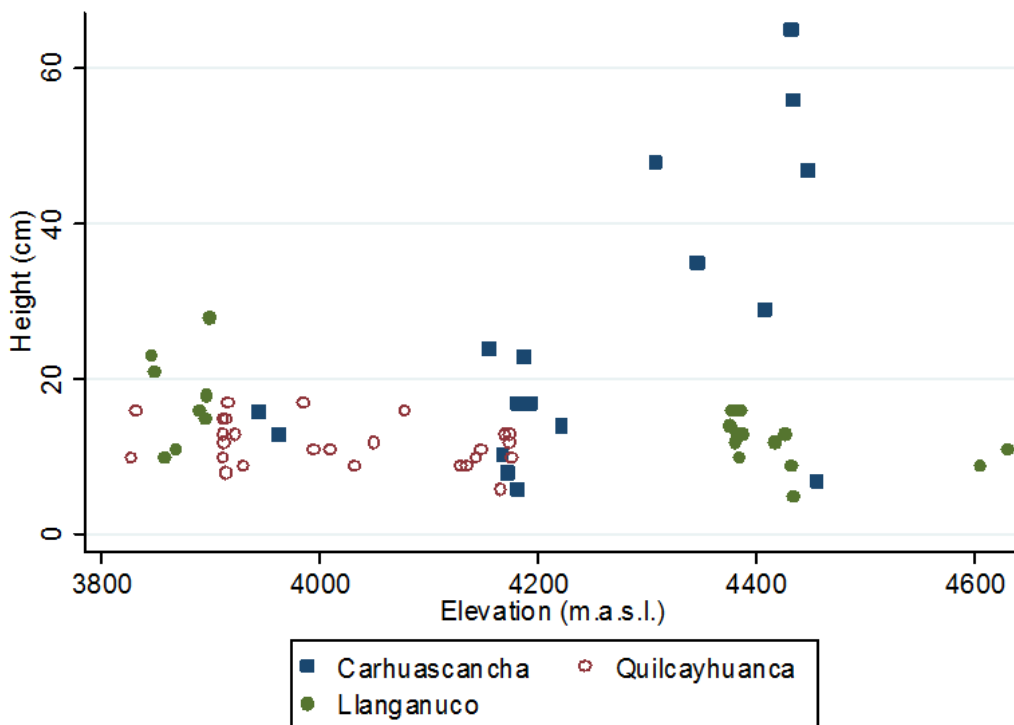


Figure 3. Two-way scatterplot showing the correlation between height of tallest species and quadrat elevation by valley.

Table 9. Measures of (dis)similarity among all pairwise valley comparisons.

Pair-wise valley comparison	No. species shared	Steinhaus similarity	Steinhaus dissimilarity	MRPP A	MRPP p-value	MRPP T-value
Llanganuco vs. Quilcayhuanca	35	34%	66%	0.0077	0.1420	-0.9935
Llanganuco vs. Carhuascancha	32	34%	66%	0.0711	0.0000	-8.6140
Quilcayhuanca vs. Carhuascancha	31	37%	63%	0.0946	0.0000	-12.5189

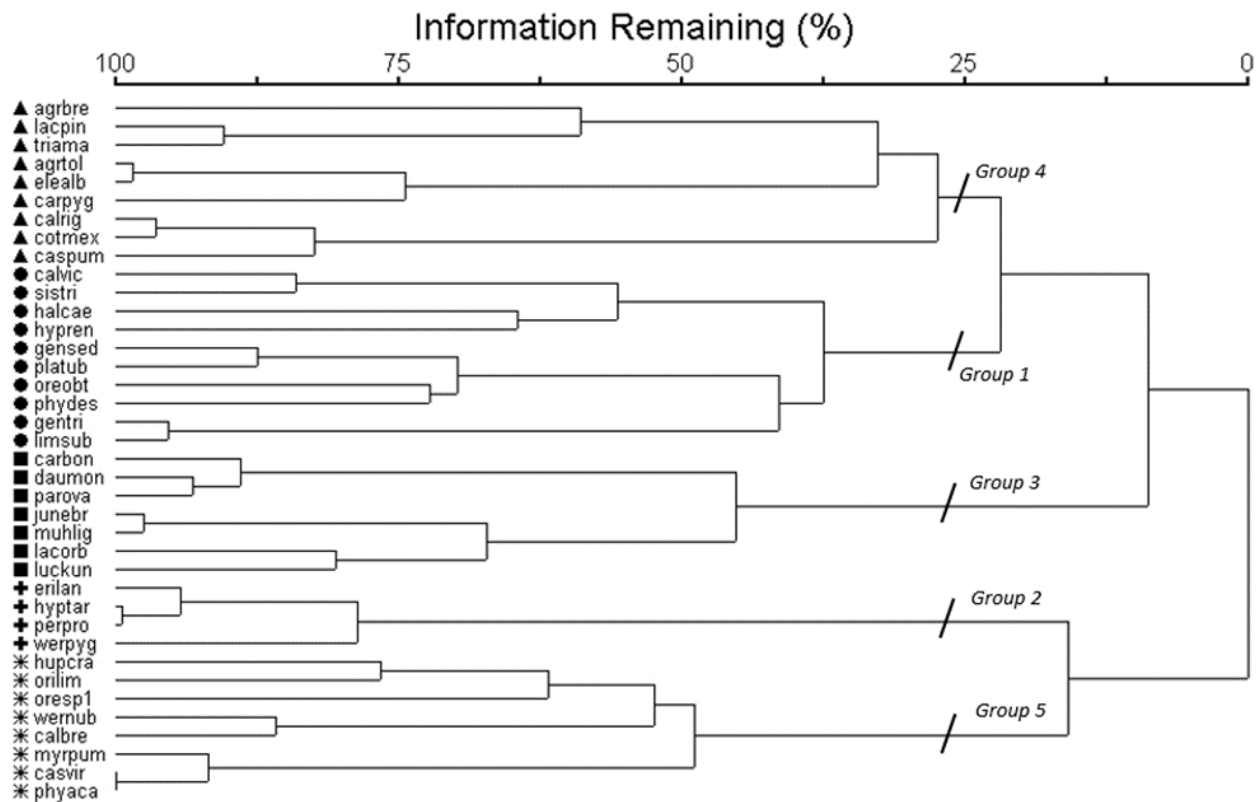


Figure 4. Cluster dendrogram of *bofedal* plant assemblages. Symbols indicate the five species assemblages. The dendrogram is scaled by Wishart's objective function, which measures the information lost at each step in the analysis. Refer to Table A1 (Appendix) for species codes and full names.

assemblage form a dense mat of vegetation that eventually develops peat (Cooper *et al.* 2010). The presence of an obligate aquatic species, *Limosella subulata*, indicates that soils are saturated year-round (León & Young 1996).

Group 2. *Werneria pygmaea* - *Pernettya prostrata*. The second cushion plant group is dominated by *Werneria pygmaea*, a peat-forming cushion plant. Interspersed in this cushion assemblage is *Pernettya prostrata*, a species with red berries that is important to wildlife (Troya *et al.* 2004). Less abundant but typical of the assemblage are two Asteraceae species, *Erigeron lanceolatus* and *Hypochaeris taraxacoides*, which occur in bogs and seeps.

Group 3. *Juncus ebracteatus* - *Carex bonplandii*. This rush-sedge assemblage is one of the most characteristic groups in the study area and is dominated by the abundant short plants (5–10 cm in height), *Juncus ebracteatus* and *Carex bonplandii*. The rosette-shaped *Lucilia kunthiana* is also common in this assemblage.

Group 4. *Eleocharis albibracteata* - *Calamagrostis rigescens* - *Lachemilla pinnata*. This spike rush - grass assemblage is dominated by *Eleocharis*

albibracteata, a spike rush often accompanied by the herbaceous *Lachemilla pinnata* in montane grasslands with moist soils in valley bottoms (Cabido *et al.* 1987, Funes *et al.* 2001). The grass *Calamagrostis rigescens* is also common in Peruvian mountain wetlands (Flores *et al.* 2005). Of note is the abundant legume in this assemblage, *Trifolium amabile*, an introduced species and an indicator of livestock impacts.

Group 5. *Werneria nubigena* - *Oritrophium limnophilum* - *Phlegmariurus crassus*. This aster - lycopod assemblage is dominated by large mats of *Werneria nubigena*, a basal rosette that spreads when overgrazing occurs (Young *et al.* 2007). *Oritrophium limnophilum* characterises this assemblage along with *Phlegmariurus crassus*, a species that requires moist soil to survive.

Factors associated with vegetation composition

Our final objective was to identify abiotic factors that could be associated with *bofedal* vegetation composition. The exploratory analysis showed that possible factors were elevation and a combination of bulk density, % OM and CEC (Figure 5). The three axes produced by the NMS analysis together

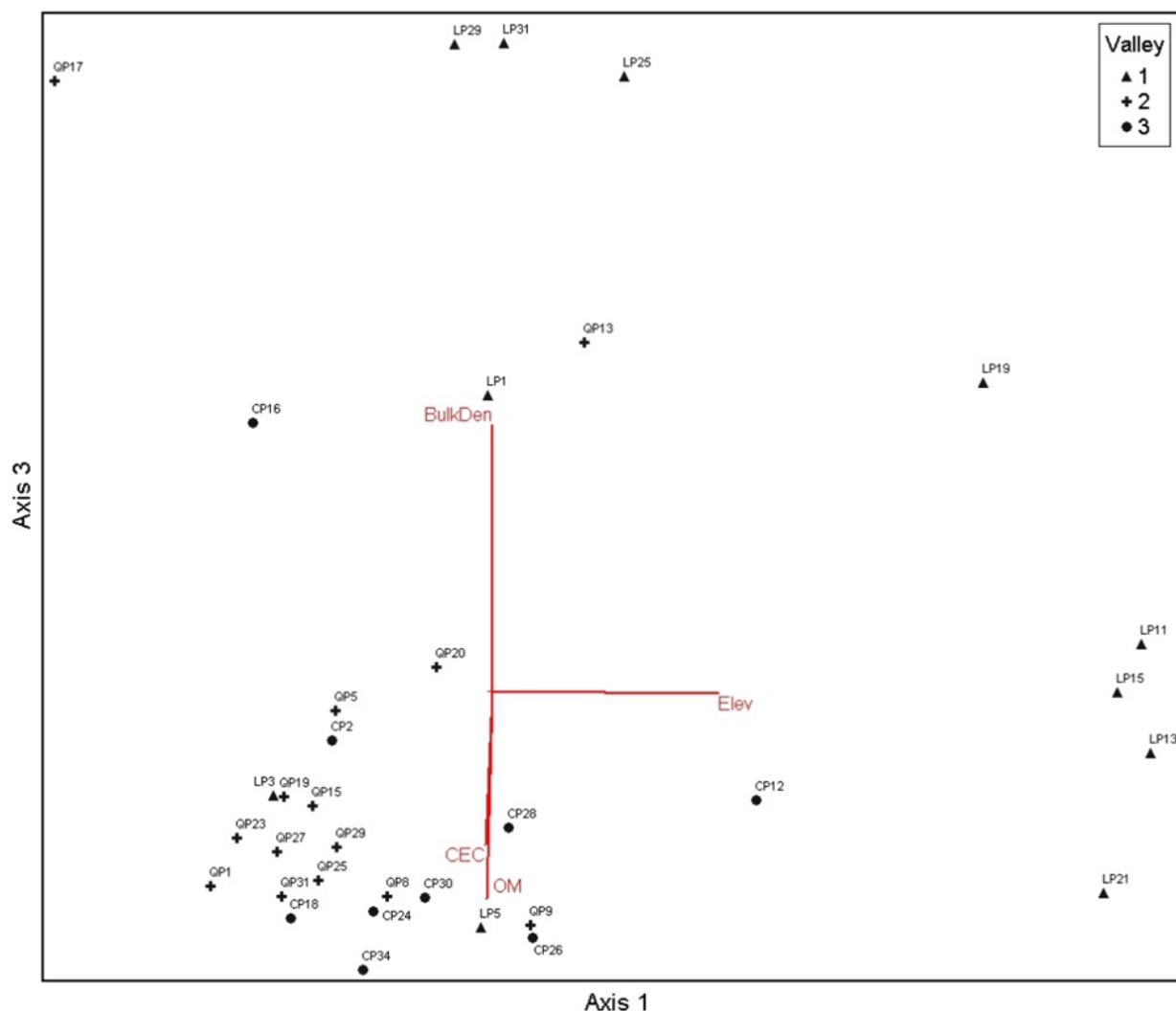


Figure 5. NMS ordination of quadrat data in *bofedales* species space with joint bi-plots of % organic matter (OM), cation exchange capacity (CEC), bulk density (BulkDen) and elevation (Elev) relative to Axes 1 and 3. Symbols correspond to valleys: ▲ = Llanganuco (1), + = Carhuascancha (2), ● = Quilcayhuanca (3). Displayed vectors have $R^2 \geq 0.2$.

represented 87 % of the variance. Axis 1 represented 35 % of that variance and is associated with elevation. Axis 2 represented 19 % of the variation, although its environmental association is unclear and further research is required. Axis 3 represented 33 % of the variation and appeared to be associated with a combination of bulk density, % OM and CEC. Because Axis 2 was unexplained, we re-ran the NMS using two axes to determine whether or not a solution with lower stress would result. The 2-axis solution stress in relation to dimensionality was 16.845 versus 10.586 from the 3-axis solution; therefore, the 3-axis solution is more reliable. The quadrats did not demonstrate a strong pattern of differentiation when grouped by valley, wetness index or pH.

DISCUSSION

The contribution of this research to peatland science is that it advances knowledge about vegetation in *bofedales* in the Peruvian Andes: it provides a baseline floristic inventory, evaluates vegetation dissimilarity and biodiversity across three valleys, distinguishes plant assemblages and identifies possible abiotic factors associated with vegetation composition. In the three valleys representative of the humid puna ecosystem, we found 112 species in 29 families. The valley-to-valley comparison shows that there is more dissimilarity in species composition than similarity, suggesting high beta diversity among plant species in *bofedales*. For each valley, the

relationships between height and elevation were different and the explanations for this are uncertain, but could be related to differences in livestock among valleys. Non-native livestock herd compositions and sizes vary from valley to valley. Herds in Carhuascancha tend to be composed of sheep, while herds in Quilcayhuanca consist of larger numbers of horses and cattle. In Llanganuco, herds are smaller, but *bofedales* are also smaller than in other valleys so the effect of trampling and grazing could be just as important. We suspect that these differences in livestock might also affect species diversity and plant assemblages, further discussed below.

Larger valleys with correspondingly larger wetland areas would be expected to contain more species because of the species richness - area relationship in tropical mountains (Sklenář *et al.* 2014). In the *jalca* ecosystem, Tovar *et al.* (2012) used the same 4 m² quadrat sampling scheme and reported mean alpha diversity of 18.0 compared to 12.6 in our study area, a difference that would be expected because Tovar *et al.* (2012) sampled a wider variety of habitats. They also reported a mean Shannon index of 2.3 versus 1.1 in this study. While the diversity measures reported here are lower than those of Tovar *et al.* (2012), sampling in more valleys in HNP would reveal additional species. More botanical sampling should be undertaken to create a comprehensive *bofedales* taxa list for the entire extent of HNP and a broader perspective on biodiversity.

The plant assemblages found here resemble the general observations made by Smith (1988), but go a step further by specifying that cushion plants are associated with species in the Cyperaceae, Asteraceae and Poaceae families. Weberbauer (1945) and Maldonado Fonkén (2014) proposed that there are four wetland types based on hydrophytic plant species that tend to occur together: *Distichia* wetland, wetland with mosses and shrubs, peaty meadows, and grass-dominated streamside wetlands. Our research shows that *bofedal* vegetation at the scale of the park displays finer variation than those four types. The five assemblages we identified could be conceived as possible new *bofedal* sub-types. For example, peaty meadows are dominated by Poaceae, Cyperaceae, and Juncaceae species; *Carex*, *Eleocharis*, *Juncus*, and *Calamagrostis* are common (among others) (Maldonado Fonkén 2014). Our Groups 3 and 4 are examples of peaty meadow subtypes. The rush-sedge assemblage we identified (Group 3) is dominated by *Juncus ebracteatus* and *Carex bonplandii*. The spike rush - grass assemblage, Group 4, is dominated by *Eleocharis albibracteata* and *Calamagrostis*

rigescens. Grass-dominated streamside wetlands consist of carpet-forming species such as *Plantago tubulosa* and *Werneria pygmaea* (Maldonado Fonkén 2014); our two cushion plant assemblages (Groups 1 and 2) are dominated by *Plantago tubulosa* and *Werneria pygmaea*, respectively. In mountain wetlands outside the tropics, Clausen *et al.* (2006) identified eight wetland types in Torres del Paine National Park, Chile. In Colorado's San Juan mountain fens, Chimner *et al.* (2010) identified 20 characteristic plant communities. Thus, the findings presented here suggest that vegetation in *bofedales* merits finer levels of categorisation than the system proposed by Weberbauer (1945) and Maldonado Fonkén (2014), an initiative that could be advanced by further quadrat-level vegetation sampling throughout Peru.

Compared to studies that took place north and south of our study area (Cooper *et al.* 2010, Salvador *et al.* 2014), the five plant assemblages we identified have similar dominant species, but there are key distinctions. In the dry puna of southern Peru, Salvador *et al.* (2014) found that the primary plant life form was the cushion plant; *Distichia muscoides* and *Plantago tubulosa* were the dominant species. In the three valleys that we sampled, *Distichia muscoides* was found in only one quadrat and *Plantago tubulosa* was present in 43 quadrats. Based on research from Cajamarca (northwest of HNP), one of Cooper *et al.*'s (2010) three cushion plant communities was characterised by *Plantago tubulosa*, *Oreobolus obtusangulus*, *Werneria pygmaea* and *Distichia acicularis*. Our Group 1 is similar in that it shares *Plantago tubulosa* and *Oreobolus obtusangulus*, but based on our analysis from HNP, the clustering separated *Werneria pygmaea* into a different assemblage with *Pernettya prostrata*. *Distichia acicularis* did not appear in our sampling. Similar to Cooper *et al.* (2010), we found an assemblage dominated by *Werneria nubigena*, which Cooper *et al.* (2010) refer to as a cushion plant community. *Werneria nubigena*, an Asteraceae, has narrow leaves that are arranged in a rosette and can reach 10 cm in length. It flowers year-round and has a showy yellow and white composite flower (Cano *et al.* 2006). Based on our observations, *Werneria nubigena* can form cushions when the abundance is high, but in low abundance it co-occurs with grasses and forbs and does not form cushions. Therefore, we separated it into an assemblage distinct from cushion plants. Of the fourteen sedge and rush dominated communities found by Cooper *et al.* (2010), two groups are similar. *Carex bonplandii* – *Drepanocladus longifolius* and *Eleocharis*

albibracteata – *Scorpidium cossonii* align with our Groups 3 and 4, but neither *Drepanocladus longifolius* nor *Scorpidium cossonii* appeared in the three valleys in HNP.

The presence of certain species as dominant species in the plant assemblages suggests that *bofedales* are affected by non-native livestock (cattle, sheep, horses). For example, *Werneria nubigena*, a sign of overgrazing (Young *et al.* 2007), is the dominant species in the *Werneria nubigena* – *Oritrophium limnophilum* – *Phlegmariurus crassus* assemblage. *Werneria nubigena* was present in 23 of our 65 quadrats and informal conversations with pastoralists confirmed that the species has been expanding spatially. Vegetation cover in *bofedales* is disturbed by herbivory, hoof action and other destructive activities (cf. Pérez 1993), creating conditions in which *Werneria nubigena* can colonise, expand, and begin to dominate plant composition. *Werneria nubigena* is unpalatable to cattle because it contains pyrrolizidine alkaloids which are poisonous to livestock and humans (Roeder *et al.* 1992, Roeder & Pflueger 1995, Bildfell 2013). The legume *Trifolium amabile* was a dominant species in Group 4, *Eleocharis albibracteata* – *Calamagrostis rigescens* – *Lachemilla pinnata*, and is another indicator of livestock activity. *Trifolium amabile* is highly palatable to livestock that then disperse the seeds (Adler & Morales 1999). Given the national park status and designation as a UNESCO Biosphere Reserve, the dominance of these species should be of concern to land managers.

Steep environmental gradients where abiotic factors change quickly over short distances are characteristic of mountains. Elevation is a well-recognised variable that consists of interrelated environmental gradients which organise mountain vegetation composition (Körner 2003). Along the elevation gradient, precipitation and temperature patterns vary and thus vegetation varies, although local conditions such as nutrient availability and disturbance history are also important (Hadley *et al.* 2013). Tovar *et al.* (2012) found that elevation and pH were the most important gradients explaining species composition; the association we found between Axis 1 and elevation was expected. We did not identify pH as a factor associated with vegetation, although it is important elsewhere (Cooper *et al.* 2010, Tovar *et al.* 2012). Overall, the range of pH values we observed was 3.6–5.4, i.e. lower than the ranges reported by Cooper *et al.* (2010) (3.2–8.2) and Salvador *et al.* (2014) (4.5–7.9) and similar to that found by Benavides (2014) (mean pH ~4.7 for undrained upland and 4.9 for drained). We note that Tovar *et al.* (2012), Cooper *et al.* (2010), and

Salvador *et al.* (2014) used groundwater for pH measurements; our values were determined by a different method (1:1 soil to water solution, see Methods) so the results may not be directly comparable. Therefore, we recommend that future pH sampling be conducted using groundwater to facilitate comparisons.

Instead of pH, we identified CEC, OM and bulk density (33 % of the variation on Axis 3) as factors that are associated with *bofedal* vegetation. Soil organic acids, lignins and other compounds are associated with increased CEC and lower pH (Rydin & Jeglum 2013). In general, as OM increases, CEC can also increase and pH can decrease. Vectors on the joint biplot show an inverse relationship between OM and bulk density: when soil OM is high there is more pore space among soil particles, thus bulk density is low. In this study, mean OM was 46 % and median was 55 %, whereas mean bulk density was 0.3 g cm⁻³ (300 kg m⁻³) and median was 0.1 g cm⁻³ (100 kg m⁻³) (Table 3). Mountain wetlands can receive large amounts of mineral inputs from neighbouring slopes and the mineral content of the soil can vary greatly through the soil profile. A recent restoration project in the dry puna, south of our study area, showed that soil OM in high Andean grasslands is responsive to rehabilitation practices and shows increasing sensitivity over time (Ducichela *et al.* 2019). Future work should sample soils at varying depths to advance our understanding of the relationship between soil characteristics and vegetation composition and configuration.

In summary, we found that CEC, OM, bulk density and elevation are factors that are associated with *bofedal* vegetation in HNP. The five plant assemblages revealed by our data demonstrate that there are possible new subtypes and high valley-to-valley dissimilarity, implying high biological diversity inside HNP. We identified five assemblages based on plant species, but we expect that other types of *bofedales* are likely to be present in HNP and that they could be classified into finer categories. A related effort would map *bofedal* types using a combination of remotely sensed data and field sampling. Future botanical sampling should include valleys at the northern, southern, eastern and western edges of the park to take account of precipitation, temperature and elevation gradients. *Bofedales* in the Peruvian Andes face a variety of threats (Salvador *et al.* 2014) and, in order to help land managers to administer policies that protect the future of *bofedales*, we advocate additional systematic and comprehensive research on these unique and biologically diverse ecosystems with various environmental roles.

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Appendix

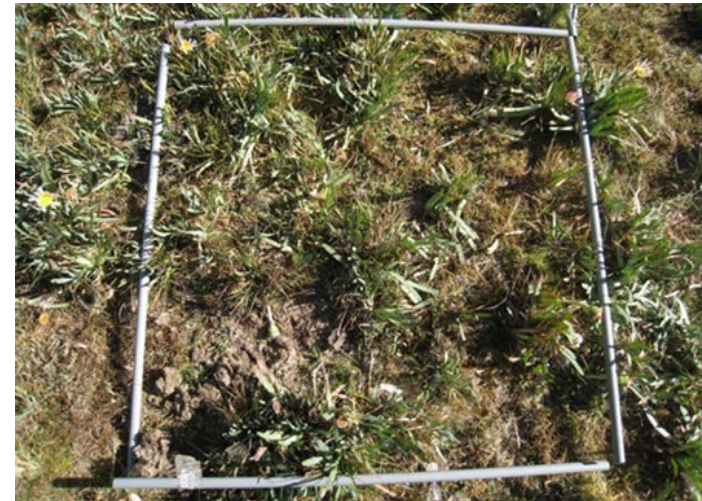


The *Plantago tubulosa* – *Oreobolus obtusangulus* Group 1.



The *Juncus ebracteatus* – *Carex bonplandii* Group 3.

Figure A1. Photographs of selected plant assemblages.



The *Werneria nubigena* – *Oritrophium limnophilum* – *Phlegmariurus crassus* Group 5

Table A1. Vascular plant taxa found in quadrats. “No. of quads” represents the number of quadrats in which the species was observed. Endemism, Growth Form, Habitat (where available), and Known Geographic Distribution were obtained from Missouri Botanical Garden’s Tropicos database (www.tropicos.org) and from Brako and Zarucchi (1993). † Indicates non-native/exotic species.

Taxa	No. of quads	Species code	Endemic to Peru	Growth form	Habitat	Known geographical distribution
APIACEAE						
<i>Chaerophyllum andicola</i> (Kunth) K.F. Chung	3	chaand	N	Herb	Grasslands, rocky slopes, shrublands	Ecuador, Peru
<i>Daucus montanus</i> Humb. & Bonpl. ex Spreng.	5	daumon	N	Herb	Disturbed areas, lomas, rocky slopes	Argentina, Bolivia, Chile, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Peru, Venezuela
<i>Eryngium humile</i> Cav.	1	eryhum	N	Herb	Grasslands, rocky slopes	Colombia, Costa Rica, Ecuador, Panama, Peru, Venezuela
<i>Lilaeopsis macloviana</i> (Gand.) A.W. Hill	2	lilmac	N	Herb	Seasonally inundated areas, submerged, terra firme forests	Argentina, Bolivia, Chile, Ecuador, Peru
ASTERACEAE						
<i>Aphanactis villosa</i> S.F. Blake	2	aphvil	N	Herb	Grasslands, rocky slopes, shrublands	Ecuador, Peru
<i>Belloa piptolepis</i> (Wedd.) Cabrera	3	belpip	N	Herb	Grasslands, shrublands	Argentina, Bolivia, Chile, Colombia, Ecuador, Peru, Venezuela
<i>Bidens andicola</i> Kunth	1	bidand	N	Herb	n.d.	Argentina, Bolivia, Colombia, Ecuador, Peru, Venezuela
<i>Cotula mexicana</i> (DC.) Cabrera	22	cotmex	N	Herb	Disturbed areas	Argentina, Bolivia, Chile, Colombia, Costa Rica, Ecuador, Mexico, Panama, Peru, Venezuela
<i>Erigeron lanceolatus</i> Wedd.	5	erilan	N	Herb	n.d.	Argentina, Bolivia, Peru
<i>Gamochaeta cabrerarum</i> Anderb.	1	gamore	Y	Herb	n.d.	Peru
<i>Hypochaeris meyeniana</i> Walp.) Benth. & Hook. f. ex Griseb	3	hypmey	N	Herb	n.d.	Bolivia, Ecuador, Peru
<i>Hypochaeris taraxacoides</i> Ball	6	hyptar	N	Herb	n.d.	Argentina, Bolivia, Chile, Peru
<i>Loricaria</i> sp.	1	lorsp1	N	Herb	n.d.	n.d.
<i>Lucilia kunthiana</i> (DC.) Zardini	15	luckun	N	Herb	Grasslands, shrublands	Colombia, Ecuador, Peru, Venezuela

Taxa	No. of quads	Species code	Endemic to Peru	Growth form	Habitat	Known geographical distribution
<i>Oritrophium limnophilum</i> (Sch. Bip.) Cuatrec.	34	orilim	N	Herb	n.d.	Bolivia, Colombia, Ecuador, Peru, Venezuela
<i>Oritrophium</i> sp.	1	orisp1	N	Herb	n.d.	n.d.
<i>Paranephelium ovatus</i> A. Gray ex Wedd.	8	parova	Y	Herb	n.d.	Bolivia, Peru
<i>Senecio breviscapus</i> DC.	2	senbre	N	Herb	n.d.	Argentina, Bolivia, Chile, Peru, South Africa
<i>Senecio condimentarius</i> Cabrera	1	sencon	N	Herb	n.d.	Peru
<i>Senecio repens</i> var. <i>Macbridei</i> (Cuatrec.) Cabrera	3	senrep	N	Herb	n.d.	Peru
<i>Werneria nubigena</i> Kunth	23	wernub	N	Herb	Disturbed areas	Bolivia, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Panama, Peru
<i>Werneria pygmaea</i> Gillies ex Hook. & Arn.	20	werpyg	N	Herb	n.d.	Argentina, Bolivia, Chile, Colombia, Ecuador, Peru, Venezuela
<i>Werneria</i> sp.	1	wersp1	N	Herb	n.d.	n.d.
BRASSICACEAE						
<i>Lepidium meyenii</i> Walp.	2	lepme	N	Herb	Disturbed areas	Bolivia, Chile, Peru,
CAMPANULACEAE						
<i>Lobelia reniformis</i> Cham.	24	hypren	N	Herb	n.d.	Bolivia, Chile, Colombia, Ecuador, Peru
CARYOPHYLLACEAE						
<i>Arenaria serpens</i> Kunth	1	arepal	N	Herb	n.d.	Argentina, Bolivia, Chile, Ecuador, Mexico, Peru
<i>Cerastium mucronatum</i> Wedd.	1	cermuc	N	Herb	n.d.	Bolivia, Peru
<i>Cerastium</i> sp.	1	cersp1	N	Herb	n.d.	n.d.
<i>Drymaria engleriana</i> (Muschl.) Baehni & J.F. Macbr.	1	dryeng	Y	Herb	n.d.	Peru
CYPERACEAE						
<i>Carex bonplandii</i> Kunth	27	carbon	N	Herb	Disturbed areas, grasslands, riversides	Argentina, Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Peru, U.S.A., Venezuela
<i>Carex hebetata</i> Boott	3	carheb	Y	Herb	Grasslands	Peru
<i>Carex pygmaea</i> Boeckeler	19	carpyg	N	Herb	n.d.	Bolivia, Colombia, Costa Rica, Ecuador, Panama, Peru

Taxa	No. of quads	Species code	Endemic to Peru	Growth form	Habitat	Known geographical distribution
<i>Eleocharis albibracteata</i> Nees & Meyen ex Kunth	42	elealb	N	Herb	Bogs, disturbed areas, grasslands	Argentina, Chile, Ecuador, Guatemala, Peru,
<i>Isolepis cf. cernua</i>	2	isocer	N	Herb	n.d.	n.d.
<i>Oreobolopsis</i> sp.	7	oresp1	N	Herb	n.d.	n.d.
<i>Oreobolus obtusangulus</i> Gaudich.	17	oreobt	N	Herb	Bogs, disturbed areas, grasslands, riversides	Argentina, Bolivia, Chile, Colombia, Ecuador, Peru, Venezuela
<i>Phylloscirpus acaulis</i> (Phil.) Geotgh. & D.A. Simpson	12	phyaca	N	Herb	Disturbed areas	Argentina, Bolivia, Chile, Ecuador, Peru
<i>Phylloscirpus deserticola</i> (Phil.) Dhooe & Goetgh.	15	phydes	N	Herb	n.d.	Argentina, Bolivia, Chile, Ecuador, Peru
<i>Rynchospora</i> sp.	1	rynspl	N	Herb	n.d.	n.d.
<i>Trichophorum rigidum</i> (Boeckeler) Goetgh., Muasya & D.A. Simpson	4	tririg	N	Herb	n.d.	Argentina, Bolivia, Brazil, Chile, Colombia, Costa Rica, Ecuador, Peru
EQUISETACEAE						
<i>Equisetum bogotense</i> Kunth	1	equbog	N	Herb	n.d.	Argentina, Bolivia, Chile, Ecuador, Panama, Paraguay, Peru, Uruguay, Venezuela
ERICACEAE						
<i>Pernettya prostrata</i> (Cav.) DC.	14	perpro	N	Shrub	Disturbed areas, forests, grasslands, rocky slopes	Argentina, Bolivia, Colombia, Costa Rica, Ecuador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Peru, Venezuela
FABACEAE						
<i>Astragalus garbancillo</i> Cav.	1	astgar	N	Herb/ Shrub	Grasslands, shrublands	Argentina, Bolivia, Peru
<i>Lupinus paniculatus</i> Desr.	1	luppan	N	Herb/ Subshrub	Riversides, rocky slopes	Bolivia, Colombia, Ecuador, Peru, Venezuela
<i>Trifolium amabile</i> Kunth	8	triam	N	Herb	n.d.	Argentina, Bolivia, Chile, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Peru, U.S.A.
GENTIANACEAE						
<i>Gentiana sedifolia</i> Kunth	37	gensed	N	Herb	Grasslands, rocky slopes	Argentina, Bolivia, Chile, Colombia, Costa Rica, Ecuador, Guatemala, Panama, Peru, Venezuela
<i>Gentianella bicolor</i> Wedd.	1	genbic	N	Herb	Grasslands	Peru

Taxa	No. of quads	Species code	Endemic to Peru	Growth form	Habitat	Known geographical distribution
<i>Gentianella poculifera</i> (Gilg) Zarucchi	1	genpoc	Y	Herb	Grasslands	Peru
<i>Gentianella tristicha</i> Gilg	9	gentri	Y	Herb	Grasslands, shrublands	Peru
<i>Halenia caespitosa</i> Gilg	12	halcae	N	Herb	Grasslands, riversides, shrublands	Bolivia, Peru
<i>Halenia umbellata</i> (Ruiz & Pav.) Gilg	2	halumb	N	Herb	Bogs, grasslands, riversides, rocky slopes	Bolivia, Peru
HYPERICACEAE						
<i>Hypericum laricifolium</i> Juss.	3	hyplar	N	Shrub, subshrub, tree	Cloud forests, shrublands	Bolivia, Colombia, Ecuador, Peru, Venezuela
<i>Hypericum silenoides</i> Juss.	2	hypsil	N	Herb	Rocky slopes	Argentina, Bolivia, Chile, Colombia, Ecuador, Mexico, Peru
IRIDACEAE						
<i>Sisyrinchium caespitificum</i> Kraenzl.	1	siscae	N	Herb	Grasslands	Ecuador, Peru
<i>Sisyrinchium chilense</i> Hook.	1	sischi	N	Herb	Grasslands	Argentina, Bolivia, Chile, Ecuador, Peru
<i>Sisyrinchium trinerved</i> Baker	5	sistri	N	Herb	Grasslands	Bolivia, Chile, Colombia, Costa Rica, Ecuador, Peru, Venezuela
JUNCACEAE						
<i>Distichia muscoides</i> Nees & Meyen	1	dismus	N	Herb	Grasslands	Argentina, Bolivia, Chile, Colombia, Ecuador, Peru,
<i>Juncus arcticus</i> Willd.	1	junart	N	Herb	Grasslands, riversides	Argentina, Bolivia, Canada, Chile, Colombia, Ecuador, Guatemala, Mexico, Norway, Peru, United States
<i>Juncus ebracteatus</i> E. Mey.	39	junebr	N	Herb	Rocky slopes, shrublands	Bolivia, Guatemala, Mexico, Peru
<i>Luzula racemosa</i> Desv.	3	luzrac	N	Herb	Grasslands, rocky slopes	Argentina, Bolivia, Chile, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Peru, Venezuela
LAMIACEAE						
<i>Stachys arvensis</i> L. †	1	staarv	N	Herb	Disturbed areas, rocky slopes	Argentina, Bolivia, Brazil, China, Ecuador, Russia, South Africa, United States, Venezuela
LYCOPODIACEAE						
<i>Phlegmariurus crassus</i> (Humb. & Bonpl. ex Willd.) B. Øllg.	21	hupcra	N	Herb	n.d.	Bolivia, Caribbean, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Panama, Paraguay, Peru, Venezuela

Taxa	No. of quads	Species code	Endemic to Peru	Growth form	Habitat	Known geographical distribution
MARCHANTIACEAE						
<i>Marchantia polymorpha</i> L.	2	marpol	N	Herb	n.d.	Nonvascular. Brazil, Chile, China, Japan, Peru, Russia, United States.
MONTIACEAE						
<i>Calandrinia acaulis</i> Kunth	1	calaca	N	Herb	Rocky slopes	Argentina, Bolivia, Chile, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Peru, Venezuela
ONAGRACEAE						
<i>Epilobium pedicellare</i> C. Presl	1	epiped	N	Herb	Riversides	Bolivia, Chile, Peru
<i>Epilobium</i> sp.	2	episp1	N	Herb	n.d.	n.d.
<i>Oenothera multicaulis</i> Ruiz & Pav.	2	oenmul	N	Herb	Grasslands, shrublands	Bolivia, Costa Rica, Ecuador, Guatemala, Mexico, Peru, Venezuela
OPHIOGLOSSACEAE						
<i>Ophioglossum crotalophoroides</i> Walter	1	ophcro	N	Herb	n.d.	Argentina, Bolivia, Brazil, Caribbean. Chile, Colombia, Costa Rica, Ecuador, Guatemala, Honduras, Mexico, Nicaragua, Peru, United States, Uruguay, Venezuela
ORCHIDACEAE						
<i>Aa</i> sp.	1	aaspe1	N	Herb	n.d.	n.d.
<i>Myrosmodes paludosa</i> (Rchb. f.) P. Ortiz	1	myrpal	N	Herb	Grasslands, shrublands	Bolivia, Colombia, Peru, Venezuela
<i>Myrosmodes pumilio</i> (Schltr.) C. Vargas	18	myrpum	N	Herb	n.d.	Bolivia, Peru
OROBANCHACEAE						
<i>Bartsia diffusa</i> Benth.	2	bardif	N	Herb	Grasslands	Bolivia, Peru
<i>Bartsia melampyroides</i> (Kunth) Benth.	3	barmel	N	Herb	Disturbed areas, grasslands	Bolivia, Ecuador, Peru
<i>Castilleja pumila</i> (Benth.) Wedd.	11	caspum	N	Herb	Grasslands	Bolivia, Chile, Colombia, Ecuador, Peru
<i>Castilleja virgatoides</i> Edwin	5	casvir	Y	Herb	n.d.	Peru
PHRYMACEAE						
<i>Mimulus glabratus</i> Kunth	2	mimgla	N	Herb	Riversides	Argentina, Bolivia, Canada, Chile, Colombia, Ecuador, Guatemala, Mexico, Nicaragua, Peru, United States, Venezuela

Taxa	No. of quads	Species code	Endemic to Peru	Growth form	Habitat	Known geographical distribution
PLANTAGINACEAE						
<i>Plantago lamprophylla</i> Pilg.	1	plalam	N	Herb	Disturbed areas, grasslands, rocky slopes, shrublands	Bolivia, Peru
<i>Plantago tubulosa</i> Decne.	43	platub	N	Herb	Bogs, grasslands, rocky slopes	Argentina, Bolivia, Chile, Colombia, Ecuador, Guatemala, Mexico, Peru
POACEAE						
<i>Aciachne pulvinata</i> Benth.	1	acipul	N	Herb	Bogs, grasslands, rocky slopes	Bolivia, Costa Rica, Ecuador, Peru, Venezuela
<i>Agrostis breviculmis</i> Hitchc.	17	agrbre	N	Herb	Disturbed areas, grasslands	Argentina, Bolivia, Brazil, Canada, Chile, Colombia, Ecuador, Peru, Venezuela
<i>Agrostis tolucensis</i> Kunth	10	agrtol	N	Herb	Disturbed areas, grasslands	Argentina, Bolivia, Chile, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Panama, Peru, Venezuela
<i>Calamagrostis brevifolia</i> (J. Presl) Steud.	12	calbre	N	Herb	Disturbed areas, grasslands, rocky slopes	Argentina, Bolivia, Peru
<i>Calamagrostis eminens</i> (J. Presl) Steud.	2	calemi	N	Herb	Bogs, riversides	Argentina, Bolivia, Chile, Colombia, Peru
<i>Calamagrostis heterophylla</i> (Wedd.) Pilg.	3	calhet	N	Herb	Grasslands, riversides	Argentina, Bolivia, Chile, Ecuador, Peru, Venezuela
<i>Calamagrostis recta</i> (Kunth) Trin. ex Steud.	3	calrec	N	Herb	Grasslands, riversides, shrublands	Argentina, Bolivia, Colombia, Ecuador, Peru, Venezuela
<i>Calamagrostis rigescens</i> (J. Presl) Scribn.	36	calrig	N	Herb	Grasslands, riversides, swamps	Argentina, Bolivia, Chile, Ecuador, Mexico, Peru
<i>Calamagrostis tarmensis</i> Pilg.	1	caltar	N	Herb	Grasslands, rocky slopes	Argentina, Bolivia, Ecuador, Peru
<i>Calamagrostis vicunarum</i> (Wedd.) Pilg.	27	calvic	N	Herb	Grasslands, rocky slopes	Argentina, Bolivia, Chile, Ecuador
<i>Eragrostis peruviana</i> (Jacq.) Trin.	2	poaper	N	Herb	Disturbed areas, lomas	Peru, Chile
<i>Festuca nigriflora</i> (Hitchc.) Negritto & Anton	1	fesnig	N	Herb	n.d.	Peru
<i>Festuca procera</i> Kunth	3	fespro	N	Herb	Disturbed areas	Bolivia, Colombia, Ecuador, Peru

Taxa	No. of quads	Species code	Endemic to Peru	Growth form	Habitat	Known geographical distribution
<i>Muhlenbergia ligularis</i> (Hack.) Hitchc.	22	muhlig	N	Herb	Disturbed areas, grasslands	Argentina, Bolivia, Colombia, Costa Rica, Ecuador, Guatemala, Peru, Venezuela
<i>Muhlenbergia peruviana</i> (P. Beauv.) Steud.	1	muhper	N	Herb	Forests, grasslands	Argentina, Bolivia, Chile, Ecuador, Guatemala, Mexico, Peru, United States
<i>Nassella brachyphylla</i> (Hitch.) Barkworth	1	nasbra	N	Herb	Grasslands	Argentina, Bolivia, Ecuador, Peru
<i>Nassella inconspicua</i> (J. Presl) Barkworth	3	nasinc	N	Herb	Grasslands	Argentina, Bolivia, Colombia, Ecuador, Peru
<i>Pennisetum clandestinum</i> Hochst. ex Chiov. †	1	pencla	N	Herb	Disturbed areas, riversides, streamsides	Argentina, Bolivia, Brazil, Burundi, Caribbean, China, Colombia, Costa Rica, Ecuador, Ethiopia, Greece, Guatemala, Honduras, India, Kenya, Mexico, Nicaragua, Panama, Paraguay, Peru, Rwanda, South Africa, Tanzania, Uganda, United States, Uruguay, Venezuela, Congo
<i>Poa annua</i> L.	3	poaann	N	Herb	Disturbed areas, forests, grasslands, lomas, riversides	Global
<i>Poa serpaiana</i> Refulio	2	poaser	N	Herb	n.d.	Argentina, Bolivia, Chile, Peru
POLYGONACEAE						
<i>Muehlenbeckia volcanica</i> (Benth.) Endl.	1	muevol	N	Herb, shrub, vine	Disturbed areas, elfin forests, grasslands, riversides, rocky slopes, shrublands	Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Peru, Venezuela
<i>Rumex acetosella</i> L. †	1	rumace	N	Herb	Disturbed areas, rocky slopes, shrublands	Argentina, Bolivia, Brazil, Canada, Caribbean, Chile, China, Colombia, Costa Rica, Ecuador, Greenland, Guatemala, India, Japan, Kazakhstan, Mexico, Mongolia, New Zealand, Panama, Peru, Russia, South Africa, South Korea, United States, Venezuela
RANUCULACEAE						
<i>Ranunculus flagelliformis</i> Sm.	2	ranfla	N	Herb	Aquatic	Argentina, Bolivia, Brazil, Caribbean, Chile, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Paraguay, Peru, Uruguay, Venezuela
<i>Ranunculus limoselloides</i> Turcz.	1	ranlim	N	Herb	Aquatic	Bolivia, Colombia, Ecuador, Peru, Venezuela
<i>Ranunculus praemorsus</i> Humb., Bonpl. & Kunth ex DC.	1	ranpra	N	Herb	Disturbed areas, grasslands	Argentina, Bolivia, Chile, Colombia, Costa Rica, Ecuador, Mexico, Panama, Peru, Venezuela

Taxa	No. of quads	Species code	Endemic to Peru	Growth form	Habitat	Known geographical distribution
ROSACEAE						
<i>Lachemilla aphanoides</i> (Mutis ex L. f.) Rothm.	1	lacaph	N	Herb	Bogs, disturbed areas, forests	Bolivia, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Panama, Peru, Venezuela
<i>Lachemilla orbiculata</i> (Ruiz & Pav.) Rydb.	7	lacorb	N	Herb	Bogs, cloud forests, disturbed areas, grasslands, shrublands	Bolivia, Colombia, Ecuador, Peru, Venezuela
<i>Lachemilla pinnata</i> (Ruiz & Pav.) Rothm.	35	laccpin	N	Herb	Cloud forests, disturbed areas, grasslands, shrublands	Argentina, Bolivia, Colombia, Chile, Costa Rica, Ecuador, Guatemala, Mexico, Peru, Venezuela
<i>Lachemilla</i> sp.	1	lacspl	N	n.d.	n.d.	n.d.
<i>Lachemilla vulcanica</i> (Schltdl. & Cham.) Rydb.	1	lacvul	N	Herb	Grasslands, rocky slopes, shrublands	Bolivia, Colombia, Ecuador, El Salvador, Guatemala, Mexico, Peru, Venezuela
RUBIACEAE						
<i>Galium corymbosum</i> Ruiz & Pav.	3	galcor	N	Herb	Disturbed areas, grasslands, riversides, rocky slopes, shrublands	Bolivia, Colombia, Ecuador, Peru, Venezuela
<i>Nertera granadensis</i> (Mutis ex L. f.) Druce	2	nergra	N	Herb	Disturbed areas, forests, grasslands	Argentina, Australia, Bolivia, Caribbean, Chile, China, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Hawaii, Honduras, Indonesia, Malaysia, Mexico, New Guinea, New Zealand, Nicaragua, Panama, Philippines, Taiwan, Venezuela
SCROPHULARIACEAE						
<i>Limosella subulate</i> E. Ives	10	limsub	N	Herb	Submerged	Canada, Ecuador, Peru, United States, Venezuela
VALERIANACEAE						
<i>Belonanthus</i> sp.	1	belspl	N	n.d.	n.d.	n.d.