

Article

The Subnival Vegetation of Moquegua, South Peru: Chasmophytes, Grasslands and Cushion Communities

Daniel B. Montesinos-Tubée ^{1,2,3,*} , Antoine M. Cleef ⁴ and Karlè V. Sýkora ¹

¹ Environmental Sciences, Plant Ecology and Nature Conservation Group, Wageningen University, Droevendaalsesteeg 3a, 6708 PB Wageningen, The Netherlands; karle.sykora@gmail.com

² Escuela Profesional de Ingeniería Ambiental, Universidad Nacional de Moquegua, Pacocha, Ciudad Jardín s/n, Mariscal Nieto, Moquegua, Peru

³ Naturalis Biodiversity Centre, Darwinweg 2, 2333 CR Leiden, The Netherlands

⁴ Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, P.O. Box 94248, Science Park 904, 1098 XH Amsterdam, The Netherlands; cleef@uva.nl

* Correspondence: dbmtperu@gmail.com

Abstract: The present work is a phytosociological synthesis and syntaxonomic overview of the vegetation of the highest subnival parts (superpuna) of the open alpine vegetation of the high plateaus (puna) of the Andes of Moquegua, South West Peru, as related to the main environmental gradients. Using TWINSpan and DCA ordination analysis, 153 phytosociological relevés were analyzed. For each association, subassociation and community, the syntaxonomy, floristic diversity and relation with environmental variables are described. The syntaxonomy and synecology of superpuna vegetation was studied in 19 localities at an altitude of 4450–4800 m. The study area has a pluviseasonal climate with yearly rainfall (December–April). Four main highland vegetation types were distinguished: 1. slope and scree chasmophyte vegetation composed of shrubs, cushions, ground rosettes and grasses, 2. grasslands (grazed and ungrazed) characterized by great species richness in shrubs, cushions, ground rosettes, grasses and herbs, 3. vegetation of plateaus with cushions, shrubs, ground rosettes, herbs and grasses and 4. nitrophilous vegetation with high cover and low species richness. Within the vegetation of the orotropical and cryotropical bioclimatic belts three phytosociological classes can be distinguished: *Argyroschometea niveae* (chasmophytic vegetation), *Calamagrostietea vicunarum* (grasslands with cushions), *Anthochloa lepidulae-Dielsiochloeta floribundae* (highland slopes and plateaus) and a nitrophylous community. One new association from rock and scree slopes was described within the *Saxifragion magellanicae* (*Argyroschometea niveae*). Within the *Calamagrostion minima*, which comprises grasslands with cushions and mat-forming plants, one new association with two subassociations could be distinguished. Within the grassland and cushion associations of the *Azorello-Festucion* (*Calamagrostietea vicunarum*), three new associations were described, comprising nine subassociations. In the *Anthochloa-Dielsiochloetalia* one new and one previously described association and one community are distinguished. In addition, the nitrophilous community of *Tarasa nototrichoides* and *Urtica flabellata* has been described. In total the vegetation comprised 172 vascular species belonging to 32 families. Our study provides the first syntaxonomic revision of chasmophytes, cushion associations and high-altitude grasslands in the Andes of North Moquegua. The proposed syntaxonomic scheme contains the associations distributed under similar habitat conditions throughout the Southern Andes of Peru, but also the associations reflecting the local floristic and environmental patterns. The subnival vegetation of Moquegua hosts some rare endangered and/or protected plant species.



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Keywords: Andes; Peru; phytosociology; superpuna; syntaxonomy

1. Introduction

The puna is one of the world's largest pastoral ecosystems in the tropical mountains and its flora, (including many endemic species) and vegetation are vulnerable to human

pressure. A reference and tool for nature conservation is highly needed. Its vegetation is however still insufficiently studied. An overview of plant species assemblages and their relation to environmental conditions is largely missing. This especially applies to the highest part of the Moquegua study area over 4400 m. The relation between diversity and species composition of the superpuna vegetation and environmental factors such as altitude, slope aspect and angle, cover of rocks and stones and soil properties is largely unknown. In the traditional vegetation classification of Bolivia and Peru, the term puna is used to identify the open alpine vegetation of the high plateaus of the Central Andes [1–6]. Reference [7] defined the puna as a level area termed Altiplano. References [8,9] use the term superpuna to refer to the highest subnival parts of the puna with isolated patches of snow. The subnival zone of tropical mountains is characterized by a variable climate. This means cold freezing nights and low to moderate temperatures during daytime [7,10–13]. Night temperature is lowest at ground level before sunrise. Nightly freezing causes daily frost heaving with a number of phenomena at soil surface level, which also has an impact on plant life.

In this research we define the superpuna as the zone between 4450 and 4800 m (permanent snowline in Moquegua) with average annual temperatures ranging from 6 degrees C at 4500 m to 0 degrees C at 4800 m a.s.l. Mean annual precipitation is low: between 400 and 600 mm per year [14].

Growth forms in the extreme habitat of the subnival zone of the puna correspond mainly to low evergreen shrub, low herbs with thick cuticle and/or hairy leaf surface, and lax and compact cushions [7].

In the north of Moquegua growth forms of the superpuna vegetation include the scarce presence of dwarf and erect shrubs, tussock grasses, and annual herbs. More abundant is the presence of ground rosettes, cushions, mats and annual grasses. Cushions are abundant in the superpuna as well; they are known to enhance diversity by nursing other species [8,15,16], although some cushions appear to be non-facilitators [17]. Due to the near absence of tussock grasses grazing and fire are practically absent.

The continuous fumarolic activity of the Ubinas volcano [18] could have strong negative effects (not studied) on the plant communities in North Moquegua.

Several authors [4,19–34] have studied plant communities of the superpuna of the Central Andes, their ecology, structure and floristic composition.

References [35,36] presented the first research on the structure and ecology of the prepuna and puna vegetation in the Andes of North Moquegua between 3470 and 4500 m.

The present contribution concerns the upslope communities between 4500 m and the lower border of snow and ice at about 4800 m in the Andes of North Moquegua. We try to provide more insight into the relation between superpuna plant communities with their floristic composition, environmental variables and the rate of anthropic influence.

Finally, we present an overview of the superpuna vegetation between 4450 and 4800 m a.s.l.

The aim of this study is to: (a) present a syntaxonomic characterisation of the superpuna vegetation in South Peru, based on full synoptic tables. This settles the basis for the legend of future vegetation mapping in order to quantify the different vegetation types, important for management and nature conservation. (b) determine the distribution of chasmophytic, grassland and plateau vegetations in Moquegua (South Peru), (c) account for their rare, local occurrence and floristic diversity, and (d) evaluate the importance of superpuna rocky slopes, grasslands and cushion communities as habitats for specific vegetation types, and for some endemic plant species in Moquegua (South Peru).

The relation between the diversity and species composition of the superpuna vegetation and factors such as altitude, slope aspect and angle, cover of rocks and stones, soil properties and the disturbance caused by grazing is described here.

2. Study Area

The research was conducted in an area of approximately 720 km² in the districts of Ichuña, Ubinas and Yunga, in the General Sánchez Cerro province and the district of Carumas in the Mariscal Nieto province, in the north of the department of Moquegua,

South Peru. The study area is located at $70^{\circ}54'02''$, $70^{\circ}32'32''$ W and $16^{\circ}06'11''$, $16^{\circ}15'31''$ S (Figure 1, Table 1) at an altitude between 4450 and 4800 m a.s.l. Average annual precipitation at the Ichuña meteorological station at 3790 m a.s.l. is 460 mm, the mean minimum temperature is 3.7°C and the mean maximum is 19.4°C [14]. Precipitation is markedly seasonal, with over 80% of the annual rainfall (600–800 mm) falling between December and April [14] and significant interannual variability [37,38]. Recent floods correspond to the El Niño phenomenon by increased annual precipitation. Soil moisture ranges from 0 in the dry season to below 10% in the rainy season [39]. No glaciers have been observed on the highland mountains of North Moquegua. Nevertheless, after heavy rainfall, snow accumulates temporarily above 4700 m altitude. On the summit of the Ubinas volcano (5672 m a.s.l.), snow can be permanent during the rainy season (December–April) and occasionally during the dry season (May–November).

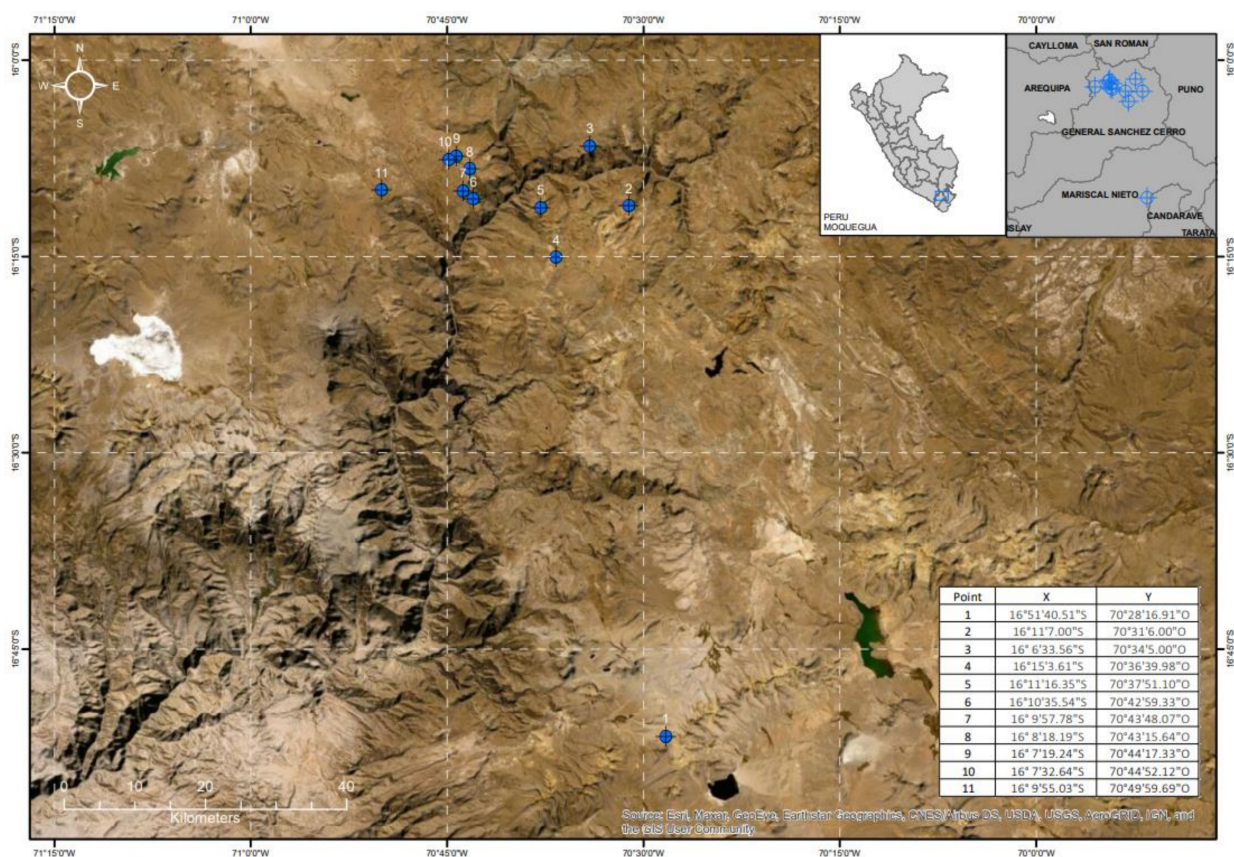


Figure 1. Location of the upper reaches of the Tambo and Ichuña rivers in the Andes of Moquegua, Peru. The numbers show the locations of the study sites as listed in Table 1.

The study area is located in the high-altitude sectors of the southwestern Andes with Pacific tributaries. Here the geology is volcanic and sedimentary with intercalations of conglomerates and sand. Ravines and crevices have infill of sandy silt and calcareous sediment [40]. The fieldwork area comprises the high plateaus and rocky slopes of the two mountain chains of volcanic origin that form the watersheds of the upper Tambo, Paltuturo and Ichuña rivers and their tributaries.

Reference [35] presented the vegetation zonation of the upper Tambo River in the Moquegua region and distinguished the orotropical and cryotropical bioclimate [41] occurring between 4150 and 4650 m and characterized by chasmophytic associations and grasslands with cushions, which occur above 4500 m in Moquegua. The cryotropical zone was identified at altitudes above 4870 m where cushion associations are also present.

Table 1. Overview of parameters for each research site (1–11) in the superpuna of the Andes of Moquegua, Peru. #rel = number of relevés at the site in question, year = year(s) in which fieldwork was done, Elevation = the altitudinal range within which the relevés were made, Slope (°) = minimal and maximal slope angle, Aspect = orientation, and vegetation = general description of the vegetation structure.

Sites	Locality	District	# rel.	Year	Elevation (m)	Slope (°)	Aspect	Environment	
1	Janchata slopes	Nevados	Carumas	5	2015	4700–4710	'5–10	SE	Scree plateaus
2	Cerro Santo Tomas, C. Huarmaca, Puqa Saya	Yanahuara	Ichuña	15	2009, 2012	4530–4665	0–60	N, NW, S, SE	Chasmophyte, scree slopes with copper, steppe grasslands with cushions, rocky slopes, open plateaus, manure communities
3	Coriri, Jatun Puqio, Qhaqhaskinkri	Ichuña	Ichuña	9	2009	4460–4540	'3–43	NW, S, SE, E, W	Steppe grasslands with cushions, grazed grasslands
4	Choco-Choco environs	Yunga	Yunga	10	2012	4660–4760	'2–35	N, W	Grasslands with cushions, scree slopes, open plateaus with cushions
5	Sura, Perusa-Chaquisura, Siliaca, Yanasaya	Yunga	Yunga	28	2011, 2012	4510–4800	'10–50	NW, N, SSW, SW, W	Chasmophyte, rocky slopes, steppe grasslands with cushions, grasslands, scree, open plateaus with cushions
6	Rancho-Pirhuani; Laguna Jallpacocha	Tassa/Pachamayo	Ubinas	18	2014	4450–4565	'5–45	NE, SE, E	Steppe grasslands with cushions, grazed grasslands, rocky slopes, scree slopes
7	Pirhuani	Tassa	Ubinas	18	2011	4470–4660	0–17	NNW, SSE, W	Steppe cushion communities
8	Cochapata lake environs	Tassa	Ubinas	10	2013	4680–4700	'4–5	SE	Steppe grasslands with cushions
9	Pacosani, Yaretaq, Larsepesca	Coalaque	Ubinas	10	2009	4615–4690	'5–47	N, NE, S, SW	Steppe grasslands with cushions, rock slopes
10	Janaqpampa, Gasawasi, Witopata	Querala	Ubinas	10	2011	4500–4640	'4–15	S, E, W	Steppe grasslands with cushions, open plateaus
11	Condor Sallana	Matazo	Ubinas	20	2013, 2014	4460–4590	0–25	N, S	Grazed grasslands with cushions, manure communities, rocky slopes

3. Methods

3.1. Data Collection

Floristics. The plant species were identified directly in the field; unidentified species were collected and later deposited in various herbaria (USM, HUSA, MOL, CPUN, CUZ, HSP, MO, L, WAG; acronyms according to [42]). Information on the taxonomy and species distribution was obtained from the literature. The nomenclature of the taxa is in accordance with [43], the electronic versions of [44–46]. Specific information on the taxonomy and species distribution was obtained from different sources [43,47–52].

Vegetation. Fieldwork was conducted over a period of five years (2009, 2011–2014) during the months of February, March, April and September.

A total of 153 relevés was made in 11 sites within an altitudinal range of 4450–4800 m a.s.l. Plot size was 25 m² for grasslands and cushion vegetation and 16 m², or 25 m² for chasmophyte and 1 m² for nitrophilous vegetation [9].

Within the different biotopes, sample plots (relevés) were randomly selected and positioned according to the principle of homogeneity as defined by the Zurich-Montpellier method [53]. We ensured that no sample relevés traversed ravines, clefts or streams. In chasmophytic environments, relevés were selected on pure rock stands including soil pockets and crevices. Contact with zonal grassland vegetation was avoided.

For each relevé, the presence of species was noted and its percentage actual cover was estimated [54,55]. Due to insufficient expertise only the presence of bryophytes and lichens was noted, but the species were not identified.

3.2. Environmental Variables

For each relevé we collected data on altitude (meters above sea level = m a.s.l.), slope inclination (degrees) and slope orientation (compass), cover of rocks and stones (percentage). Within each relevé, five subsamples were taken from the upper 10 cm of the soil and combined into one bulked sample for pH analysis in the laboratory (only for the relevés done in 2009). The presence of manure was determined by the amount of dung found in each relevé and classed as 0: absence; I: 1–30%; II: 31–70%; III: >71% (dung cover). Grazing intensity was determined by the percentage of tussock grasses showing signs of grazing at the moment of field analysis, and was later converted into the same I-III values.

3.3. Data Analysis

For computer calculations the percentage values were transformed into a nine-point ordinal cover/abundance scale [56]. The scales used were: 1% = 1; 2% = 2; 3% = 3; 4–7% = 4; 8–20% = 5; 21–37 = 6; 38–68% = 7; 69–88% = 8 and 89–100% = 9.

3.4. Classification

The relevés were classified by means of TWINSpan [57]. In Table 2 species constancies are given in percentage values.

The first cluster analysis with 373 nr of relevés (153 this survey and 220 nr from literature) revealed an outgroup (61 relevés by [4,20,22,28,31,32,35,58–61] which was removed prior to the second run with the remaining 312 relevés including the relevés from the present survey as well as relevés from literature (Table 3, see heading of Table 3 for detailed description of the communities from other studies included in the analysis).

Table 2. Table with the type relevés of associations and subassociations described as new (including one community and a pro-visual association). Community # indicated for each association and subassociation; Relevé# for the type relevé or representative relevé. Altitude (meters above sea level). Inclination (degrees). Orientation. Total number of species (# SPP). VEGC % for vegetation cover percentage in that single relevé. Rocks and stones in percentage cover. Grazing and manure (expressed as I: 1–30%; II: 31–70%; III: >71%).

Community #	1	2.1	2.2	3.1	3.2	3.3	4.1	4.2	4.3	4.4	5.1	5.2	6.1	6.2	7	8	9
Relevé #	2	6	20	3	8	20	7	17	33	41	14	20	6	14	2	2	8
ALTITUDE	4580	4585	4470	4450	4510	4500	4670	4610	4680	4590	4800	4590	4650	4710	4790	4745	4460
INCLINATION	25	5	5	5	20	45	10	5	5	10	10	25	5	10	15	45	0
ORIENTATION	S	N	W	NE	N	NW	SW	W	SE	N	W	S	SSE	SE	SSW	NW	-
# SPP	8	18	22	8	15	22	18	12	6	20	16	22	8	8	14	6	5
VEGC %	20	55	45	20	35	60	50	30	35	35	40	45	30	15	15	5	80
ROCKS %	5	5	10	40	40	10	0	20	10	5	20	10	0	5	8	8	0
STONES %	55	5	20	10	10	30	35	35	30	30	40	24	30	90	34	90	0
GRAZING (I-III)	0	0	1	0	1	1	1	0	0	0	0	0	1	0	0	1	3
Argyrochosmetea niveae																	
Saxifragetalia magellanicae,																	
Saxifragion magellanicae																	
<i>Saxifraga magellanica</i>	4
Saxifrago																	
magellanicae-Leucherietum																	
daucifoliae																	
<i>Leucheria daucifolia</i>	4
<i>Weberbaueria arequipa</i>	2
Calamagrostietea vicunarum																	
<i>Calamagrostis vicunarum</i>	.	.	1	1	.	.	.	2	.	1
Parastrephietalia quadrangularis																	
<i>Parastrephia quadrangularis</i>	.	.	4	4	4	8
<i>Tetraglochin cristatum</i>	.	8	3	.	.	8	.	2
<i>Descurainia depressa</i>	1
<i>Pycnophyllum molle</i>	.	10	4	.	.	.	20	10	15	7	8	.	8
<i>Hypochaeris meyeniana</i>	.	.	2	.	1	2
<i>Ephedra rupestris</i>	3
<i>Weberbaueria spathulifolia</i>	2	.	3	.	.	1
<i>Belloa piptolepis</i>	1	1	1	2
<i>Senecio candollei</i>	1	2
<i>Senecio humillimus</i>	2	4
<i>Brayopsis calycina</i>	.	1	1	1	1
<i>Chaetanthera stuebelii</i>	1	.	.	1

Table 2. Cont.

Community #	1	2.1	2.2	3.1	3.2	3.3	4.1	4.2	4.3	4.4	5.1	5.2	6.1	6.2	7	8	9
<i>Nototriche anthemidifolia</i>	.	1	2	1	.	1	1
<i>Draba macleanii</i>	.	2	2
<i>Hypochaeris eriolaena</i>	1
<i>Plantago sericea</i> var. <i>lanuginosa</i>	.	.	1	1
<i>Werneria aretioides</i>	.	.	2	2	2
<i>Senecio spinosus</i>	.	3	1
<i>Werneria pectinata</i>	1	.	1	.	.	2
<i>Wahlenbergia peruviana</i>	1
<i>Nototriche digitulifolia</i>	.	.	.	1
<i>Nototriche pedicularifolia</i>	.	2
<i>Lupinus ananeanus</i>	.	.	3	.	.	3
<i>Cerastium subspicatum</i>	.	.	.	1
<i>Conyza deserticola</i>	.	.	1
<i>Gomphrena meyeniana</i>	.	.	2
Calamagrostietea minimae																	
<i>Calamagrostis minima</i>	.	1	1
<i>Oreomyrrhis andicola</i>	.	1
<i>Werneria nubigena</i>	.	.	2
Astragalo minimi-Azorelletum																	
diapensioidis																	
<i>Azorella diapensioides</i>	.	6	4
<i>Astragalus minimus</i>	.	10	2	.	2	2	1
<i>Bougueria nubicola</i>	.	2	1	.	.	1	1
<i>Werneria apiculata</i>	.	2	2
<i>Junellia minima</i>	.	1
Subassociation Typicum																	
<i>Werneria melanandra</i>	.	1
<i>Nototriche longirostris</i>	.	2	.	.	.	1
aciachnetosum pulvinatae																	
<i>Aciachne pulvinata</i>	.	.	2
Azorello-Festucion																	
<i>Azorella compacta</i>	.	.	.	8	10	15	.	.	12	4	4	4
<i>Festuca orthophylla</i>	2	5
<i>Baccharis caespitosa</i>	1	2
<i>Belloa</i> sp. (# 3945)	1	1
<i>Bowlesia tropaeolifolia</i>	1

Table 2. Cont.

Community #	1	2.1	2.2	3.1	3.2	3.3	4.1	4.2	4.3	4.4	5.1	5.2	6.1	6.2	7	8	9
<i>Cumulopuntia boliviana</i> subsp. <i>ignescens</i>	3
<i>Senecio evacoides</i>	2
<i>Stangea wandae</i>	1	.	1
Astragalo pusillii-Parastrephietum quadrangularis																	
<i>Astragalus pusillus</i>	.	.	.	1	1	2
sisyrinchietosum trinervis																	
<i>Sisyrinchium trinervis</i>	.	.	.	1
baccharidetosum tricuneatae																	
<i>Baccharis tricuneata</i>	2	3	4
<i>Descurainia</i> sp. (# 0940)	1
Subassociation Typicum																	
<i>Sisyrinchium brevipes</i>	.	1	.	.	.	1
Senecioni																	
moqueguensis-Pycnophylletum molle																	
<i>Senecio moqueguensis</i>	3	3	4	4
<i>Nototriche argentea</i>	1
<i>Perezia coerulescens</i> var. <i>amplibracteata</i>	1
Subassociation Typicum																	
<i>Mniodes</i> sp. (# 2477)	3	2
<i>Senecio helianthemoides</i>	1
senecionetosum tassaensis																	
<i>Senecio tassaensis</i>	1
<i>Xenophyllum weddellii</i>	2
gentianelletosum primuloides																	
<i>Gentianella primuloides</i>	1
<i>Senecio graveolens</i>	1
arenarietosum acaulis																	
<i>Arenaria acaulis</i>	1
<i>Nototriche sepalioba</i>	1
<i>Cerastium behmianum</i>	1
<i>Nototriche pusilla</i>	1
<i>Senecio sykora</i>	1
<i>Poa brevis</i>	1

Table 3. Cont.

#order	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
<i>Bowlesia tropaeolifolia</i>			4	2	18											+			43	6		20					
<i>Baccharis tricuneata</i>			35	33	46					22	75	75	33	100													1
<i>Cumulopuntia boliviana</i> subsp. <i>ignescens</i>			22		14					43		25		20													+
<i>Bartsia elongata</i>				9	14							25		40													
<i>Caiophora rosulata</i>				9	18																						
<i>Senecio evacoides</i>				2	32									20					14		25						
<i>Stangea wandae</i>				16	27																						
Astragalo pusillii-Parastrephietum quadrangularis																											
<i>Astragalus pusillus</i>			65							4																	3
<i>Sisyrinchium brevipes</i>		8	22																								
<i>Sisyrinchium trinervis</i>			17																								
<i>Laennecia artemisioides</i>			17																								
<i>Valeriana aschersoniana</i>			4																								
<i>Belloa longifolia</i>			4								13	50		20										1			
<i>Descurainia</i> sp. (# 0940)			4																								
<i>Junellia pappigera</i>			4																								
Senecioni moqueguensis-Pycnophylletum molle																											
<i>Senecio moqueguensis</i>			84																								
<i>Senecio tassaensis</i>			4	26		13																					
<i>Nototriche argentea</i>			21	5																							1
<i>Arenaria acaulis</i>			16																								
<i>Gentianella primuloides</i>			16																								
<i>Nototriche sepaliloba</i>			16																								
<i>Cerastium behmianum</i>			14																								
<i>Xenophyllum weddellii</i>			14																								
<i>Nototriche pusilla</i>			12																								
<i>Oritrophium</i> sp. (# 2194b)			12																								
<i>Senecio sykora</i>			12																								
<i>Perezia coeruleascens</i> var. <i>amplibracteata</i>			9																								
<i>Werneria heteroloba</i>			9																								
<i>Myrosmodes</i> sp. (# 2287)			7																								
<i>Poa brevis</i>			7																								
<i>Senecio graveolens</i>			7							4	13		17										13				

Table 3. Cont.

#order	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27			
Nototricho obcuneatae-Xenophylletum poposi Galán de Mera, Cáceres & Gonzáles 2003																														
<i>Mniodes coarctata</i>				16		88																						+	4	
<i>Xenophyllum poposum</i>						81				9																		4		
<i>Nototriche erinacea</i>						56																								
<i>Senecio trifurcifolius</i>						31																								
<i>Poa</i> sp. (# 3099)						25																								
<i>Nototriche</i> sp.2 (# 4228a)						19																								
<i>Senecio</i> sp.4 (# 4228b)						13																								
Poo aequiglumae-Xenophylletum dactylophyllum																														
<i>Nototriche</i> sp.3 (# 2447)										100																				
<i>Poa aequigluma</i>										100																				
<i>Poa spicigera</i>										100											63									
<i>Xenophyllum dactylophyllum</i>										80																		1		
Community of <i>Senecio algens</i>																														
<i>Senecio algens</i>				2						80					2						17	13		13	1			1		
<i>Senecio</i> sp.5 (# 3942)										100																				
Class																														
Community of <i>Tarasa nototrichoides</i> and <i>Urtica flabellata</i>																														
<i>Urtica flabellata</i>										100																				
<i>Lachemilla pinnata</i>		38	4							100					1															+
<i>Tarasa nototrichoides</i>		4	4							90																				
<i>Perezia multiflora</i>				17						50		13																		
<i>Jaborosa squarrosa</i>										40		13																		
<i>Valeriana</i> sp. (Image DSC075, 03/2014)										10																				
CRASSULETEA CONNATAE																														
<i>Muhlenbergia peruviana</i>		25	13	2								13	83																	
<i>Crassula connata</i>			17																											
ARGYROCHOSMETEA NIVEAE; <i>Salpichroetalia glandulosae</i>																														
<i>Asplenium peruvianum</i>				9											4						71	11		100						
<i>Belloa kunthiana</i>					9																									
<i>Belloa schultzei</i>		4		2																	29	6	38							

Table 3. Cont.

#order	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	
Species from other communities																												
<i>Lupinus paruroensis</i>										17	13		67															
<i>Chersodoma jodopappa</i>										4		13	33	20														
<i>Deyeuxia heterophylla</i>											25	13	67	20														
<i>Deyeuxia breviaristata</i>											13																+	3
<i>Astragalus arequipensis</i>											13																	
<i>Festuca rigescens</i>											13												13				+	
<i>Lupinus saxatilis</i>											38			40														
<i>Erigeron incarum</i>											13		17															
<i>Luzula racemosa</i>										4														38	1			
<i>Festuca dolichophylla</i>												100	100	100						14			25					
<i>Deyeuxia cabrerai</i>													17								6	13	13			+	2	
<i>Paranephelium ovatus</i>												75	17	60											1			
<i>Coreopsis fasciculata</i>												75		60														
<i>Plantago sericea</i>												13	67															
<i>Plantago linearis</i>												25		20														
<i>Nassella pubiflora</i>												25	17															
<i>Dissanthelinum macusaniense</i>													17											25				
<i>Nassella mucronata</i>												38	83	60														
<i>Trifolium amabile</i>												63	17															
<i>Bromus catharticus</i>												38		20														
<i>Lupinus microphyllus</i>													17	20														
<i>Senecio modestus</i>															1	1							40	13				
<i>Draba brackenridgei</i>																				29								
<i>Mniodes andina</i>																							88					
<i>Oxalis andina</i>															1	+							60		1			
<i>Senecio rhizomatus</i>															1	+							20					
<i>Cystopteris fragilis</i>																+							20					
<i>Asplenium triphyllum</i>																1						11	40					
<i>Senecio culcitoides</i>																	1		14	28	13		50					
<i>Woodsia montevidensis</i>																		1	14									
<i>Caiophora horrida</i>																		1							1			
<i>Sisymbrium peruvianum</i>																		1			6							

Table 3. Cont.

#order	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
<i>Stipa rigida</i>																	1					20	63				
<i>Xenophyllum ciliolatum</i>																							25	2			
<i>Silene andicola</i>																							13	1	+	2	
<i>Poa humilluma</i>																							38	1			
<i>Adesmia patancana</i>																											1
<i>Perezia ciliosa</i>																											1

Other species: In 10 *Baccharis incarum* 57; in 10 *Nassella brachyphylla* 13, *Echinopsis pamparuii* 9, *Baccharis genistelloides* 9, *Hypochaeris taraxacoides* 9, *Stipa nardoides* 4, *Stipa rigidiseta* 4, *Plantago monticola* 4, *Nassella asplundii* 4, *Polylepis tarapacana* 13, *Arenaria serpens* 9, *Dissanthelium peruvianum* 9, *Werneria* sp. 4, *Oxalis pachyrrhiza* 4, *Calamagrostis intermedia* 4, *Caiochophora chuquitensis* 4, *Bomarea dulcis* 4, *Dissanthelinum breve* 4; in 11 *Stipa obtusa* 25, *Opuntia lagopus* 13, *Baccharis buxifolia* 13, *Adesmia miraflorensis* 13, *Polylepis rugulosa* 25, *Senecio adenophylloides* 13, *Senecio rudbeckiifolius* 13, *Stipa annua* 13; in 12 *Nassella pubiflora* 25, *Tunilla soehrensii* 13, *Quinchamalium procumbens* 13, *Echinopsis pampana* 13, *Vulpia megalura* 38, *Tagetes multiflora* 25, *Bidens pilosa* 25, *Gilia laciniata* 13, *Lepechinia meyenii* 13, *Nassella depauperata* 13, *Schkhuria multiflora* 13, *Chondrosium simplex* 13, *Hordeum muticum* 13, *Hypochaeris chillensis* 13, *Erodium cicutarium* 13, *Lepidium chichicara* 13; in 13 *Bartsia camporum* 50, *Mutisia arequipensis* 17, *Gnaphalium dombeyanum* 17; in 14 *Agrostis gelida* 100; in 16 *Asplenium castaneum* +, *Peperomia peruviana* 2, *Oxalis arenaria* 1; in 17 *Draba cryptantha* 2; in 18 *Gnaphalium* sp. 1, *Cerastium mucronatum* 1, *Phacelia pinnata* 1, *Lobivia caespitosa* 1; in 19 *Bomarea uniflora* 57, *Bowlesia sodiroana* 14, *Oxalis petrophila* 14, *Valeriana plectritoides* var. *pallida* 14, *Galium aparine* 14, *Poa horridula* 14; in 20 *Draba cuzcoensis* 6, *Ribes brachybothrys* 6; in 22 *Peperomia peruviana* 60, *Oxalis arenaria* 40, *Asplenium castaneum* 20, *Englerocharis peruviana* 20; in 23 *Xenophyllum decorum* 88, *Plettkea cryptantha* 38, *Xenophyllum digitatum* 13, *Chaetanthera cochlearifolia* 63, *Weberbaueria rosulans* 13, *Niphogeton dissecta* 25, *Gentianella weberbaueri* 13, *Englerocharis peruviana* 50, *Nototriche aretioides* 38, *Nototriche pinnata* 13, *Plantago lamprophylla* 13, *Bromus villosissimus* 38, *Pycnophyllum weberbaueri* 13, *Pernettya prostrata* 13, *Niphogeton scabra* 13, *Astragalus brackenridgei* 13, *Deyeuxia tarmensis* 13, *Senecio tephrosioides* 13, *Deyeuxia ovata* 25, *Deyeuxia rigescens* 13, *Deyeuxia glacialis* 13, *Senecio canescens* 13, *Ephedra americana* 38, *Melpomene moliniformis* 13, *Valeriana candamoana* 38; in 24 *Poa gymnantha* 18, *Astragalus micranthellus* 1, *Bartsia crenata* 1, *Bromus lanatus* 1, *Chaetanthera boliviensis* 1, *Chaetanthera villosa* 1, *Deyeuxia cephalanta* 1, *Deyeuxia densiflora* 1, *Deyeuxia glaciaria* 1, *Gnaphalium badium* 1, *Niphogeton scabra* 1, *Poa aequigluma* 1, *Pycnophyllum filiforme* 1, *Senecio puchii* 1, *Valeriana interrupta* 1, *Viola nivalis* 1; in 25 *Deyeuxia deserticola* 9; in 26 *Nototriche* sp.

The second TWINSpan analysis was run with 6 cutlevels resulting in 64 clusters. The clusters were checked for the presence of differential species in different hierarchical TWINSpan cut-levels. Species are considered to be differential by their occurrence in clusters and contrasted with their absence or less frequent occurrence or smaller total estimate in other clusters [56]. Clusters without differential species were fused resulting in a final number of 27 clusters.

A synoptic-syntaxon table (Table 2) was constructed by reordering the species into syntaxonomic species groups after comparison with publications from [21,22,24,27,58,59].

Full association tables are presented in Supplementary Tables S1–S9. The character and differential species in the description of the associations are mentioned in order of their diagnostic value.

The assignment to class order, alliance, association and subassociation is based on the presence of diagnostic species as mentioned in relevant syntaxonomic publications. Besides the hierarchical structure of the table clearly shows the syntaxonomic level allowing the distinction and assignment of associations on the lowest level but one and characterised by their own diagnostic species. At the lowest level subassociations are distinguished based on the presence of differential species. Two vegetation types could not be described within the Braun-Blanquet system due to lack of data and were simply named community.

New syntaxa were described following the International Code of Phytosociological Nomenclature [62] and new syntaxonomic units were defined after reviewing [21,22,24,27,58,59].

The relation between each syntaxon and the environmental variables rocks, stones, slope degree and the vegetation cover was presented as box-and-whisker charts. Besides a chart is presented showing their altitudinal distribution.

3.5. Gradient Analysis

Detrended Correspondence Analysis (DCA; CANOCO 4.5, [63]) was used to study the relation between species composition and environmental variables.

The first DCA run with all 153 relevés resulted into two floristically and environmentally very dissimilar groups. The grassland and cushion vegetation was clearly separated from the vegetation from rock fissures (chasmophytic vegetation), scree (cryoturbate vegetation) and the nitrophylous vegetation. In order to better reveal the inner gradients DCA analysis was performed again, but now on both groups separately: the grassland and cushion vegetation with 112 samples and 153 species and the rock fissures, scree and the nitrophylous vegetation with 41 samples and 56 species.

4. Results

Classification of Relevés and Description of Vegetation Units

The classification resulted in 17 clusters separated by differential species (see Supplementary Tables S1–S9, in Table 2, the synoptic table only the 7 associations and 2 communities are represented). In this section we present an overview of these vegetation units, with information about physiognomy, composition, ecology and distribution. After comparison with literature, all vegetation units but one could be described as new associations. One vegetation unit could be assigned to the *Nototricho obcuneatae-Xenophylletum poposi* Galán de Mera, Cáceres & González 2003. The syntaxonomic affinity of the vegetation units is discussed below.

Saxifraga magellanicae-*Leucheria daucifoliae* ass. nov.

(Table 2, col. 1; Table 3, col. 1, Supplementary Table S1, Typus: Rel 2; Figure 2).

Physiognomy and composition: Association of chasmophyte vegetation, with a variable cover by cushions, herbs and grasses. It consists of 4–20 cm tall cushions and herbs with a cover of 10–20% in combination with tussock grasses and dwarf shrubs (*Ephedra rupestris*) with a cover of 5%. Among the surface layer species with substantial cover are *Leucheria dauciflora*, *Saxifraga magellanica*, *Calandrinia acaulis*, *Weberbaueria spathulifolia* and *Microsteris gracilis*. The cushion *Pycnophyllum molle*, present in two relevés, facilitates the

presence of the rare orange-flowered *Gentianella incurva*. The grass layer is composed of the tussock *Stipa ichu* and the small grass *Anthochloa lepidula*.

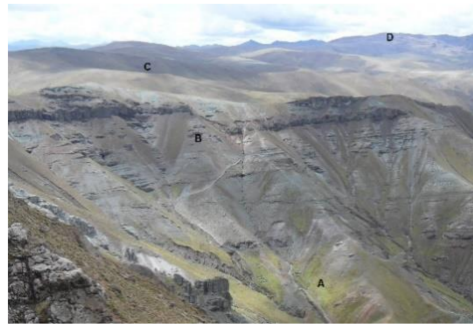


Figure 2. Superpuna landscape at 4500–4800 m (Cachilaya-Yanapuquio sites, Ichuña district). A. Community of *Misbrookea strigosissima* & *Stipa ichu* (Calamagrostietea vicunarum). B. *Saxifraga magellanica*-*Leucheria daucifoliae* (*Argyrochosmeteetea niveae*). C. *Astragalo minimi*-*Azorelletum diapensioidis* subassociation typicum (Calamagrostietea vicunarum). D. *Nototrichion obtusum* (*Anthochloa lepidulae*-*Dielsiochloetea floribundae*).

Diagnostic species: Character species are *Leucheria dauciflora*, *Perezia nivalis*, *Saxifraga magellanica*, *Gentianella incurva*, *Weberbaueria arequipa* and *Perezia pinnatifida*. Differential against other classes are *Poa candamoana* and *Stangea rhizanta*.

Ecology and distribution: This Andean chasmophyte association is generally found delimited by grassland, plateaus and steep rock formations, at edges of slopes or on hilltops. It is located at altitudes of 4580–4590 m, on south-facing slopes of 5–25°. The soils are mainly formed by unstable scree high in copper minerals, with stone particles and grayish-green mottling in the upper soil horizons. This association can be found on the rocky slopes of the Ichuña River valley, in the north of the Ichuña district.

Astragalo minimi-*Azorelletum diapensioidis* ass. nov.

(Table 2, col. 2.1–2.2; Table 3, col. 2; Supplementary Table S2, Typus: Rel. 6; Figure 3A).



Figure 3. Overview of the grasslands with cushions of *Azorella compacta* in the surroundings of the road between Carmen Chaclaya and Matazo in the Ubinas district (4460–4830 m a.s.l.). A. *Astragalo pusilli*-*Parastrephietum quadrangularis* (Calamagrostietea vicunarum). B. *Senecioni moqueguensis*-*Pycnophylletum molle* (Calamagrostietea vicunarum). C. *Plantagini rigidae*-*Distichietea muscoidis*. D. *Nototrichion obtusum* (*Anthochloa lepidulae*-*Dielsiochloetea floribundae*).

Physiognomy and composition: Grassland vegetation with high density and diversity of dwarf shrubs, cushions, grasses, ground rosettes and annual herbs. Vegetation cover is between 20–80%, 57% on average. The 20–40 (50) cm tall resinous shrubs of *Parastrephia quadrangularis* cover 10% in four relevés only. Cushions attain 15–30% of the total cover and are represented by *Azorella diapensioides* and *Pycnophyllum molle*. *Pycnophyllum glomeratum* attains low cover in two relevés only. The grasses are mostly represented by *Festuca orthophylla*, which reaches high cover in most of the relevés. The ground layer is represented by

few species with relatively higher cover: *Dissanthelium calycinum*, *Hypochaeris meyeniana*, *Brayopsis calycina*, *Werneria pectinata*, *Belloa piptolepis*, *Astragalus minimus*, *Werneria apiculata*, *Aciachne pulvinata*, *Bouguiera nubicola*, *Oreomyrrhis andicola*, the dwarf shrub *Tetraglochin cristatum*, among others. The absence of *Festuca dolichophylla* and *Baccharis tricuneata* is diagnostic. Ferns are absent. The mat-forming *Astragalus minimus* is dominant and forms dwarf and compact mats that extend to 30–40 cm in diameter; in common with other species of cushion plants, these cushion plants also host other species. This association is negatively characterized by the absence of *Azorella compacta*.

Diagnostic species: Character species are: *Astragalus minimus*, *Azorella diapensioides*, *Bouguiera nubicola*, *Junellia minima*, *Nototriche turritela*, *Nototriche longirostris*, *Ourisia muscosa*, *Viola hillii* and *Werneria apiculata*. Differential species include: *Crassula connata*, *Gomphrena meyeniana*, *Oxalis calachaccensis*, *Cyperus seslerioides* and *Lupinus cuzcensis*.

Ecology and distribution: The association develops between 4460–4670 m altitude, covering extensive plateaus on slopes of about 11° with varied aspect. Soil texture is composed of fine scree, clay and sandy clay, with few rocks and stones. The association occurs in the highlands of the Ichuña district, near Cachilaya, Coriri, Jatun Puqio and Qhaqhaskinkri and the southern lower slopes of Pirhuani peak (Ubinas district). The association borders the syntaxa formed by *Azorella compacta*, grasslands and chasmophytic units.

Subassociation Typicum

(Table 2, col. 2.1; Supplementary Table S2, Typus: Rel. 6).

Physiognomy and composition: Characterized by the abundance of *Astragalus minimus* together with *Azorella diapensioides*, *Pycnophyllum molle*, *Tetraglochin cristatum* and *Werneria melanandra*. Other differences include the absence of several species belonging to the plateaus, which have greater species diversity, probably because more nutrients are available in the soil.

Diagnostic species: The subassociation typicum is differentiated by *Werneria melanandra*, *Nototriche longirostris* and *Junellia minima*.

Ecology and distribution: This subassociation develops on plateaus and slopes with a mixture of clayey sand and scree with concentrations of copper minerals, at altitudes ranging from 4580 to 4590 m in the sector of Puqa Saya, in the Ichuña district.

aciachnetosum pulvinatae subass. nov.

(Table 2, col. 2.2; Supplementary Table S2, Typus: Rel. 20).

Physiognomy and composition: By comparison with the *subassociation typicum*, the herb layer is more species-rich, herbs and cushions are more abundant; *Azorella diapensioides* is common.

Diagnostic species: The subassociation is species-rich and many differential species were identified: *Aciachne pulvinata*, *Belloa schultzei*, *Conyza deserticola*, *Crassula connata*, *Cyperus seslerioides*, *Mancoa hispida*, *Ourisia muscosa*, *Oxalis calachaccensis* and *Viola hillii*.

Ecology and distribution: The vegetation of this subassociation grows on extensive plateaus covered by clayey sand and with a relatively high cover of stones; rocks are almost absent. The subassociation develops at altitudes between 4460 and 4670 m a.s.l. greatly in slope orientation, rockiness percentage and grazing.

Astragalo pusilli-Parastrephietum quadrangularis ass. nov.

(Table 2, col. 3.1–3.3; Table 3, col. 3; Supplementary Table S3, Typus: Rel. 20; Figure 3A).

Physiognomy and composition: The association is characterized by the co-occurrence of the aromatic shrub *Senecio nutans* and the leptophyllous shrub *Parastrephia quadrangularis*. Ref. [19] refer to this association as orotropical and dry, situated on volcanic sediments and alluvial materials from the Pleistocene, which form large rocky slopes with soils of variable depth.

Diagnostic species: The following species can be considered to be character species of this association: *Astragalus pusillus*, *Sisyrinchium brevipes*, *Sisyrinchium trinervis*, *Laennecia artemisioides* and with lower frequency *Valeriana aschersoniana*, *Belloa longifolia*, *Descurainia* sp. (# 0940) and *Junellia pappigera*.

In addition, species such as the nitrophilous *Perezia multiflora*, *Galium corymbosum*, *Loricaria graveolens*, *Oxalis nubigena*, *Lobivia maximiliana*, *Asplenium peruvianum*, *Adesmia spinosissima*, *Oxalis debilis* and *Weberbaueria peruviana* are considered to be differential against the other alliances. This association differs from other similar associations by the permanent presence of *Parastrephia quadrangularis*, *Azorella compacta* and the tussock *Stipa ichu*. In contrast with other associations described for the same class, *Gomphrena meyeniana*, *Senecio evacoides*, *Pycnophyllum glomeratum*, *Nototriche mandoniana* and *Werneria aretioides* are absent.

Ecology and distribution: The *Astragalo pusilli-Parastrephietum quadrangularis* is widespread on the southern slopes of Peru in areas with intense grazing. In our study area it occurs between 4450–4560 m a.s.l. The association develops on slopes (mean inclination: 22°) with a relatively high cover of rocks (mean: 28%) and stones (20%). We distinguished three new subassociations distributed in the Rancho-Pirhuani area and environs of Condor Sallana, near Matazo locality (Ubinas district), Siliaca (Yunga district) and Qhaqhaskinkri in the Ichuña district.

sisyrinchietosum trinervis subass. nov.

(Table 2, col. 3.1; Supplementary Table S3, Typus: Rel. 3).

Physiognomy and composition: Characterized by the relative abundance of *Sisyrinchium trinervis* together with *Pycnophyllum molle*, *Paronychia andina* and *Parastrephia quadrangularis*. Annual herbs are relatively abundant but low in cover; like the cushions and shrubs, their cover is between 15 and 20%. The cushion *Azorella compacta* is present in four relevés.

Diagnostic species: The *sisyrinchietosum trinervis* is differentiated by *Sisyrinchium trinervis* and *Nototriche digitulifolia*.

Ecology and distribution: The *sisyrinchietosum trinervis* grows on bare soils on slopes with 5–20° inclination and facing N to NE. Rocks cover between 25–50% and stones between 10–15%. Three out of ten relevés appeared to be intensively grazed. The *sisyrinchietosum trinervis* occurs around 4450 m a.s.l. in the Rancho-Pirhuani area, near Tassa locality in the Ubinas district and it borders the chasmophytic *Loricario graveolentis-Pycnophylletum mollis* [51] and the *Calamagrostion minima* (this study, [51]).

baccharidetosum tricuneatae subass. nov.

(Table 2, col. 3.2; Supplementary Table S3, Typus: Rel. 8).

Physiognomy and composition: Characterized by the abundance of *Baccharis tricuneata* together with *Stipa ichu*, *Azorella compacta*, *Parastrephia quadrangularis* and *Belloa piptolepis*. The herb layer is dominated by *Calamagrostis vicunarum*, *Werneria pectinata*, *Galium corymbosum* and *Bartsia diffusa*. The cushion *Pycnophyllum molle* occurs in four relevés and *Senecio nutans* is found in five relevés only.

Diagnostic species: The *baccharidetosum tricuneatae* is mainly differentiated by *Baccharis tricuneata*, *Cumulopuntia boliviana* subsp. *ignescens*, *Galium corymbosum*, *Bartsia diffusa*, *Senecio nutans*, *Oxalis nubigena*, *Perezia multiflora*, *Muhlenbergia peruviana*, *Werneria pectinata* and by some other species with low cover only, such as *Descurainia* sp. (# 0940), *Junellia pappigera* and *Valeriana aschersoniana*.

Ecology and distribution: This subassociation develops on plateaus and slopes with clayey soils; rocks cover 20–50% of the surface. Most relevés are intensively grazed and contain manure. The *baccharidetosum tricuneatae* grows around 4500 m a.s.l. Its vegetation cover is about 45%. It is found in the surroundings of the road between Carmen Chaclaya and Matazo sites in the Ubinas district.

Subassociation Typicum

(Table 3, col. 3.3; Supplementary Table S3, Typus: Rel. 20).

Physiognomy and composition: By comparison with the other subassociations of the *Astragalo pusilli-Parastrephietum quadrangularis*, the vegetation cover and species richness are higher. The species composition comprises several companions such as: *Adesmia spinosissima*, *Astragalus peruvianus*, *Bartsia diffusa*, *Calamagrostis curvula*, *Galium corymbosum*, *Geranium sessiliflorum*, *Lepidium meyenii*, *Luzula vulcanica*, *Microsteris gracilis*, *Paronychia andina*,

Senecio nutans and *Stipa ichu*, the last species probably as an effect of grazing. The shrub *Parastrephia quadrangularis* is abundant and covers 10–15%, the cushion *Azorella compacta* also attains a high cover compared to the other units, and so does the spiny shrub *Tetraglochin cristatum*.

Diagnostic species: This subassociation is mainly differentiated by *Astragalus pusillus*, *Sisyrinchium brevipes* and *Conyza* sp. (# 2601), but also by the low frequency of *Cardionema ramosissimum* and *Mancoa hispida*.

Ecology and distribution: The *subassociation typicum* occurs at altitudes averaging 4500 m on stony slopes in the Coriri and Qhaqhaskinkri sites in the Ichuña district. On average, the measured pH was 5.6.

Senecioni moqueguensis-Pycnophylletum mollis ass. nov.

(Table 2, col. 4.1–4.4; Table 3, col. 4; Supplementary Table S4, Typus: Rel. 7; Figure 4).



Figure 4. Overview of the extensive slopes with *Senecioni moqueguensis-Pycnophylletum mollis sub-association typicum* in the surroundings of the group of lakes between the localities of Coalaque and Querala, in the Ubinas district at an altitude of 4550 m a.s.l. Species visible in the Figure: *Azorella compacta* (cushion), *Festuca orthophylla* (tussock grass), *Baccharis tricuneata* and *Parastrephia lucida* (shrubs).

Physiognomy and composition: Plateau vegetation with abundant cushion and mat-forming plants. Vegetation cover varies between 30–70%. Bare soil is frequently covered by fine stone particles. Shrubs are less frequent and cover between 4–8% (20–40 cm height); they are mainly represented by *Baccharis tricuneata* and *Parastrephia lucida*.

Diagnostic species: Character species are *Senecio moqueguensis*, *Senecio tassaensis*, *Nototriche sepaliloba*, *Cerastium behmianum*, *Oritrophium* sp. (# 2194b), *Werneria heteroloba*, *Xenophyllum weddellii*, *Nototriche argentea*, *Arenaria acaulis*, *Gentainella primuloides*, and some other species with lower presence like *Perezia coerulescens* var. *amplibracteata* and *Senecio* sp.1 (# 4217a). Differentials against other associations include: *Mniodes coarctata*, *Geranium sessiliflorum*, *Calandrinia acaulis*, *Hypochaeris eriolaena* and *Werneria aretioides*.

Ecology and distribution: The vegetation represented by the *Senecioni moqueguensis-Pycnophylletum mollis* spreads over areas with partial rock cover (13%) and stones (28%) on the extensive plateaus at an altitude of 4500–4830 m in North Moquegua. The slopes (about 11° with varied aspect) for this association are characterized by the abundance of the cushion *Pycnophyllum molle* and, with less presence, *Azorella compacta*. Wild animals were seen in the landscape during fieldwork. Dung from domesticated bull (*Bos taurus*), vicuña (*Vicugna vicugna*) and deer (*Hippocamelus antisensis*) was recognized in a few relevés across the sites. There were no signs of grazing. The wild animals tend to graze other species such as small grasses and herbs. The distribution is limited to Gasawasi-Witopata plateaus, the northern lower slopes of Pirhuani peak, the extensive plateaus surrounding the group of lakes upslope Coalaque and Querala localities, the Matazo locality environs (Ubinas district) and the Choco-Choco lower mountain slopes in Yunga district.

Subassociation typicum

(Table 2, col. 4.1; Supplementary Table S4, Typus: Rel. 7).

Physiognomy and composition: By comparison with the other subassociations of the *Senecioni moqueguensis-Pycnophylletum mollis*, the vegetation attains lower cover and lower species richness. Stones (24%) have a higher cover than rocks (9%). The cushion *Pycnophyllum molle*, *Senecio moqueguensis* (mat-forming), *Mniodes* sp. (# 2477) (a rigid cushion with grayish leaves in a rosette and inconspicuous yellow flowers) and *Azorella compacta* are frequent. Tussock grasses are represented by *Festuca orthophylla* in twelve relevés. Shrubs are well represented by *Baccharis tricuneata* and *Parastrephia lucida*.

Diagnostic species: This subassociation typicum is differentiated by *Mniodes* sp. (# 2477), *Myrosmodes* sp. (# 2287), *Lupinus* sp. (# 2424) and *Senecio scorzoniferifolius*. *Weberbaueria spathulifolia*, *Hypochaeris eriolaena*, *Poa candamoana*, *Perezia coerulescens* and *Lepidium meyenii* are differential against the other subassociations.

Ecology and distribution: The subassociation typicum grows between 4530 and 4700 m, on the extensive plateaus (5–20°) and rocky slopes (20–45°) of the Gasawasi-Witopata site, the northern lower slopes of Pirhuani peak, the extensive plateaus surrounding the group of lakes upslope Coalaque and Querala localities (Ubinas district) and the Choco-Choco lower mountain slopes in Yunga district. Vegetation cover attains 20–70%; soils are mainly clayey sands.

senecionetosum tassaensis subass. nov.

(Table 2, col. 4.2; Supplementary Table S4, Typus: Rel. 17).

Physiognomy and composition: Characterized by the low abundance of *Xenophyllum weddellii* and of *Stangea wandae*. *Pycnophyllum molle*, *Senecio moqueguensis*, *Werneria aretioides* and *Belloa piptolepis* attain high cover. Other differences include the absence of shrubs, except for *Tetraglochin cristatum*, which acquires a decumbent habit on the slopes. The cushion *Azorella compacta* is less frequent in the company of *Pycnophyllum molle*. Species richness is relatively high, probably due to the presence of species related to grazing and manure.

Diagnostic species: The senecionetosum tassaensis is mainly differentiated by species such as *Senecio tassaensis*, *Xenophyllum weddellii*, *Oritrophium* sp. (# 2194b) and *Werneria heteroloba*.

Ecology and distribution: This subassociation develops on plateaus (5°) and slopes (8–14°) with a mixture of clayey sand, at altitudes between 4510 and 4700 m on the northern plateaus of the Ubinas district.

gentianelletesum primuloides subass. nov.

(Table 2, col. 4.3; Supplementary Table S4, Typus: Rel. 33).

Physiognomy and composition: This subassociation is characterized by thirty-four species recorded from 7 relevés. *Senecio moqueguensis* has low constancy and cover and occurs in combination with *Pycnophyllum molle*, *P. glomeratum*, *Azorella compacta*, *Festuca orthophylla*, *Parastrephia lucida* and *Stangea rhizantha*.

Diagnostic species: The gentianelletesum primuloides is differentiated by species such as *Gentianella primuloides*, *Senecio graveolens*, *Xenophyllum digitatum* and *Viola* sp. (# 4217a).

Ecology and distribution: The gentianelletesum primuloides grows between 4590 and 4680 m, on the extensive plateaus (5–10°) of the Yunga district. Vegetation cover attains 35–65%.

arenarietosum acaulis subass. nov.

(Table 2, col. 4.4; Supplementary Table S4, Typus: Rel. 41).

Physiognomy and composition: Characterized by the abundance of *Senecio moqueguensis* together with *Pycnophyllum molle*, *Azorella compacta*, *Parastrephia lucida*, *Mniodes coarctata* and *Werneria pectinata*.

Diagnostic species: The arenarietosum acaulis is differentiated by *Arenaria acaulis*, *Nototriche sepaliloba*, *Cerastium behmianum*, *Nototriche pusilla*, *Senecio sykora*, *Poa brevis*, *Spergularia andina* and *Werneria* sp. (# 3940).

Ecology and distribution: The vegetation of the subassociation grows on rocky soils, on slopes and plateaus at altitudes averaging 4580 m in the Condor Sallana environs close to Matazo locality (Ubinas district).

Calamagrostio trichophyllae-Azorelletum compactae ass. nov.

(Table 2, col. 5.1–5.2; Table 3, col. 5; Supplementary Table S5, Typus: Rel. 14; Figure 5).



Figure 5. Overview of the scree slopes with cushions of *Azorella compacta* on the lower slopes of Choco-Choco mountain in the Yunga district at 4750 m a.s.l.

Physiognomy and composition: In a total of twenty-two relevés many endemics from Peru were recorded. Shrubs are more frequent than in the preceding associations. The diagnostic cushion *Azorella compacta* can reach up to 50 cm in height with 1.5 m of diameter. Other cushions and mat-forming species are also common (*Pycnophyllum molle*, *P. glomeratum*, *Brayopsis calycina*, *Senecio humillimus*, *S. evacoides*, *Erigeron rosulatus*), together with many rosette herbs and grasses. Shrubs are mostly represented by the constant *Parastrephia lucida* and, with low cover, also by *Baccharis tricuneata*, *B. caespitosa*, *Senecio nutans* and the caespitose chamaephyte *Ephedra rupestris*. Cacti are represented by the cushion-forming *Cumulopuntia boliviana* subsp. *ignescens*. *Tetraglochin cristatum* is absent.

Diagnostic species: Diagnostic species of this species-rich association are *Calamagrostis trichophylla*, *Nototriche mandoniana*, *Silene mandonii* and *Perezia pungens*. Character species are the following: *Chaetanthera peruviana*, *Cumulopuntia boliviana* subsp. *ignescens*, *Microsteris gracilis*, *Plantago sericea* var. *lanuginosa*, *Poa candamoana* and *Stangea rhizantha*.

Ecology and distribution: The vegetation of this association is widely distributed on steep rocky slopes and plateaus with clayey-sandy soils and scree. This vegetation grows on the highest peaks and plateaus of the study sites between 4590–4800 m in Yanapuquio (Ichuña district), Laguna Jallpacocho environs (Ubinas district) and Perusa (Yunga district). The vegetation consists of both annual and perennial species.

Subassociation typicum subass. nov.

(Table 2, col. 5.1; Supplementary Table S5, Typus: Rel. 14).

Physiognomy and composition: The shrub *Parastrephia lucida* is abundant and covers 8–13%. The cushions *Azorella compacta* are as well represented as those of *Pycnophyllum molle* and also have a relatively high cover and presence.

Diagnostic species: This subassociation is differentiated by *Mniodes caespititia*, *Senecio* sp.2 (# 3935), *Erigeron lanceolatus*, *Werneria glaberrima* and *Nototriche pedatiloba*. *Stangea rhizantha*, *Microsteris gracilis* and *Cumulopuntia boliviana* subsp. *ignescens* are differentials against the other subassociation.

Ecology and distribution: The vegetation of the subassociation occurs at an altitude of between 4715 and 4800 m on slopes with a mixture of scree and sandy-clay and has a wide distribution on the lower slopes of the Choco-Choco Mountain (Yunga district).

drabetosum soratensis subass. nov.

(Table 2, col. 5.2; Supplementary Table S5, Typus: Rel. 20).

Physiognomy and composition: This subassociation is characterized by high species diversity; 44 species were recorded from 7 relevés. *Draba soratensis* has high constancy and cover and occurs in combination with *Azorella compacta*, *Pycnophyllum molle*, *Parastrephia lucida*, *Baccharis caespitosa*, *B. tricuneata*, *Ephedra rupestris*, *Belloa piptolepis*, *Pycnophyllum glomeratum* and *Poa candamoana*.

Diagnostic species: The *drabetosum soratensis* is differentiated by *Draba soratensis*, a dwarf rosette herb with greenish ciliated leaves and white flowers, and by species such as *Bartsia* sp. (# 3092), *Poa gilgiana*, *Agrostis breviculmis*, *Lupinus chilensis* and *Viola granulosa*.

Ecology and distribution: The *drabetosum soratensis* grows between 4590 and 4665 m on the summits and slopes of the mountains north of the Ichuña locality in the Yanapuquio site (Ichuña district).

Assoc: *Nototricho obcuneatae-Xenophylletum poposi* Galán de Mera, Cáceres & González 2003

(Table 2, col. 6.1–6.2; Table 3, col. 6; Supplementary Table S6; Figure 6).



Figure 6. Overview of the *Nototricho obcuneatae-Xenophylletum poposi* on the summits of Pirhuani peak (4730 m a.s.l.) in the Ubinas district. Occasional snow cover occurs during the rainy season.

Physiognomy and composition: Plateau vegetation with abundance of cushions represented by *Mniodes coarctata* (5–10 cm height, 40–60 cm of diameter) and *Senecio adenophyllum* (60–80 cm) and *Xenophyllum poposum* (10–20 cm). The vegetation cover is 10–50%. The shrub layer is composed of *Senecio adenophyllum*, *Xenophyllum poposum*, and with a lower cover of *Parastrephia lucida* and *Senecio nutans*. In the herb layer cushions are relatively abundant (*Mniodes coarctata*, *Pycnophyllum molle*, *P. glomeratum*), attaining 10–20% of the total percentage cover. The herbs comprise *Anthochloa lepidula* and *Calamagrostis curvula*.

Diagnostic species: Character species are *Xenophyllum poposum* and *Mniodes coarctata*. Moreover, *Senecio tassaensis*, *Pycnophyllum molle*, *Werneria pectinata*, *Mniodes* sp. (# 2477) and *Astragalus uniflorus* are differential species against the other syntaxa of the *Nototrichion obcuneatae*.

Ecology and distribution: The *Nototricho obcuneatae-Xenophylletum poposi* grows at 4650–4735 m on 2–10° slopes (facing N, NE, NNW, S, SE, SSE, W or WNW). The superficial, stony and bare soils occur on the summits of the Pirhuani peak (Ubinas district), the lower mountain peaks of Choco-Choco (Yunga district) and the scree plateaus of the puna desert of the Janchata lower slopes (Carumas district).

nototrichietosum erinaceae subass. nov.

(Table 2, col. 6.1; Supplementary Table S6, Typus: Rel. 6).

Physiognomy and composition: By comparison with the other subassociation of the *Nototricho obcuneatae-Xenophylletum poposi*, the vegetation attains higher cover and species richness. Stones (40%) have a higher cover than rocks (4%). The cushion-forming *Pycnophyllum molle*, *Mniodes coarctata* and *Pycnophyllum glomeratum* are frequent. Tussock grasses are absent. Shrubs are represented by *Senecio nutans* and *Parastrephia lucida*, both with low cover.

Diagnostic species: This subassociation is differentiated by *Nototriche erinacea*. Differentials against the other subassociation are: *Pycnophyllum molle*, *P. glomeratum*, *Senecio nutans*, *S. tassaensis*, *Parastrephia lucida*, *Luzula vulcanica* and *Mniodes* sp. (# 2477)

Ecology and distribution: The *nototrichietosum erinaceae* grows between 4650 and 4735 m, on the extensive plateaus (5–10°) of the Pirhuani peak (Ubinas district) and the lower mountain peaks of Choco-Choco (Yunga district). Vegetation cover attains 20–45%; soils are a mixture of clayey sand.

senecionetosum trifurcifolii subass. nov.

(Table 2, col. 6.2; Supplementary Table S6, Typus: Rel. 14; Figure 7).



Figure 7. Overview of the scree and volcanic sand deposits at the Janchata lower slopes (4700 m a.s.l.) where *Nototricho obtusatae*-*Xenophylletum poposi senecionetosum trifurcifolii* occurs.

The description of this subassociation is based on 5 relevés containing 12 vascular species.

Physiognomy and composition: Association of vegetation growing on a mixture of scree and volcanic sand deposits, with low diversity of species and extensive bare soils. It consists of 4–20 cm tall resinous shrubs (*Senecio trifurcifolius*) with a cover of 5–10% in combination with few grasses and herbs attaining less than 5% cover. The cushion *Mniodes coarctata* and mat-forming *Xenophyllum poposum* co-occur with a cover of 5–7%.

Diagnostic species: Character species are *Senecio trifurcifolius* and *Senecio* sp.4 (# 4228b). Differentials against the other subassociation are *Nototriche obtusata* and *Trisetum spicatum*.

Ecology and distribution: This Andean chasmophyte subassociation is generally found on the extensive plateaus formed by the volcanic lower slopes and locally known as “puna desert”. It is located at altitudes of 4700–4710 m (probably extending up to 4800 m a.s.l.), and a slope of 5–10° facing southeast. The soils are mainly formed by scree and white volcanic sand deposits. This vegetation can be found on the Janchata lower slopes (Carumas district) and presumably also occur on the lower pumice slopes of the Huaynaputina and Ticsani volcanoes. It is worth mentioning that several herds of vicuña (*Vicugna vicugna*) were seen during fieldwork.

Poa aequiglumae-*Xenophylletum dactylophylli* ass. nova

(Table 2, col. 7; Table 3, col. 7; Supplementary Table S7, Typus: Rel. 2).

Five relevés were made, containing 15 species.

Physiognomy and composition: Characteristic are the rocky and scree slopes with low vegetation cover and low species diversity. The resinous dwarf shrub *Xenophyllum dactylophyllum* is common, together with the short grass *Anthochloa lepidula* and the ground rosette *Nototriche obtusata*. Vegetation cover is about 10–15%. Cushion plants are almost absent, except for *Pycnophyllum glomeratum*, which was found in only one relevé, with low cover. Shrubs are represented by *Senecio nutans* and *Parastrephia lucida* with very low cover. Tussock grasses are absent.

Diagnostic species: Character species are *Xenophyllum dactylophyllum*, *Nototriche* sp.3 (# 2447), *Poa aequigluma* and *Poa spicigera*.

Ecology and distribution: Cryotropical association with SSW aspect, with extension to an altitude of 4800 m a.s.l. The association was only found on the Choco-Choco rocky slopes (Yunga district) and is assumed to occur on other slopes and summits above 4800 m in the neighboring departments in South Peru.

5. Community of *Senecio algens*

(Table 2, col. 8; Table 3, col. 8; Supplementary Table S8, representative Rel. 2).

Physiognomy and composition: Almost bare scree slopes with low species diversity. The unique appearance of the shrub *Senecio* sp.5 (# 3942) (apparently a new species) is very characteristic of the landscape and the less than 10 cm high *Senecio algens* develops with low cover between the scree stones. 90% of the soils are formed by white scree and rarely

by volcanic rocks (except in one relevé). Vegetation cover is about 5%, the slope is 35–45°, facing W or NW.

Diagnostic species: Characteristic species are *Senecio algens* and *Senecio* sp.5 (# 3942). *Stangea rhizantha* is differential against the other units of the alliance.

Ecology and distribution: Cryrotropical community distributed at about 4750 m a.s.l. The community was only found on the Choco-Choco scree slopes (Yunga district) and is assumed to occur on other mountain summits above 4700 m in the neighboring departments of South Peru. Ref. [22] recognized the occurrence of the community at lower altitude with a mixture of species belonging to grasslands. Ref. [64] indicates that *S. algens* can be found on chasmophytic rocky slopes as well as in cryoturbate conditions, however, [22] recognized the occurrence of the community at lower and higher altitude with a mixture of species belonging to the puna grasslands.

Tarasa nototrichoides and *Urtica flabellata* community

(Table 2, col. 9; Table 3, col. 9; Supplementary Table S9, representative Rel. 8, Figure 8).



Figure 8. Detail of *Urtica flabellata* among llama and alpaca dung at 4460 m a.s.l.

Physiognomy, composition and syntaxonomy: Due to the nitrogen-rich accumulations of manure, species such as *Urtica flabellata* become dominant; in some areas, together with other species, it covers almost 100% of the soil surface.

Diagnostic species: *Urtica flabellata*, *Jaborosa squarrosa* and *Valeriana* sp. (Image DSC075, 03/2014) have only been found in this community. Other diagnostic species are *Lachemilla pinnata*, *Perezia multiflora* and *Tarasa nototrichoides*. *Dissanthelium calycinum* occurs in all relevés.

Ecology and distribution: Nitrophilous community growing on llama and alpaca patches in grassland plateaus near grazing sites. The vegetation typically develops during the rainy season within a short 2–3-month period. The community of *Tarasa nototrichoides* and *Urtica flabellata* can be found between 4460 to 4650 m in North Moquegua, in a wide variety of habitats. Ref. [46] Includes the distribution of *Urtica flabellata* in the high Andes from Colombia to Argentina; therefore this puna and superpuna community can be assumed to occur in a wide geographical area in the high Andes. The ecological and floristical optimum for this unit is found in the orotropical and cryrotropical bioclimatic belts. The distribution range of the unit is approximately between 4000–4800 m a.s.l.

6. Gradients and Zonation

As after the first DCA with all 153 samples the relevés clearly fell into two very dissimilar groups representing very different site conditions, subsequently two separate analyses were performed. One group contains the grasslands and tussock vegetation of the *Calamagrostion* and *Azorello-Festucion* and the other group consists of vegetation growing on

mobile scree slopes (*Nototrichion*). The DCA diagrams (Figures 9 and 10) show the relation between the vegetation units and environmental variables. In Figure 9, the main gradient in species composition (axis 1) is strongly correlated with altitude ($r = 0.65$), scree ($r = 0.31$), vegetation cover ($r = -0.24$), grazing ($r = -0.22$), manure ($r = -0.16$), stones ($r = 0.03$) and number of species ($r = -0.06$). The relation between the second axis and environmental variables is low, except for number of species ($r = 0.34$), vegetation cover ($r = 0.31$) and slope inclination ($r = 0.27$).

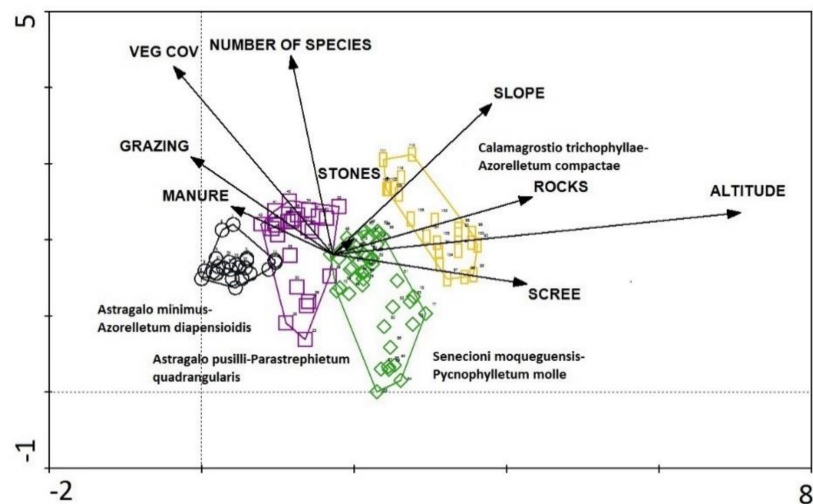


Figure 9. Ordination diagram (DCA, axis 1 and 2) of associations 2–5. The relevés belonging to the 4 different associations have been delineated. # SPP refers to the total number of species, % rocks and stones = estimated cover of rocks and stones in each relevé. VC refers to total vegetation cover, altitude is expressed in meters above sea level, manure and grazing is expressed in I: 1–30%; II: 31–70%; III: >71%, and scree is expressed by the percentage total cover.

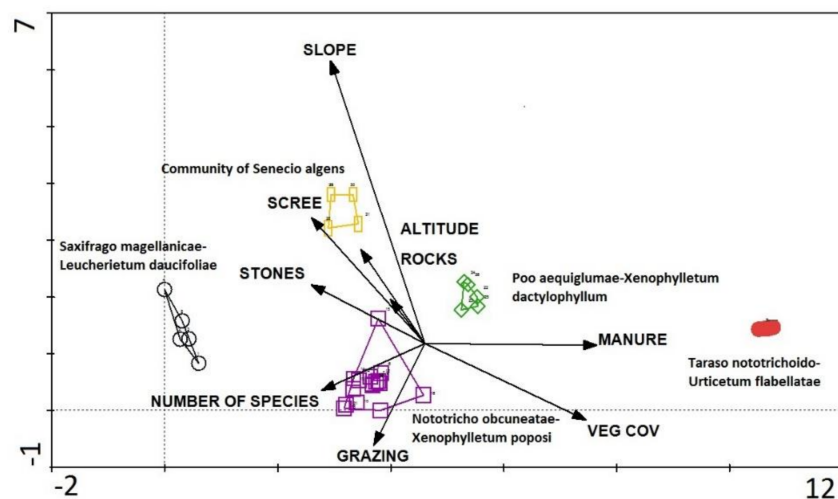


Figure 10. Ordination diagram (DCA, axis 1 and 2) of communities 1, 6–9. The relevés of three associations, one community and one provisional association have been delineated. For caption definitions refer to Figure 9.

The grasslands with cushions (*Astragalo pusilli-Parastrephietum quadrangulare* and *Astragalo minimi-Azorelletum diapensioidis*) are positively correlated with grazing, number of species, vegetation cover and manure. The cushion association (*Senecioni moqueguensis-Pycnophylletum mollis*) is correlated with rocks, altitude and scree. The other cushion

associations from higher altitudes (*Calamagrostio trichophyllae-Azorelletum compactae*) are correlated with altitude, percentage of stones, slope and rocks.

In Figure 10, the main gradient in species composition (axis 1) is strongly correlated with vegetation cover ($r = 0.81$), manure ($r = 0.88$), and further with stone cover percentage ($r = -0.57$), scree ($r = -0.56$), number of species ($r = -0.54$), slope inclination ($r = -0.43$), altitude ($r = -0.31$), grazing ($r = -0.28$), and rock percentage ($r = -0.16$). The relation between the second axis and environmental variables is relatively low except, for inclination ($r = 0.67$), grazing ($r = -0.29$), scree ($r = 0.25$), altitude ($r = 0.20$) and number of species ($r = -0.19$). The nitrophilous community of *Tarasa nototrichoides* and *Urtica flabellata* is positively correlated with manure and vegetation cover and negatively correlated with stones, scree, slope, number of species and rock percentage. The chasmophytic unit, *Saxifraga magellanicae-Leucheriaetum daucifoliae*, plotted on the lower side of axis 2 is positively correlated with number of species, stones, slope and scree but negatively with manure and vegetation cover.

The *Nototricho obtusatae-Xenophylletum poposi* correlated positively with number of species and negatively with manure and vegetation cover. The community of *Senecio algens* shows a positive correlation with scree, stone percentage and slope degree.

The relation between vegetation and environmental factors as shown by the ordination diagrams corresponds to the results as shown by Figure 11 in which the mean values for (a) slope degree, (b) vegetation cover, (c) rocks and (d) stones are given. The *Calamagrostio trichophyllae-Azorelletum compactae* develops on steeper slopes, as does the community of *Senecio algens*. In contrast, the community of *Tarasa nototrichoides* and *Urtica flabellata* develops on level surfaces. In graph b, vegetation cover is higher in the following units: community of *Tarasa nototrichoides* and *Urtica flabellata*, *Astragalo pusilli-Parastrephietum quadrangulare subassociation typicum*, *Astragalo minimi-Azorelletum diapensioidis aciachnetosum pulvinatae* and *Senecioni moqueguensis-Pycnophylletum mollis subassociation typicum*. The lowest vegetation cover (less than 20%) was recorded for the community of *Senecio algens*, *Nototricho obtusatae-Xenophylletum poposi senecionetosum trifurcifolii*, *Poo aequiglumae-Xenophylletum dactylophylli* and *Astragalo pusilli-Parastrephietum quadrangulare sisyrrinchietosum trinervis*. *Astragalo pusilli-Parastrephietum quadrangulare* grows on sites with a high rock cover. This is especially the case in two subassociations belonging to this association: the *sisyrrinchietosum trinervis* and *baccharidetosum tricuneatae*. The mean rock cover is less than 10% in the *Saxifraga magellanicae-Leucheriaetum daucifoliae* (comm. 1), *Astragalo pusilli-Azorelletum diapensioidis* (comm. 2) and community of *Senecio algens* (comm. 8). The community of *Tarasa nototrichoides* and *Urtica flabellata* (comm. 9) grows on sites without bare rock.

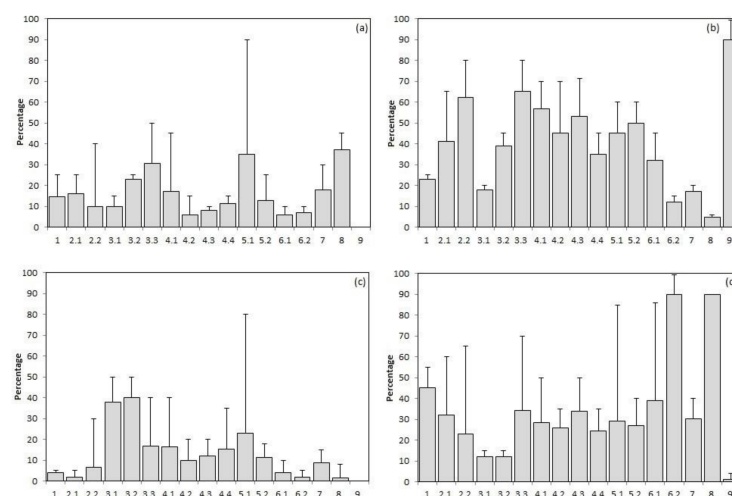


Figure 11. Bar charts showing the mean percentage values with standard deviation for (a) slope degree, (b) vegetation cover, (c) rocks and (d) stones.

In the community of *Senecio algens* (comm. 8) the surface is almost fully covered by stones (>90%) as well as in the *Nototricho obcuneatae-Xenophylletum poposi senecionetosum trifurcifolii*. Within the *Saxifraga magellanicae-Leucherietum daucifoliae* (comm. 1) the stone cover is 40 to 50%. Stones are almost absent in the community of *Tarasa nototrichoides* and *Urtica flabellata* (comm. 9).

Figure 12 shows the observed and expected altitudinal distribution of the syntaxa described in this overview. The gray boxes represent the distribution as based on the present field survey and the boxes in dashed lines the expected distribution based on the co-occurrence of the following character species of the syntaxa distinguished [48,65–67]: *Saxifraga magellanica* with *Leucheria daucifolia*; *Astragalus minimus* and *Azorella diapensioides*; *Senecio nutans* and *Parastrephia quadrangularis*; *Senecio moqueguensis* together with *Azorella compacta*; *Anthochloa lepidula* and *Azorella compacta*; *Nototriche obcuneata* with *Xenophyllum poposum*; *Xenophyllum dactylophyllum*; *Senecio algens*; *Dissanthelium calycinum* with *Urtica flabellata*. The expected altitudinal distribution of the different associations and community of *Tarasa nototrichoides* and *Urtica flabellata* is as follows: (1) *Saxifraga magellanicae-Leucherietum daucifoliae* (4500–4800 m a.s.l.), (2) *Astragalo minimi-Azorelletum diapensioidis* (4350–4700 m a.s.l.), (3) *Astragalo pusilli-Parastrephietum quadrangularis* (4250–4650 m a.s.l.), (4) *Senecioni moqueguensis-Pycnophylletum mollis* (4500–4800 m a.s.l.), (5) *Calamagrostio trichophyllae-Azorelletum compactae* (4550–4800 m a.s.l.), (6) *Nototricho obcuneatae-Xenophylletum poposi* (4600–4800 m a.s.l.), (7) *Poo aequiglumae-Xenophylletum dactylophylli* (4750–4950 m a.s.l.), (8) Community of *Senecio algens* (4450–4800 m a.s.l.) and (9) community of *Tarasa nototrichoides* and *Urtica flabellata* (4200–4700 m a.s.l.).

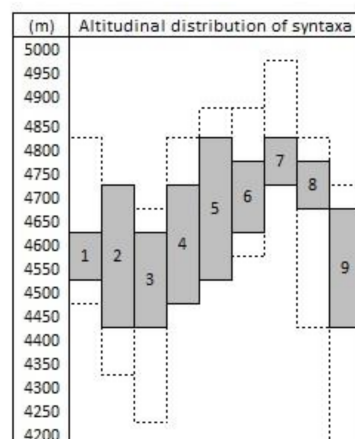


Figure 12. Altitudinal distribution of syntaxa (association, subassociation) and communities of the study area based on the relevés (solid lines) and references and field observations (dashed lines) from Moquegua by the first author [43–45,48]. (1) *Saxifraga magellanicae-Leucherietum daucifoliae*, (2) *Astragalo minimi-Azorelletum diapensioidis*, (3) *Astragalo pusilli-Parastrephietum quadrangularis*, (4) *Senecioni moqueguensis-Pycnophylletum mollis*, (5) *Calamagrostio trichophyllae-Azorelletum compactae*, (6) *Nototricho obcuneatae-Xenophylletum poposi*, (7) *Poo aequiglumae-Xenophylletum dactylophylli*, (8) Community of *Senecio algens*, (9) community of *Tarasa nototrichoides* and *Urtica flabellata*.

Family composition shows the same trend as observed in the Andean prepuna and puna of Moquegua [35,36], where the Composites dominate the vegetation. In the grasslands of Moquegua, species richness is greatest within the woody species belonging to the Composites, Fabaceae and Orobanchaceae, while in the ground layer the number of species is highest in the Malvaceae, Caryophyllaceae and Poaceae, followed by Plantaginaceae and Violaceae.

7. Floristic Composition Alfa-Diversity

In total, 172 vascular species belonging to 80 genera and 32 families were recorded. The flora list of the total relevé dataset is dominated by Asteraceae (60 spp.), Malvaceae (14

spp.), Poaceae (14 spp.), Brassicaceae (11 spp.), Caryophyllaceae (10 spp.), Fabaceae (9 spp.) and Apiaceae (4 spp.). The shrubs (postrate or erect, 5–70 cm height) are represented by 26 species, herbs (including rosettes) by 93 species, cushions by 14 species, mat-forming plants by 22 species, grasses by 13 species), and ferns and succulents by one species each.

In Figure 13, box-and-whisker plots show the species diversity of the different associations, subassociations and one community. The species richness of the Chasmophytic association can not be compared to the richness of the grassland and cushion vegetation as with 16 m² the plot size is 9 m² smaller (see Figure 13). The chasmophytic association *Saxifraga magellanicae*-*Leucherietum daucifoliae* has a maximum of 15 species and a median of 11 species.

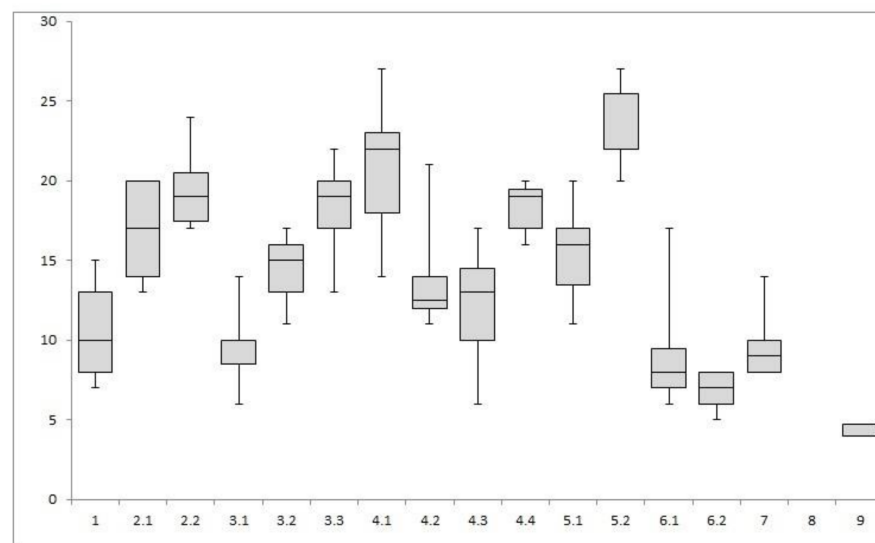


Figure 13. Box-and-whisker plots representing species richness per syntaxon in chasmophyte vegetation (1, plot sizes 16 m²), grasslands with cushions (2–4, 25 m²), cushion communities (5–8, 25 m²) and one nitrophilous unit (9, 1 m²). The line in the boxes represents the median values, the boxes the 25 and 75% percentiles and the lines the minimum and maximum values found in each syntaxon.

The highest species diversity was recorded in the *Senecioni moqueguensis*-*Pycnophylletum mollis* (comm. 4) and *Calamagrostio trichophyllae*-*Azorelletum compactae* (comm. 5), which have a median of 15 species and a maximum of 26 and 25 species respectively. Within the grasslands with cushions, species diversity in the *Astragalo minimi*-*Azorelletum diapensioidis* (comm. 2, median of 18 species and maximum of 23 species) is greater than that of the *Astragalo pusilli*-*Parastrephietum quadrangularis* (comm. 3), median of 13 species and maximum of 22 species. The species diversity is least in the *Nototricho obtusatae*-*Xenophylletum poposi* (comm. 7) and in the community of *Senecio algens* (comm. 9), with a median of 6 species and maximum of 16 species; this is probably due to the extreme conditions in their high altitude growth sites.

The plot sizes of the relevés made in the nitrophilous community are only 1 m² and only 4 to 6 species were counted per plot.

Within the chasmophytic association species richness generally decreases with elevation. However, species richness was observed to increase locally between 4500 and 4700 m in the cushion associations, probably as a result of nursing effects, sometimes in great abundance as seen in *Azorella* and *Pycnophyllum* [8,16]. Although lichens and mosses were not included in our phytosociological analysis, we noted their low diversity in the study sites. Low cover of *Thamnolia vermicularis* was observed in the *Poo aequiglumae*-*Xenophylletum dactylophylli*.

8. Syntaxonomic Affinity

The syntaxonomic relation of the communities described in this research was studied by comparison with literature. A large dataset was collected from [4,20–22,24,25,27,31,32,58–61,68]. After cluster analysis with all data an outgroup was detected and these relevés were excluded from a second run. The remaining 27 clusters are represented in Table 3 in which the species are ordered into syntaxonomic species groups to show their syntaxonomic affinity. New syntaxonomic units were defined after reviewing [20–22,25,27,58,59].

The vegetation of rock crevices, grassland and cushion vegetation, and vegetation of mobile scree slopes could respectively be assigned to the *Argyrochosmetea niveae*, *Calamagrostietea vicunarum*, *Anthochloo lepidulae-Dielsiochloetea floribundae*. The class, order and alliance of the nitrophilous community should be defined by further research.

Based on the presence of *Saxifraga magellanica*, the new association *Saxifrago magellanicae-Leucherietum daucifoliae* has been assigned to the class *Argyrochosmetea niveae*, the order *Saxifragetalia magellanicae* and the alliance *Saxifragion magellanicae*. It grows on deep soils with fine scree across rock crevices, in the north of Moquegua, South Peru. Ref. [61] described the class *Argyrochosmetea niveae* as occurring at an altitude of 2500–3500 m in Junín (Central Peru), with *Argyrochosma nivea*, a fern species characteristic of rock crevices. Ref. [20] confirmed the presence of this species in the south of Peru, and we refer to the *Argyrochosmetea niveae* based on the occurrence of the superpuna alliance *Saxifragion magellanicae* [19] represented by *Saxifraga magellanica*.

The order and alliance combine the basaltic and andesite soils along the Andes of Peru, from Lima to Tacna regions [22].

Saxifraga magellanica grows on the south-facing highlands of the Yanahuara River in the Ichuña district. *Saxifraga magellanica* is a cushion-forming herbaceous rosette with whitish flowers; its distribution area is from Ecuador to South Argentina [46].

Four new associations were assigned to the order *Parastrephietalia quadrangularis* of the class *Calamagrostietea vicunarum* based on the presence of *Calamagrostis vicunarum* and many species of the *Parastrephietalia* (see Table 3).

Reference [22] proposed the class name *Deyeuxietea vicunarum*. According to [46] *Deyeuxia vicunarum* should be considered to be a synonym for *Calamagrostis vicunarum* and *Calamagrostis vicunarum* is the most frequently used name in the main taxonomic databases. Consequently, we suggest that the name *Calamagrostietea vicunarum* Rivas-Martínez & Tovar 1982 should be maintained instead of the new class name *Deyeuxietea vicunarum* Rivas-Martínez & Tovar 1982.

The *Calamagrostietea vicunarum* grows on clay and loamy clay (rarely on sand) on rocky slopes, plateaus and hills at 4450–4800 m a.s.l. in the Andean regions of North Moquegua, downslope it is in contact with the grassland vegetation dominated by *Lupinus paruroensis* and the giant bromeliad *Puya raimondii* and upslope with units of the *Anthochloo-Dielsiochloetea*.

The *Parastrephietalia quadrangularis* combines the puna grasslands extending from southwest Peru to West Bolivia, Northwest Argentina and Northwest Chile.

The *Astragalo minimi-Azorelletum diapensioidis* ass. nov. is assigned to the alliance *Calamagrostion minimae*. It is characterized by the presence of cushion plants, dwarf shrubs, tussock grasses, annual grasses and herbs. The high cover of the cushion *Azorella diapensioides* together with the mat-forming *Astragalus minimus* characterizes the association described within this alliance. The alliance occurs in the grassland puna known as “cesped de puna” formed by small herbs and ground rosettes with long root systems, mostly developing on open and uniform slopes with shallow soils. The alliance is known to occur in the highlands of Peru and Bolivia, between 4500 and 5000 m [29,58].

The *Astragalo minimi-Azorelletum diapensioidis* (*Calamagrostion minimae*) differs greatly from the *Belloo piptolepis-Dissanthelietum calycini azorelletosum diapensioidis* [20] and *Baccharido caespitosae-Azorelletum diapensioidis* [36] because of the absence of *Festuca dolichophylla*, *Baccharis caespitosa* and other elements of the puna. We have included this association in the *Calamagrostion minimae* [29] because of the abundance of cushion plants such as *Azorella*

diapensioides and the presence of small grasses such as *Calamagrostis minima*, and the absence of some species characterizing the *Azorello-Festucion* and *Nototrichion obcuneatae*.

Three new associations, *Astragalo pusilli-Parastrephietum quadrangularis*, the *Senecioni moqueguensis-Pycnophylletum mollis* and the *Calamagrostio trichophyllae-Azorelletum compactae* were assigned to the alliance *Azorello compactae-Festucion orthophyllae* (Supplementary Tables S3–S5).

The grassland with cushion vegetation of South Peru is grouped into the *Azorello compactae-Festucion orthophyllae* [20,21,59]. *Azorella compacta* can be found in some restricted Andean regions in South Peru [6,39,65,69], Bolivia [70], Argentina [71,72] and Chile [73,74]. The *Azorello compactae-Festucion orthophyllae* represents the large tracts of superpuna grasslands in South Peru, in the Moquegua region where *Festuca orthophylla*, *Tetraglochin cristatum*, *Parastrephia quadrangularis* and *P. lucida* are common. *Festuca orthophylla* is the tussock grass that dominates the superpuna grasslands of Moquegua in association with the resinous shrub *Parastrephia quadrangularis*, which is replaced by *Parastrephia lucida* at altitudes higher than 4500 m and is well represented in the superpuna.

The *Azorello compactae-Festucion orthophyllae* comprises vegetation represented by grasslands with cushions, open plateaus with cushions, vertical cushion formations and scree units with cushions and dwarf shrubs. The relatively high presence and cover of the composite resinous shrub *Parastrephia lucida* that replaces *Parastrephia quadrangularis* in the altitudinal gradient characterize the associations described. The cushions *Pycnophyllum molle* and *Azorella compacta* are relatively abundant, together with the relative high cover of the tussock *Festuca orthophylla* which replaces *Festuca dolichophylla* as well as from the higher altitudinal gradient context. *Festuca dolichophylla* (which is a species from the lower altitudinal gradient)

This alliance dominates extensive areas in the puna and superpuna of North Moquegua [36], occurring in the Arequipa, Tacna and Puno departments [20,59]. In our study region, it occurs between 4450–4800 m a.s.l. The inclination varies from 0 to 90° and the orientation is variable. Grazing intensity varies; some grasslands are heavily grazed while others can be considered to be ungrazed.

The tussock *Festuca orthophylla* is distributed in our study sites at altitudes between 4450 and 4800 m, becoming more abundant at 4650 m and higher. The tussock grass distribution is in agreement with [75], who recorded *Festuca dolichophylla* in the subhumid puna of Bolivia at 3500–4000 m and 4500 m and *Festuca orthophylla* at higher altitudes, in the super puna and subnival puna (uppermost part of the superpuna). Above 4500 m *Festuca orthophylla* co-occurs with cushion plants such as *Azorella* and *Pycnophyllum*.

The new associations and subassociations with *Azorella compacta* described here differ from each other not only in species composition but also in altitude and distribution.

In the *Calamagrostio trichophyllae-Azorelletum compactae* ass. nov. the character species of the alliance *Azorello-Festucion*, *Azorella compacta* and *Festuca orthophylla* are very frequent. *Anthochloa lepidula*, considered to be a character species of the *Anthochloo-Dielsiochloetea*, appears to have a very wide syntaxonomic amplitude. *Anthochloa lepidula*, *Dissanthelium calycinum* and *Senecio adenophyllus*, character species of the *Nototrichion obcuneatae*, are only present at low frequency. By contrast, *Azorella compacta* and *Baccharis caespitosa*, both character species of the *Azorello-Festucion*, are relatively frequent. Consequently, this association is considered to belong to the *Azorello-Festucion* instead of the *Anthochloo-Dielsiochloetea* and *Nototrichion obcuneatae*.

Two associations and one community have been assigned to the alliance *Nototrichion obcuneatae* of the order and class, *Anthochloa lepidulae-Dielsiochloetalia floribundae* Rivas-Martínez & Tovar 1982 and *Anthochloa lepidulae-Dielsiochloetea floribundae* (for diagnostic species see Table 2).

According to [29] *Anthochloa lepidula* and *Dielsiochloa floribunda* are character species of the *Anthochloa lepidulae-Dielsiochloetea floribundae*. According to our table, however, although *Anthochloa lepidula* has a higher presence in this class, it appears to have a very wide syntaxonomic amplitude. Although the associations are well represented by character

species, these are almost absent from the higher units. This might be due to the very extreme climatic conditions on the mountain summits.

The *Anthochloo-Dielsiochloetea* is highland vegetation characterized by ground rosettes, cushion and dwarf shrubs, herbs and grasses. Soils are of cryoturbate origin with sparse stoniness and fissures in gelid rocks, located near the vegetation line [29] in the superpuna region.

The alliance of *Nototrichion obtuneatae* [19], combines a series of subnival associations identified in the Andean regions of the Moquegua department.

The *Anthochloo lepidulae-Dielsiochloetalia* occurs in the central Andes of Peru [68], southern Andes of Peru [20], Bolivia, Chile and NW Argentina [24,25,29] above 4600 m a.s.l.

The cryotropical units described within *Nototrichion obtuneatae* (Supplementary Tables S6–S8) under the names *Nototricho obtuneatae-Xenophylletum poposi* [20] and *Poa aequiglumae-Xenophylletum dactylophylli* are similar to those described in Peru [60] and Bolivia [28,32] as having similar floristic affinities, such as *Anthochloa lepidula*, *Nototriche obtuneata* and *Senecio adenophyllus*. Both associations are more similar to those units described in Arequipa by [22] and Bolivia [32]. Our knowledge about the structure of these cryotropical communities is incomplete because of the lack of studies in the different geographical regions of South Peru and Northwest Bolivia.

The alliance is found on mobile scree slopes. As a consequence of solifluction, the plants are dispersed in sheltered hollows [20]. Based on the distribution of its character elements (*Nototriche obtuneata*, *Xenophyllum poposum*) it is a cryotropical (dry-humid) alliance of the southern highlands of Peru and Bolivia [20,22,43,76]. It is characterized by the presence of ground rosettes with thick roots, resinous shrubs and cushions, herbs and small grasses. The associations belonging to this alliance can further be found in South Peru [20,22], SW Bolivia and NW Argentina (described as *Chaetantherion sphaeroidalis* by [20] where the species *Chaetanthera sphaeroidalis* is absent in our study region).

9. Nitrophilous Vegetation

Nitrophilous communities dominated by nitrophytes are found on patches of llama and alpaca dung in grassland plateaus and slopes in the South Andes of Peru. The communities have been found in rock shelters, where cattle and wildlife shelter during the night and heavy rain, and near traditional cattle corrals and farmhouses. Little is known about the occurrence of these specific plant communities in the Andes. It seems that populations of *Urtica flabellata* are widespread in the C Andes [77]. According to [6], *Urtica flabellata* as a ruderal species and colonizer of llama dung that can often be found in puna regions together with *Cajophora cirsiifolia* and tall *Lupinus* species.

We distinguished two nitrophilous communities, the community of *Senecio algens* and the *Tarasa nototrichoides* and *Urtica flabellata* community. As these vegetation types are still insufficiently studied and suggestions of proper alliances or associations are still missing in literature, no association names were suggested in this paper.

The community resembling the community of *Senecio algens* [22] was named accordingly.

Nitrophilous communities, but floristically more impoverished, can also be recognized in northern, Central and southern Peru [60,61], and Bolivia [60,61,77]. Reference [61] was based on data from the Central Andes; he was not aware of Bolivian records. Ref. [60] describe the close affinity of these communities to the class *Nicotiano glutinosae-Ambrosietea arborescentis* Galán de Mera & Cáceres in [19], which represents ruderal vegetation from lower altitudes with a very distinct structure and floristic composition.

In the prepuna (supratropical belt) in Central Peru (Prov. Yauli, dept. Junín) [61] described the *Urtico flabellatae-Cajophoretum sepiariae* between 3600 and 3800 m in the region South of La Oroya. He supposed that this association could belong to a still undescribed class. Additional observations were made of alpine *Urtica flabellata* communities on the West slope of the Andes between 3000 and 3600 m, above Huánuco 3900–4000 m, in North Peru above Cajamarca and near Huaraz and Cusco. We agree with the concept of Gutte that a true ruderal class seems to exist in the alpine zone of Peru. However, in our relevés of

the superpuna of Moquegua the only species in common with [61] are the character species *Urtica flabellata* and *Perezia multiflora*. *Urtica flabellata* is also shared with the *Urtica flabellatae-Urocarpidetum peruviani* [60] (3320–3850 m a.s.l.). *Urtica flabellata* is found throughout the country and also from neighbouring Bolivia. It is known that *Urtica flabellata* also occurs in the páramos of Ecuador and Colombia [9]. On calcareous bedrock (Colombian Páramo Almorzadero) *Lachemilla pinnata* is associated with *Urtica flabellata* as well. For an adequate description of the class on the level of order and alliances, more relevés are needed. Thus far there are no relevés available for páramos. We conclude that these communities need further research using relevé data collection from both puna and páramo.

10. Discussion

There are few previous studies on species composition and diversity of superpuna grassland syntaxa in South Peru for comparison with our vegetation description. Refs. [4,20–22,60,61,77] address the phytosociological classification and description of plant associations and communities in the central and southern Peruvian Andes. Other studies from North Chile [24,25] and Bolivia [27,28,31–33]; were compared with our results and appear to differ significantly in species composition and distribution. Refs. [35,36] describe the prepuna shrublands, puna chasmophytes and grassland associations and communities occurring in the north of Moquegua under the classes *Echinopsio-Proustietea cuneifoliae* (prepuna shrublands) occurring at an average altitude of 3500 m, *Argyrochosmetea niveae* (chasmophytic vegetation) and *Calamagrostietea vicunarum* (puna grasslands) occurring between 3800 and 4500 m a.s.l. These associations lack the presence of cushion plants (*Azorella compacta*, *Pycnophyllum* spp.) and the tussock grass *Festuca orthophylla*.

11. Conspectus of the Syntaxa

Chasmophytic vegetation (*Argyrochosmetea niveae*)

Class: *Argyrochosmetea niveae* Gutte 1986

Order: *Saxifragetalia magellanicae* Galán de Mera & Cáceres in Galán de Mera et al. 2002

Alliance: *Saxifragion magellanicae* Galán de Mera & Cáceres in Galán de Mera et al. 2002

Association:

Saxifrago magellanicae-Leucherietum daucifoliae ass. nov.

12. Grassland and Cushion Vegetation (*Calamagrostietea vicunarum*)

Class: *Calamagrostietea vicunarum* Rivas-Martínez & Tovar 1982

Order: *Parastrephietalia quadrangularis* Navarro 1993

Alliance: *Calamagrostion minimae* Rivas-Martínez & Tovar 1982

Association and subassociations:

Astragalo minimi-Azorelletum diapensioidis ass. nov.

Subassociation *typicum*

aciachnetosum pulvinatae subass. nov.

Alliance: *Azorello compactae-Festucion orthophyllae* Galán de Mera, Cáceres & González 2003

Associations and subassociations:

Astragalo pusilli-Parastrephietum quadrangularis ass. nov.

sisyrinchietosum trinervis subass. nov.

baccharidetosum tricuneatae subass. nov.

Subassociation *typicum*

Senecioni moqueguensis-Pycnophylletum mollis ass. nov.

Subassociation *typicum*

senecionetosum tassaensis subass. nov.

gentianelletesum primuloides subass. nov.

arenarietosum acaulis subass. nov.

Calamagrostio trichophyllae-Azorelletum compactae ass. nov.

Subassociation *typicum*

drabetosum soratensis subass. nov.

13. Cryoturbate Vegetation (*Anthochloo lepidulae*-*Dielsiochloetea floribundae*)

Class: *Anthochloo lepidulae*-*Dielsiochloetea floribundae* Rivas-Martínez & Tovar 1982

Order: *Anthochloo lepidulae*-*Dielsiochloetalia floribundae* Rivas-Martínez & Tovar 1982

Alliance: *Nototrichion obtusatae* Galán de Mera, Cáceres & González 2003

Associations and subassociations:

Nototricho obtusatae-*Xenophylletum poposi* Galán de Mera, Cáceres & González 2003
nototrichetosum erinaceae subass. nov.

senecionetosum trifurcifolii subass. nov.

Poo aequiglumae-*Xenophylletum dactylophylli* ass. nov.

Community of *Senecio algens*

14. Nitrophilous Vegetation

Class, order and alliance: Still to be defined by further research.

Community of *Tarasa nototrichoides* and *Urtica flabellata*

15. Concluding Remarks

Our vegetation research in northern Moquegua (South Peru), an area not studied previously, extends the knowledge of the syntaxonomy, floristic diversity and synecology of *Azorella compacta* and *Pycnophyllum molle* vegetation structure, and of chasmophytic and nitrophilous communities. It comprises four alliances, seven new associations and thirteen subassociations, representing an important basis for a future overview and synopsis of the Andean vegetation of tropical South America. The vegetation studied in Moquegua appears to be floristically different from comparable vegetation in North Chile and Bolivia. Further research is needed, however, to study the relation with chasmophytic and plateau associations with cushions in the highlands of other mountainous regions in South America.

The present overview is also important as a reference and tool for nature conservation. Apart from the impressive cushion plants, many endemic species are found in the newly described syntaxa, highlighting the need for conservation schemes and measures. In recent years, the superpuna syntaxa have been increasingly affected by grazing and road construction. The natural vegetation is being disturbed and cushions of *Azorella compacta* have regularly been removed for use as fuel. Fire has been regularly observed on several mountain slopes. These fires were probably set on purpose as part of a festivity in June. Fortunately, due to advice and information given to the local communities by the first author, this practice is now gradually decreasing (personal observation), and conservation programs have been started. At the same time, interviews with the local communities suggest that the pastures are being grazed in a way that prevents overgrazing. Negative effects have been observed only in some grassland syntaxa where livestock and wild grazers are abundant. In addition to livestock, wild grazers including vicuñas (*Vicugna vicugna*), viscacha (*Lagidium peruanum*), taruca (*Hippocamelus antisensis*) and suri (lesser rhea, *Rhea pennata*) are known to occur in the region. This highlights the vulnerability of the flora and vegetation of the Andes to human pressure, and requires further studies.

Supplementary Materials: The following are available online at <https://www.mdpi.com/2673-4133/2/1/5/s1>: Supplementary Table S1. *Saxifraga magellanicae*-*Leucheria daucifoliae*, Supplementary Table S2. *Astragalo minimi*-*Azorelletum diapensioidis*, Supplementary Table S3. *Astragalo pusilli*-*Parastrephietum quadrangularis*, Supplementary Table S4. *Senecioni moqueguensis*-*Pycnophylletum mollis*, Supplementary Table S5. *Calamagrostio trichophyllae*-*Azorelletum compactae*, Supplementary Table S6. *Nototricho obtusatae*-*Xenophylletum poposi*, Supplementary Table S7. *Poo aequiglumae*-*Xenophylletum dactylophylli*, Supplementary Table S8. Community of *Senecio algens*, Supplementary Table S9. Community of *Tarasa nototrichoides* and *Urtica flabellate*.

Author Contributions: D.B.M.-T. planned the research and conducted the field sampling, D.B.M.-T. and K.V.S. performed the statistical analyses and all authors (D.B.M.-T., A.M.C. and K.V.S.) jointly wrote and revised the manuscript. Conceptualization, D.B.M.-T., A.M.C. and K.V.S.; Methodology, D.B.M.-T. and K.V.S.; Software, D.B.M.-T.; Validation, D.B.M.-T., A.M.C. and K.V.S.; Formal Analysis,

A.M.C. and K.V.S.; Investigation, D.B.M.-T.; Resources, A.M.C. and K.V.S.; Data Curation, D.B.M.-T., A.M.C. and K.V.S.; Writing—Original Draft Preparation, D.B.M.-T.; Writing—Review & Editing, D.B.M.-T., A.M.C. and K.V.S.; Visualization, D.B.M.-T., A.M.C. and K.V.S.; Supervision, A.M.C. and K.V.S.; Project Administration, K.V.S.; Funding Acquisition, A.M.C. and K.V.S. All authors have read and agreed to the published version of the manuscript.

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