

Plant community variation across a puna landscape in the Chilean Andes

Variación en la comunidad vegetal de un paisaje de puna en los Andes chilenos

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ABSTRACT

We describe patterns of plant species and growth form abundance in the puna vegetation of Parque Nacional Lauca, Chile. At more than 4,300 m, the extreme habitat of the study site supported relatively few species. These few species, however, represented a diverse array of growth forms that were organized with respect to distinct environmental gradients. Both species richness and growth form diversity increased with the degree of habitat rockiness and on more xeric north and east facing slopes. These xeric, rocky sites supported the greatest overall abundance of cushion forms. Less rocky sites with more soil development supported a greater abundance of tussock grass and shrub forms. Congeneric species occupied distinct microhabitats and were often markedly divergent in growth form. These patterns suggest that water and thermal stress are critical forces shaping functional form as well as community organization in the high Andean puna.

Key words: Altiplano, cushion plants, growth form, high Andean vegetation.

RESUMEN

Describimos los patrones de abundancia de las especies vegetales y las formas de vida en la vegetación de puna en el Parque Nacional Lauca, Chile. A una altitud que excede los 4.300 m de altitud, el hábitat extremo de nuestro sitio de estudio presenta relativamente pocas especies. Dichas especies, sin embargo, representan un arreglo diverso de formas de vida organizadas con respecto a distintos gradientes ambientales. Tanto la riqueza de especies como el hábito de crecimiento aumentaron en los suelos más rocosos y en las pendientes expuestas al norte y al este, cuya vegetación es más xerófila. Dichos sitios presentaron la mayor abundancia en formas de cojines. Los sitios menos rocosos con un suelo más desarrollado presentaron una mayor abundancia de pastos y arbustos. Distintos microhábitats fueron ocupados por especies congénéricas que con frecuencia divergieron en su hábito de crecimiento. Los patrones observados sugieren que el agua y el estrés térmico son fuerzas críticas que moldean la forma funcional de las especies vegetales así como la organización de las comunidades de plantas en la puna altoandina.

Palabras clave: altiplano, plantas en cojín, forma de vida, vegetación altoandina.

INTRODUCTION

The puna of the central Andean altiplano is a center of regional plant and animal endemism (Locklin 2001). Although relatively species poor compared to the moister páramo vegetation of the northern Andes (Luteyn 1999) or to mid-elevation pre-puna communities, the puna is unusual because of its unique assemblages of cushion and mat-forming species (Hodge 1946). Many of these species,

most notably the large cushion *Azorella compacta*, have been intensively harvested for fuel and medicinal uses (Hodge 1960, Wickens 1995). The vegetation also supports herds of wild and domesticated camelids, which form the social and economic core of Aymara pastoral societies (Bowman 1990, Caro 1992).

Our understanding of the dry puna vegetation is mostly restricted to broad phytosociological classifications (Ruthsatz 1977, Villagrán et al. 1981, 1982, Bonaventura et al. 1995, Lubert &

Gajardo 2005). Comparatively few studies have quantified how individual species and growth form abundance varies across local physiographic gradients. This lack of information makes it difficult to formulate effective species based management plans or to predict how stressors such as climate change and increased human exploitation might influence ecosystem function.

A remarkably pristine, yet accessible example of dry puna vegetation exists in Parque Nacional Lauca, Region 1, northern Chile (Fig. 1). Floristically the park is more similar to that of southern Peru and Bolivia than it is to the Chilean floristic province further south (Rundel & Palma 2000). Rainfall at this latitude is derived from summer fronts breaching the cordillera from the Amazon basin. Annual precipitation declines rapidly down the western Andean slope from mean annual totals over 300 mm near the crest of the Cordillera Occidental to less than 1mm on the Pacific coast. At its lower margins (2,900-3,900 m) the park contains diverse pre-puna

shrublands (Rundel et al. 2003). Above 4000 m wetland formations (bofedales) are common on the level plateau, and *Polylepis* woodlands are scattered on rocky north facing slopes between 4,400 m and 4,900 m (Rundel & Palma 2000). The majority of the Lauca basin above 4000 m, however, supports a high Andean steppe-shrubland (Rundel & Palma 2000).

This high steppe-shrubland corresponds with the “high-Andean belt” in the phytosociological scheme of Ruthsatz (1977) and Villagrán et al. (1981, 1982). Villagrán et al. (1982) divided this high-Andean belt into two broad associations based on growth form dominance: one dominated by the tussock grass *Festuca orthophylla* and the shrub *Parastrephia lucida* on sandy plains, and one dominated by the large cushion *Azorella compacta* on rocky volcanic slopes. In addition, Arroyo et al. (1982, 1988) examined how broad geographic differences in aridity and thermal stress influence patterns of growth form dominance along the western slopes of the Andes. They found that woody growth forms

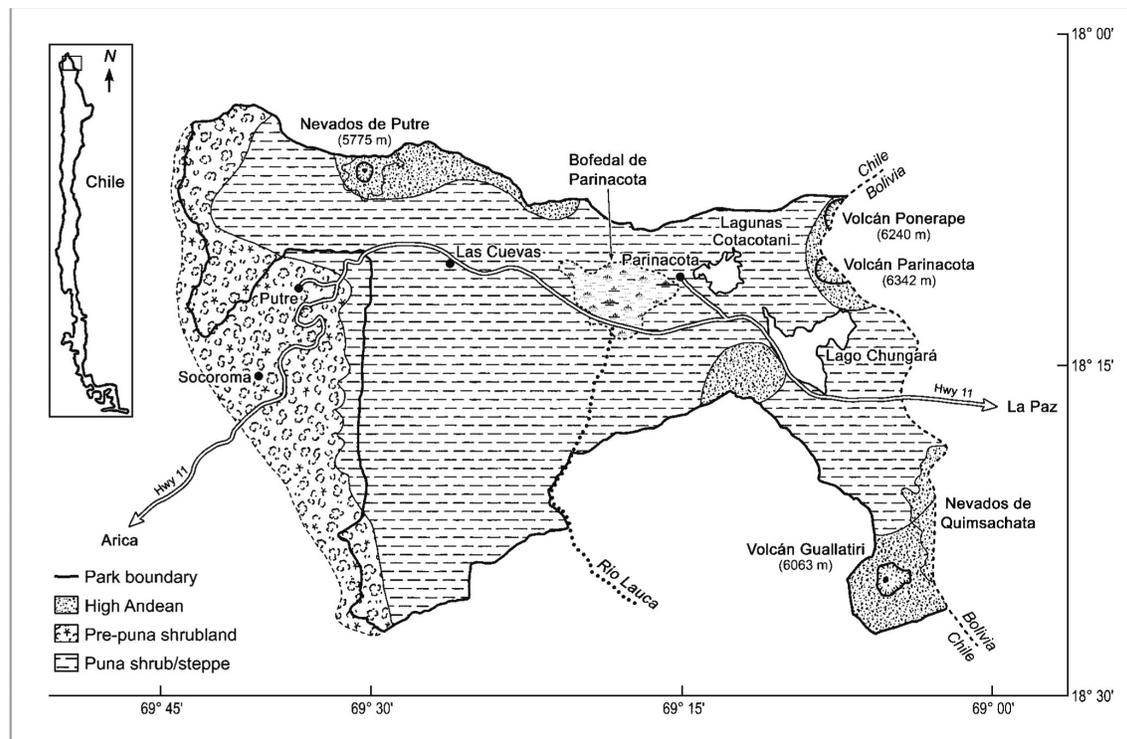


Fig. 1: Map of Parque Nacional Lauca showing the location of the study area containing the 80 sampled slopes.

El mapa de Parque Nacional Lauca que demostraba la localización del área del estudio que contenía los 80 muestreos pendientes.

increase in dominance with aridity and that cold temperatures promote the dominance of longer lived and more deeply rooted forms.

In this study, we describe variation in community composition within the high-Andean belt at a finer spatial scale. We investigate how habitat variation across the topographically complex puna landscape of Lauca National park influences patterns of species and growth form abundance. We relate these findings to a concordant study (Kleier 2001) that documented the ecophysiological characteristics of the dominant species in this ecosystem.

MATERIAL AND METHODS

Study area

This study was conducted along the northeastern edge of Parque Nacional Lauca approximately 250 km east of Arica, Chile (Fig. 1). The study site was a roughly 25 km² area bounded by the small Aymara village of Parinacota (18°12' S, 69°16' W) and by the volcanic peaks of Guane Guane (5,200 m), Parinacota, (6,342 m) and Choquelimpie (5,327 m). Elevation within the site ranged from 4,360-4,425 m

At the village of Parinacota precipitation is low and highly seasonal, with most of the 321 mm annual precipitation falling between December and March (Rundel & Palma 2000). Air temperatures vary little seasonally, but regularly reach 25 °C during the day and drop below freezing on most nights. Under the clear skies typical of the dry season, the flux in diurnal temperature can be as much as 45 °C (Kleier 2001).

The rugged topography of the study site consists of a network of steep andesite flows dating from the late Pleistocene to the present (Wörner et al. 1988). These flows create a complex landscape, and habitat variables can vary widely over small spatial scales. Environmental variation is principally related to slope aspect, steepness and substrate characteristics. Soils on slopes throughout the study area are generally thin, lack profile development, and are composed mostly of coarse sand and gravel. In addition, the relative proportion of soil to rock varies widely on slopes, from mostly soil with few rocks to

mostly rock with soil present only in cracks and crevices.

Sampling procedure

We conducted this study in November 1997 at the end of the dry season. The abundance of annual species was low, and we restricted our study to perennial species. We initially identified 93 distinct slopes within the 25 km² study area. Slopes were at least 500 m apart and separated from each other by bofedales or other non-slope habitat. We characterized each of the 93 slopes by aspect and substrate, and grouped slopes into four aspect x substrate groups: NE rocky, NE sandy, SW rocky, SW sandy. Typically, adjacent slopes varied dramatically in aspect or substrate so that these two independent variables were not correlated in space with each other over the 25 km² study area. We randomly removed slopes from our sample pool to attain equal sample sizes for each habitat category (n = 20 slopes), for a total of 80 sample slopes.

We sampled vegetation using the line intercept method. For each of the 80 slopes we randomly positioned a 25 m line transect perpendicular to the slope. These provided 80 spatially independent vegetation transects that were a representative sample of the four principal habitat categories in the study area. Along each transect we recorded the total length (to the nearest 5 cm) of the projected intercepted canopy for each species. This value was divided by the total length of the transect to give a proportion cover estimate for each species. This method has been widely used to produce accurate cover estimates in arid shrublands, although the method can underestimate species richness (Brun & Box 1963, Korb et al. 2003).

We measured the relative proportion of rock (particles >10 cm diameter) and "soil" (particles < 10 cm diameter) composing the substrate at each transect location. Most of the rock particles in this classification were larger than 50 cm diameter. Unlike desert pavement, which is underlain by soil a few centimeters below the rocky aggregation, the predominately rocky habitat in this study had only deep or interstitial soil layers. We further classified the non-rock component of the substrate based on texture. We quantified the relative proportion of coarse gravel (< 10 cm, > 2 mm) to sand (< 2 mm) for each transect. At each sample

location, we measured the slope inclination and aspect to the nearest degree. We measured inclination using a hand held clinometer and aspect using a compass. For analysis, we recoded the aspect measurements so that their rank order represented a continuous gradient from northeast to southwest.

Analysis

For each transect we calculated the percentage canopy cover of each species and species richness. We also grouped individual species into four growth form categories: tussock grasses, woody shrubs, mats and cushions. Tussock grass species were shallowly rooted and ranged in height from 20-50 cm. Woody shrub species were deeply rooted and ranged in height from 0.5-1 m. Both mat and cushion growth forms have highly branched stems with short internodes. Mat species were shallowly rooted and less than 5 cm in height. Cushion species were both shallowly and deeply rooted and greater than 5 cm in height. There was one succulent cushion (*Cumulopuntia ignescens* (Vaupel) F. Ritter). Using growth form instead of species identifications we calculated an index of growth form diversity using the Shannon-Weiner diversity index.

We used canonical correspondence analysis (CCA) to depict the pattern of species abundances in direct relationship to gradients in the environmental variables (ter Braak 1986). Correlation scores were derived from linear combinations of environmental variables. Species scores were centered, standardized to unit variance and visualized in two-dimensional ordination space. We tested the null hypothesis that there was no relationship between the species abundance patterns and the environmental gradients using a Monte Carlo test with 1,000 randomizations of the environmental variable matrix.

To examine how patterns of growth form dominance related to the gradients in environmental variables we repeated the ordination but used the abundances of the four growth form categories instead of species. We ran all ordinations using PC-ORD v.4.10 (McCune & Mefford 1999).

We used multivariate linear regression to predict the variance in total plant cover, species richness, and growth form diversity as

functions of the measured environmental variables. Cover values were arcsine transformed for analysis. Regression models were run using SYSTAT v. 8.0.

RESULTS

We found 15 species of perennial plants along the 80 transects (Table 1). We also found 10 additional perennial species at low frequency within the study area but not encountered on the transects. These were small, herbaceous species in rocky overhangs and crevices. They represented low rosette or loose cushion growth forms such as *Senecio candollei* Wedd., *Senecio haenkeanus* Cuatr., *Valeriana nivalis* Wedd., and *Urtica andicola* Wedd. The following analyses are restricted to the dominant species encountered along the 80 transects.

Mean (\pm SE) plant cover in the study area was only 35.0 % \pm 1.5 %. The sparse cover decreased further as the relative proportion of rocks to soil increased (Table 2). However, species richness and growth form diversity increased with rock cover and was higher on north and east facing slopes compared to south and west facing slopes (Table 2).

The CCA analyses described clear relationships between the environmental variables using both species and growth form abundances (Table 3). In both ordinations, axis 1 represented a gradient of increasing rock cover, axis 2 represented a gradient in aspect from south-facing slopes to north-facing slopes and axis 3 represented a gradient of increasing slope angle. All three axes influenced the pattern of species abundance, but only substrate and aspect had a strong influence on growth form abundance (Table 3).

North and east facing rocky slopes supported the richest assemblage, both in terms of species and number of growth form types. All but two of the 15 species and all of the four growth forms were represented here (Table 1). The cover of cushion growth forms was highest in this habitat, driven largely by the high abundance of the large cushion *Azorella compacta* (Table 1, Fig 4). South and west facing rocky slopes were more depauperate, supporting an association composed mostly of the small cushion *Pycnophyllum molle* and the tussock grass *Deyeuxia deserticola* (Table 1, Fig. 2 and 4).

TABLE 1

Perennial plant species found across four physiographic habitats in the dry puna of Parque Nacional Lauca. Mean canopy cover in percent (\pm SE) values were derived from 20 25 m line transects in each habitat. Number of transects (n), total species richness (S) and evenness (E) are given for each habitat subdivision. Growth form (GF) categories are: C = cushions; S = shrubs; M = mats; T = tussock grasses

Especies vegetales perennes presentes a lo largo de cuatro hábitats fisiográficos en la puna seca del Parque Nacional Lauca. Promedios de cobertura del dosel (\pm SE) fueron derivados a partir de 20 transectos lineales de 25 m en cada hábitat. La riqueza número de transectos, total (S) y la homogeneidad (E) se presentan para cada subdivisión de hábitat. Las categorías de forma de vida (GF) son: C = cojines; S = arbustos; M = tapetes y T = pastos

Species	Family	GF	NE rocky n = 20; S = 13 E = 0.80 Cover	NE sandy n = 20; S = 8 E = 0.60 Cover	SW rocky n = 20; S = 10; E = 0.53 Cover	SW sandy n = 20; S = 6; E = 0.52 Cover	All habitats n = 80; S = 15; E = 0.61 Cover
<i>Azorella compacta</i> Phil.	Apiaceae	C	10.1 \pm 1.7	—	3.0 \pm 1.0	—	3.4 \pm 0.7
<i>Azorella</i> sp.	Apiaceae	M	—	0.9 \pm 0.6	—	1.6 \pm 0.7	0.6 \pm 0.2
<i>Baccharis santelicensis</i> Phil.	Asteraceae	S	0.3 \pm 1.3	0.1 \pm 0.1	—	—	0.7 \pm 0.4
<i>Belloa schultzei</i> (Wedd.) Cabr.	Asteraceae	M	> 0.0	—	—	—	> 0.0
<i>Cumulopuntia ignescens</i> (Vaupel) Ritter	Cactaceae	C	0.4 \pm 0.2	—	0.1 \pm 0.1	—	0.1 \pm 0.1
<i>Deyeuxia deserticola</i> Phil.	Poaceae	T	0.4 \pm 0.2	—	0.1 \pm 0.1	—	0.1 \pm 0.1
<i>Dielisiochloa floribunda</i> (Pilg.) Pilg.	Poaceae	T	0.6 \pm 0.3	0.3 \pm 0.3	0.2 \pm 0.2	0.1 \pm 0.1	0.3 \pm 0.1
<i>Festuca orthophylla</i> Pilg.	Poaceae	T	2.3 \pm 0.9	16.5 \pm 3.5	22.9 \pm 4.6	20.0 \pm 3.0	15.0 \pm 1.8
<i>Parastrephia lucida</i> (Meyen) Cabrera	ASTERACEAE	S	1.5 \pm 1.3	22.8 \pm 4.0	1.8 \pm 0.8	11.0 \pm 3.2	9.2 \pm 1.6
<i>Parastrephia quadrangularis</i> (Meyen) Cabrera	Asteraceae	S	6.2 \pm 1.4	0.1 \pm 0.1	1.0 \pm 0.5	—	1.9 \pm 0.1
<i>Pycnophyllum bryoides</i> (Phil) Rohrb.	Caryophyllaceae	M	2.5 \pm 0.9	0.8 \pm 0.6	0.5 \pm 0.3	0.9 \pm 0.5	1.3 \pm 0.4
<i>Pycnophyllum macropetalum</i> Mattf.	Caryophyllaceae	C	0.7 \pm 0.4	—	—	—	0.2 \pm 0.1
<i>Pycnophyllum molle</i> Rémy	Caryophyllaceae	C	1.2 \pm 0.4	—	4.2 \pm 1.5	—	1.3 \pm 0.4
<i>Senecio nutans</i> Schultz-Bip	Asteraceae	S	0.9 \pm 0.2	—	0.3 \pm 0.2	—	0.3 \pm 0.1
<i>Senecio rufescens</i> DC.	Asteraceae	S	—	1.9 \pm 1.3	—	0.7 \pm 0.5	0.6 \pm 0.3
Total canopy cover			27.1 \pm 3.0	43.4 \pm 2.4	34.0 \pm 3.2	34.3 \pm 2.3	35.0 \pm 1.5

TABLE 2

Multivariate linear models describing the influence of environmental variables on total plant cover, species richness and growth form diversity

Modelos multivariados lineales que describen la influencia de las variables ambientales en la cubierta vegetal total, la riqueza de especies y la diversidad en las formas de vida

(A) Total cover
($R^2 = 0.253$, $F_{4, 75} = 6.27$, $P < 0.001$)

Parameter	β -coefficient	t-value	P-value
Aspect	-0.753	-0.975	0.333
Slope angle	0.141	-0.980	0.330
Rock cover	-0.250	-3.672	< 0.001
Percent soil sand	-0.029	-0.632	0.529

(B) Species richness
($R^2 = 0.455$, $F_{4, 75} = 15.668$, $P < 0.001$)

Parameter	β -coefficient	t-value	P-value
Aspect	-0.470	-4.283	< 0.001
Slope angle	-0.010	-0.488	0.627
Rock cover	0.034	2.454	< 0.001
Percent soil sand	-0.008	-0.519	0.605

(C) Growth form diversity
($R^2 = 0.262$, $F_{4, 75} = 6.655$, $P < 0.001$)

Parameter	β -coefficient	t-value	P-value
Aspect	-0.094	-2.933	0.004
Slope angle	-0.010	-1.639	0.105
Rock cover	0.012	2.887	0.005
Percent soil sand	0.003	0.752	0.454

Slopes with few rocks and soil composed mostly of sand supported two associations dominated by woody shrubs and tussock grasses. North and east facing sandy slopes supported an association dominated by the woody shrub *Parastrephia lucida* (Table 1, Fig. 4). An unidentified mat-forming species of *Azorella* and the woody shrub *Senecio rufescens* were also associated with this habitat (Fig. 2). South and west facing sandy slopes supported an association strongly dominated by the tussock grass *Festuca orthophylla* (Table 1, Fig. 2 and 4). Concordantly, the overall tussock grass abundance peaked in this habitat.

Species associated with rocky slopes assorted strongly with respect to slope angle (Fig. 3). In addition, closely related taxa occupied consistently different habitats. For example, each of the three *Pycnophyllum* species had distinct habitat associations: *P. macropetalum* occupied the steepest rocky north slopes, *P. molle* occupied rocky south slopes and *P. bryoides* occupied habitats with intermediate degrees of rockiness and steepness. Similar segregation patterns exist for the three bunch grass species, the two *Senecio* species, the two *Azorella* species and the two *Parastrephia* species (Fig. 2 and 3).

DISCUSSION

The vegetation association described in this study lies near the upper elevational limit of vascular plant species. Broad-scale regional

TABLE 3

Summary of canonical correspondence analysis statistics for the relationship of species (SP) and growth form (GF) abundances to the measured environmental variables. All eigenvalues and correlation coefficients were significantly different ($P = 0.01$) from Monte Carlo simulations

Resumen estadístico del análisis de correspondencia canónica entre las relaciones entre las abundancias de especies (SP) y formas de vida (GF) y las variables ambientales que fueron medidas. Todos los valores característicos y coeficientes de correlación fueron estadísticamente diferentes ($P = 0,01$) a partir de simulaciones de Monte Carlo

Parameter	Axis 1		Axis 2		Axis 3	
	SP	GF	SP	GF	SP	GF
Eigenvalue	0.537	0.254	0.202	0.142	0.134	0.013
Pearson correlation with environment data	0.801	0.689	0.592	0.496	0.623	0.234
Cumulative % of variance explained in SP or GF	15.6	18.8	21.5	29.4	25.4	30.3

vegetation studies in the northern and central Chilean Andes have demonstrated that both plant cover and diversity decrease significantly with elevation (Villagrán et al. 1981, 1982, Cavieres et al. 2000). Using data collected along a transect from Turi to Cerro León and from Arica to Parque Nacional Lauca, Villagrán et al. (1981,1982) defined a high-Andean vegetation association composed primarily of tussock grasses and cushion forms. The average total plant cover and species diversity reported for this study is similar to those reported by Villagrán et al. (1981, 1982) for the high-Andean belt. Despite the low cover and overall diversity, the vegetation within this High-Andean belt displays relatively complex patterns of variation over small spatial scales.

Rocky slopes in this study supported a relatively diverse association of growth forms including many cushion forms, while sandy flats supported a more depauperate tussock grass and shrub dominated steppe. This broad physiognomic pattern has been documented at other puna sites on the western Andean slope in northern Chile (Villagrán et al. 1981, 1982), and in the eastern cordillera of northern Argentina (Ruthsatz 1977, Bonaventura et al.1995). In the more mesic páramo ecosystem of the northern Andes, tussock grasses are the dominant growth form, but cushion forms become co-dominant with tussocks and arborescent shrubs on the highest rocky slopes and in xeric rain shadows (Balslev & De Vries 1991, Ramsay & Oxley 1997, Luteyn 1999).

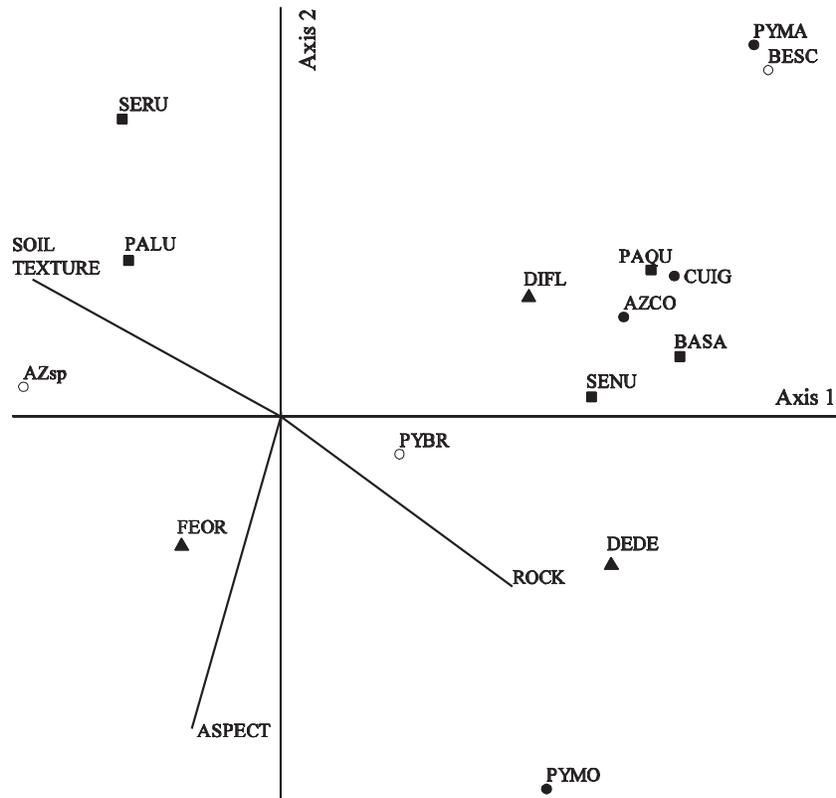


Fig. 2: Ordination of species using the first two CCA axes. Solid arrows represent correlations of the axes with environmental variables. Symbols represent growth form: cushions = closed circles, mats = open circles, shrubs = squares, grasses = triangles. See Table 1 for full species names, Table 2 for summary axis statistics. Transect scores are omitted for clarity.

Ordenación de especies utilizando los primeros dos ejes de ACC (análisis de correspondencia canónica). Las líneas sólidas representan correlaciones de los ejes con las variables ambientales. Los símbolos representan la forma de vida: cojín = círculos cerrados, tapetes = círculos abiertos, arbustos = cuadrados, pastos = triángulos. Ver en Tabla 1 los nombres completos de las especies, en Tabla 2 el resumen estadístico de los ejes. Los valores de los transectos fueron omitidos para mayor claridad.

The high species richness and growth form diversity found on rocky slopes is potentially related to the greater microhabitat diversity created by the complex surface topography of these habitats. Both water and heat availability can vary greatly over the scale of a few centimeters in relation to the proximity and orientation of rocks (Kleier 2001).

In these habitats, plant growth form appears to have a direct adaptive relationship with

patterns of water and temperature stress. Steep rocky slopes are generally more xeric habitats than shallow sandy slopes. Rocky slope soils are coarser and have low water retention. In addition, north-facing slopes at this latitude receive greater incident solar radiation than flats (Kleier 2001). Working at the same site as the present study, Kleier (2001) showed that the large cushion *A. compacta* avoids critical water stress by virtue of high tissue water

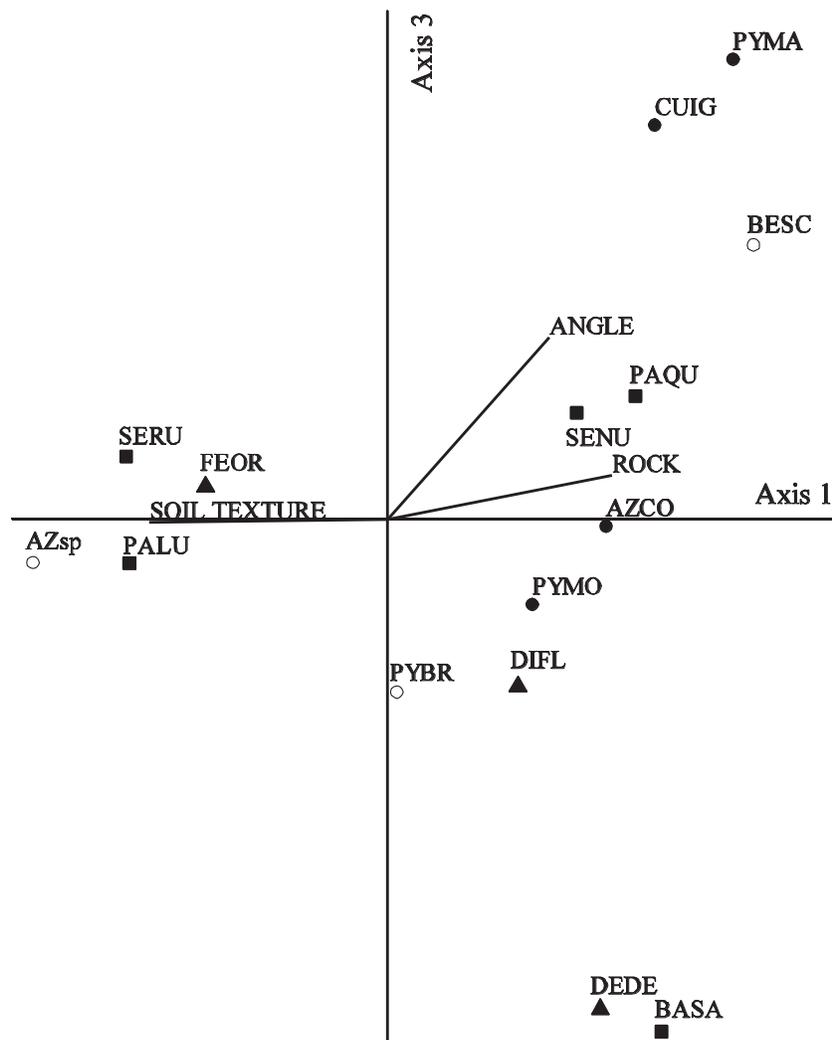


Fig. 3: Ordination of species using the first and third ordination axes. Solid arrows represent correlations of the axes with environmental variables. Symbols represent growth form: cushions = closed circles, mats = open circles, shrubs = squares, grasses = triangles. See Table 1 for full species names, Table 2 for summary axis statistics. Transect scores are omitted for clarity.

Ordenación de especies usando el primer y tercer eje de ordenación. Las líneas sólidas representan correlaciones de los ejes con las variables ambientales. Los símbolos representan la forma de vida: cojín = círculos cerrados, tapetes = círculos abiertos, arbustos = cuadrados, pastos = triángulos. Ver en Tabla 1 los nombres completos de las especies, en Cuadro 2 el resumen estadístico de los ejes. Los valores de los transectos fueron omitidos para mayor claridad.

storage capacity compared to other growth forms. High water storage capacity has thermal benefits as well. Following stomatal closure, *A. compacta* cushions retain radiative heat from rocks, and this heat storage prevents plant surface temperatures from dropping below -3°C and soil temperatures under plants from dropping below freezing (Kleier 2001). Heat retention during sub-freezing nights might also be important for the CAM succulent *C. ignescens*. The ability of cushion forms to utilize the heat reserves of rocky substrates probably affords a significant advantage in these microhabitats (Hodge 1946). Both the ability to store water reserves and to moderate diurnal temperature flux is a strategy that maximizes the overall time during which photosynthesis is possible.

In contrast to cushion forms, tussock grasses and mat species have limited ability to moderate extreme temperature and water stress fluxes, but they appear to be suited to achieving high photosynthetic rates during brief periods of favorable conditions. The sets of closely related species in this study appear to segregate along this niche axis; they are markedly divergent in growth form and display pronounced habitat segregation.

The two *Azorella* species encountered in this study exemplify this segregation. The large cushion *A. compacta* is matched with a still unidentified mat forming species. This species has shallow lateral roots suited for absorbing ephemeral shallow soil water reserves. In addition, the mat *Azorella* experiences more pronounced diurnal temperature fluctuations (Kleier 2001).



Fig. 4: Major physiographic habitats in the puna of Lauca National Park, 4,300-4,500 m of altitude. (A) North facing rocky slope dominated by *Azorella compacta* and *Parastrephia quadrangularis*. (B) South facing rocky slope dominated by *Pycnophyllum molle* and *Deyeuxia deserticola*. (C) North facing sandy slope dominated by *Parastrephia lucida*. (D) South facing sandy slope dominated by *Festuca orthophylla*.

Principales hábitats fisiográficos en la puna seca del Parque Nacional Lauca, 4.300-4.500 m de altitud. (A) Pendientes rocosas con exposición norte dominadas por *Azorella compacta* y *Parastrephia quadrangularis*. (B) Pendientes rocosas con exposición sur dominadas por *Pycnophyllum molle* y *Deyeuxia deserticola*. (C) Pendientes arenosas con exposición sur dominadas por *Parastrephia lucida*. (D) Pendientes arenosas con exposición sur dominadas por *Festuca orthophylla*.

Similarly, the three *Pycnophyllum* species displayed distinct strategies in relationship to water and thermal stress. The mat *P. bryoides* has many small scale-like leaves arranged in a loose canopy. It was found on shallow slopes with mixed sand and rock. In contrast the most cushion-like species, *P. macropetalum*, has large cylindrical leaves arranged in a tight canopy. It was associated with the steepest and rockiest north facing slopes. *Pycnophyllum molle* has an intermediate growth form and was found in habitats with intermediate slope angles and rockiness. A similar segregation of the three *Pycnophyllum* species along an elevational gradient has been observed at a regional scale, with *P. molle* and *P. macropetalum* replacing *P. bryoides* at higher elevations (Villagrán et al. 1981, Villagrán et al. 1982).

The Asteraceae shrubs appear to mostly partition the water stress gradient. *Parastrephia quadrangularis* on rocky northeast slopes has smaller more scale like leaves relative to *P. lucida* on sandy flats. A general trend toward microphyllly is also seen in the species inhabiting the xeric northeast facing slopes of the pre-altiplano shrublands (Rundel et al. 2003). Similarly, *Senecio rufescens* is a wash species at lower elevation in the pre-altiplano shrublands (Rundel et al. 2003) and was found on sandy flats in this study. In contrast *S. nutans*, which has smaller succulent leaves, inhabited rocky slopes.

The diverse range of growth forms found on rocky slopes was in sharp contrast to the grass-shrub monotony of sandy slopes. This relationship between rockiness and increased species and growth form richness has also been observed at other high Andean locations in northern Chile (Villagrán et al. 1981), on the eastern flank of the Andes in northwest Argentina (Bonaventura et al. 1995) and lowland warm deserts (Barbour & Díaz 1973). At the Lauca study site, plant cover was highest on shallow sandy slopes where soils were most developed and water availability was greatest. A number of studies have demonstrated that increases in grassland productivity and plant biomass produce concomitant decreases in diversity (Goldberg & Miller 1990). It is possible that the overall reduced productivity of rocky slopes coupled with their greater structural complexity allows a variety of species and growth forms to coexist.

Although relatively depauperate in species and overall abundance, the vegetation of the High-Andean belt varies in complex ways over relatively small spatial scales. Species appear to finely partition physical microhabitats. The patterns of growth form dominance and species association observed in this study are consistent with the hypothesis that water and thermal stress are important agents structuring vegetation patterns in this stressful habitat. Other factors such as exposure to wind and herbivore pressure that vary between microhabitats likely play an important role as well. Experimental studies are needed to identify the relative importance of different mechanisms in structuring the puna vegetation. Analyzing how both species associations and growth form dominance vary in relationship to environmental gradients is an ideal framework for understanding the key mechanisms that pattern tropical alpine vegetation. More work comparing the functional associations of species between different tropical alpine habitats and regions will likely prove valuable in understanding how their unique diversity and ecosystem services are organized.

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