RESEARCH PAPER

Plant diversity and structure in desert communities of the Andean piedmont in Ica, Peru

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Abstract

Aims: There is extensive documentation of the floristic composition and plant diversity patterns in the South American coastal deserts and the adjoining arid Puna. Surprisingly, the vegetation along the transition zone from these deserts in the coastal lowlands to the Puna highlands has been little studied. The main goal of this study was to characterize and compare the structure of plant communities in two localities in the Ica department, with the aim of contributing to the floristic knowledge of the desertic western Andean slopes along the lowlands to Andean transition zone. **Study area:** Huancacasa and La Bolivar localities located at approximately 740 and 3,000 m a.s.l. in the Ica department, Peru. **Methods:** We sampled 10 plots of 100 m × 60 m located between 740–1,600 m a.s.l. in La Bolivar and 15 modified Whittaker plots (MWPs) of 20 m × 5 m located between 2,800–3,000 m a.s.l. in Huancacasa and recorded species richness and abundance. We estimated alpha diversity, performed Non-Metric Multidimensional Scaling (NMDS) and one-way Similarity (ANOSIM) analyses and plotted rank-abundance curves. **Results:** We recorded 215 species and morphospecies with coastal and Andean distribution, including 43 species (21.3%) that are either considered endemic to Peru or have been considered under some form of threat by Peruvian or international standards. Both plant communities differed in terms of composition, species richness, abundance, and dominant growth form, with higher values in the communities located at higher elevations. We added 83 species as new records for the Ica department. **Conclusions:** Our research reinforced the need to increase exploration and documentation of the vegetation within the lowland to highland transition zone along the dry western slopes of the Andes. Our results from such a transition in Ica department in southern Peru, show that much of its plant diversity seems to be, as yet, largely unknown.

Taxonomic reference: The Plant List (2013).

Abbreviations: ANOSIM = one-way Analysis of Similarities; BMAP = Biodiversity Monitoring and Assessment Program; IUCN = International Union for Conservation of Nature; NMDS = Non-Metric Multidimensional Scaling; USM = Universidad Nacional Mayor de San Marcos (Herbarium).

Keywords

Andean biodiversity, Atacama, coastal desert, community structure, endemism, floristic records, mountain, southern Peru, threatened species

Introduction

A major feature of the Pacific coast and western slopes of South America are the arid and semi-arid ecosystems extending from the coastal lowlands to the upper slopes of the western Andes that include the well-known Peruvian and Atacama deserts and their associated fog-oasis "lomas" (Walter and Breckle 2004; Rundel et al. 2007). At elevations above 4,000 m a.s.l., these deserts are replaced by more humid ecosystems in the North-Central

Moist Andes (north of 14°S latitude) and similarly arid ecosystems prevail towards the south in the South-Central Dry Andes (Josse et al. 2003). These latter arid ecosystems include varying forms of scrub communities dominated by *Cactaceae* (Sarmiento 1975), before reaching the highland Puna formations starting at 3,200–3,600 m a.s.l. There is extensive documentation on the floristic composition and plant diversity patterns of coastal deserts (e.g. Luebert 2011, and references therein), which harbor important levels of plant endemism (Rundel et al. 1991; Moat et al. 2021), and the arid Puna (e.g. Luebert and Gajardo 2000; López et al. 2006; Montesinos et al. 2012, 2015a). Surprisingly, the vegetation along the transition zone from the deserts in the coastal lowlands to the Puna highlands has been little studied (but see Galán de Mera et al. 2009 and Chicalla-Rios 2021). Phytogeographically, these dry western slopes of the Central Andes have been linked to both the desert and the Puna (Sarmiento 1975), although Rundel et al. (2007) suggested they had closer affinities with the Puna vegetation.

Studies of the flora and vegetation of the coastal desert in Peru have focused on the hills and coastal wetlands (Johnston 1931; Weberbauer 1945; Ferreyra 1953, 1962, 1983, 1993; Müller 1985; Rundel et al. 1991; León et al. 1996; Galán de Mera et al. 1997, 2003, 2010; Cano et al. 1999; Dillon et al. 2011). Additionally, there have been efforts to document the flora on the south coast of the country (Dillon 1997a, 1997b; Arakaki and Cano 2003; Leon et al. 2004; Galán de Mera et al. 2009; Montesinos and Mondragón 2013; Quipuscoa et al. 2016). The department of Ica has received particular attention (León et al. 1997; Roque and Cano 1999; Cano et al. 2005; Jiménez et al. 2008) and the Catalogue of the flowering plants and gymnosperms of Peru published in 1993 recorded only 149 species for the entire department (Brako and Zarucchi 1993). Recent works indicate that in this department there are more than 500 species, dominated by *Asteraceae*, *Poaceae*, *Fabaceae*, *Solanaceae*, *Malvaceae* and *Cactaceae* (Whaley et al. 2010b, 2019).

Documentation of the flora of the department of Ica has concentrated mainly on the plant communities of the coastal plains, including *Tillandsia* mats, dry forests, dunes, riparian vegetation, wetlands, orchards, scrublands, lomas, cacti thickets and mixed xerophytic thickets with trees that support populations of epiphytic bromeliads and lichens (Whaley et al. 2019). However, the floristic composition of higher areas of the department, where the Andean mountains narrow and descend from 4,000 m a.s.l. in the Arid western Andes to the central Pacific coast at about 750 m a.s.l. has been less explored and documented, except for some phytosociological (Galán de Mera et al. 2003, 2004, 2009) and floristic studies (Whaley et al. 2019). Together, all these studies show that despite being considered as a desertic region, the department of Ica is home to a considerable number of species of the Peruvian flora, including several endemics and threatened species (León et al. 2006; Ministerio de Agricultura y Riego 2006). In this context, there remains important botanical knowledge gaps in the department of Ica (Roque and

Cano 1999). This situation is exacerbated by the fact that several species and ecosystems in Ica are threatened by the combined effect of urban expansion, pollution, overgrazing and climatic changes (Beresford-Jones et al. 2009).

Within the framework of a Biodiversity Monitoring and Evaluation Program (BMAP), a collaboration between the Smithsonian Institute and the PERU LNG company in the southern coast and highlands of Peru, we had the opportunity to study the vegetation of the western slopes of the department of Ica (Dallmeier et al. 2013). Although the BMAP was initially only focused on gathering information on the population ecology of *Cleistocactus acanthurus* and *C. hystrix* (*Cactaceae*), the study was later extended to document the accompanying vascular plant communities. The present contribution provides a general overview of the desert flora in the western Andean slopes of southern Peru and compares vegetation characteristics, diversity, and community structure between two locations along the elevation gradient.

Study area

The department of Ica is located in the central coast of Peru and is dominated by an extensive desertic coastal plain adjacent to the Pacific Ocean (Whaley et al. 2010b) that receives less than 8 mm annual rainfall (Dávila et al. 1981; Olivares et al. 1994). Further inland the landscape is dominated by the dry western slopes of the Andes, transitioning from desert to cacti woodlands at lower and middle elevations (750–3,100 m a.s.l.) and then rapidly ascending to the dry Puna at higher elevations (above 4,000 m a.s.l.). Our study focused on two locations along these dry western slopes (Figure 1).

La Bolívar (740–1,790 m a.s.l., Figure 2), is located adjacent to the sand plains of the province of Pisco (13.73°S, 75.75°W). It belongs to the thermotropical belt of southern Peru (Galán de Mera et al. 2017), and according to its elevation has a per-arid and semi-warm climate with an annual average of 80 mm of precipitation (Olivares et al. 1994). Temperature varies between 17 °C to 24 °C (Olivares et al. 1994), with an annual mean of 19.4 °C (free CHELSA data set 1981–2010, Karger et al. 2017) and a relative humidity of 78% (Olivares et al. 1994). It constitutes the lower slopes of the western Andes characterized by heavily dissected hills that intersect with moderately dissected streams (Langstroth et al. 2013), formed by semi-consolidated heterometric and heterogeneous alluvial and fluvial deposits of medium to high permeability (Olivares et al. 1994). Ecologically, it corresponds to the Pre-Montane Desert and Pre-Montane Desert Scrub formations, containing cacti such as *Neoraimondia arequipensis* and *Armatocereus procerus* along with some seasonal herbs and shrub deciduous species such as *Orthopterygium huaucui*, *Cnidoscolus basiacanthus*, and *Bulnesia retama* (Figure 2, Whaley et al. 2010a).

The second area, Huancacasa (2,600–3,000 m a.s.l., Figure 3), is located higher up of the western Andean slopes that border the Huancavelica department (13.73°S, 75.51°W). It
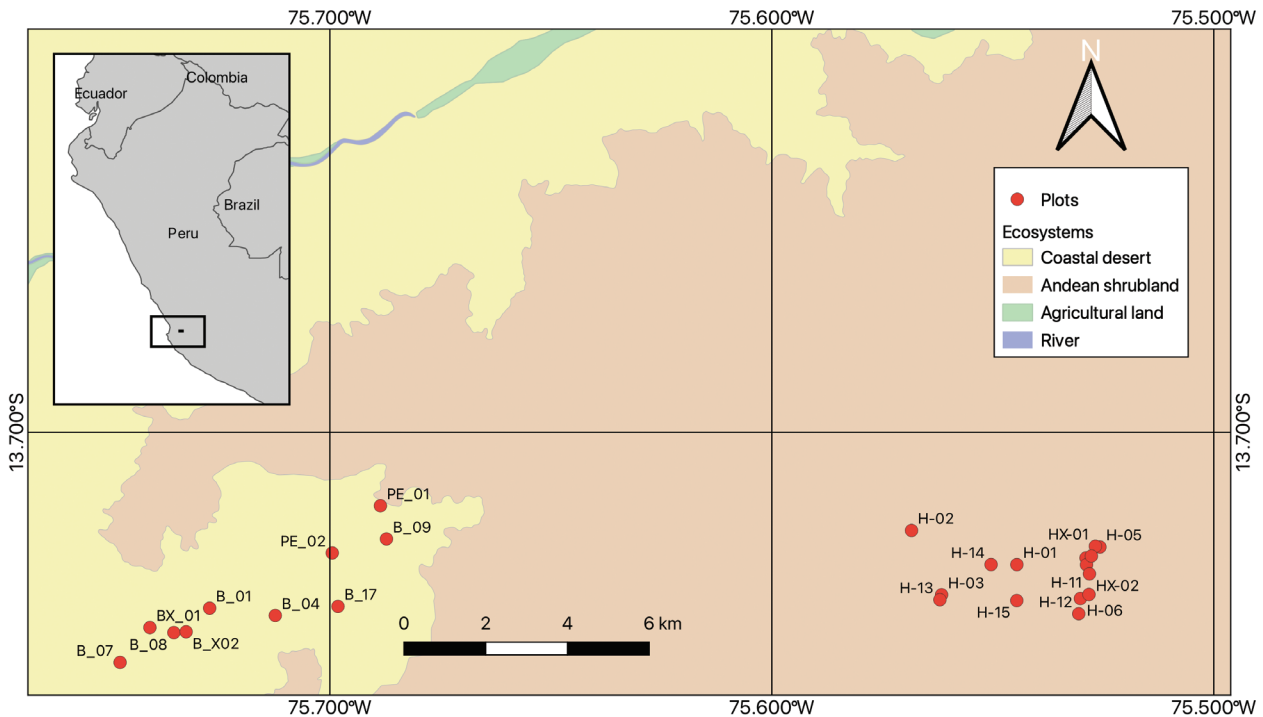
Figure 1. Plot location and codes in the study area, showing the two main natural ecosystems (coastal desert and Andean shrubland), as well as agricultural areas restricted to valleys. Framed area in inset shows location of study area in Peru.

belongs to the mesotropical belt (Galán de Mera et al. 2017), and according to its elevation has a semi-arid and temperate climate with an annual average of 380 mm of precipitation (Olivares et al. 1994), an annual mean temperature of 11.3 °C (free CHELSA data set 1981–2010, Karger et al. 2017) and a relative humidity of 67% (Olivares et al. 1994). It is characterized by hills and ridges that form the division between the upper part of the San Juan and Murcielago creeks, that are crossed by a large number of minor streams that change the physiography of the relief making it less rugged (Langstroth et al. 2013). Ecologically it corresponds to the Lower Montane Thorny Steppe formations with mostly ephemeral vegetation with annual species such as *Glandularia* sp., *Tarasa operculata*, *Heliotropium* sp., *Senecio* sp. and *Trixis cacalioides*, together with dispersed columnar cacti such as *Armatocereus matucanensis*, *Browningia candelaris*, *Corryocactus brevistylus* subsp. *puquiensis* and *Weberbauerocereus rahuii* (Figure 3, Arenas and Fernandez 2009).

Methods

To record the composition and abundance of the vegetation we sampled both localities during the months of February and March 2014. We surveyed 10 plots of 100 m × 60 m located between 740–1,600 m a.s.l. in La Bolivar (Novoa and Mendívil 2011; Novoa and Vega 2013) and 15 modified Whittaker plots (MWPs) (Barnett and Stohlgren 2003) of 20 m × 5 m located between 2,800–3,000 m a.s.l. in Huancacasa (Table 1). Plots were originally installed to monitor cacti populations only (Novoa and Mendívil 2011), with surveys of the associated vegetation added in

2014. Consequently, the differing plot sizes responded to differences observed in cacti abundances in each locality in our original research protocol (lower cacti abundances and density in La Bolivar required bigger plots to survey equivalent populations). Site accessibility and logistics were the main factors for site selection for each plot, followed by topographic position and slope. Where possible, we chose plots at the bottom of the valley, slope, and ridge in each locality. Vegetation physiognomy was visually homogeneous within each plot. Species abundance within each plot was measured as the number of individuals per plot. Inserting our coordinates per plot in the free CHELSA data set 1981–2010 we obtained mean annual temperature and annual precipitation (Karger et al. 2017). Elevation was recorded in the field and landform was assigned using the Topographic Position Index tool in QGIS (QGIS.org 2001). This tool calculates the index by comparing the elevation of each data point to its surroundings (Guisan et al. 1999). Points higher than their surroundings have a positive index value, for example ridges and hilltops. The value is negative for areas like valleys. Values of this index are then categorized into ten different landforms (Jenness 2006).

Given collection restrictions in the area due to the presence of natural populations of threatened and CITES species such as *Cleistocactus acanthurus* and *C. hystrix*, we followed collecting guidelines issued by the Peruvian National Forest Service Nacional Forestal (SERFOR) as per our permit and took a minimum-sampling approach by collecting only species that could not be identified unambiguously in the field, with three duplicates per species, following conventional herbarium procedures (Sánchez-González and González 2007). All collections were deposited in the USM
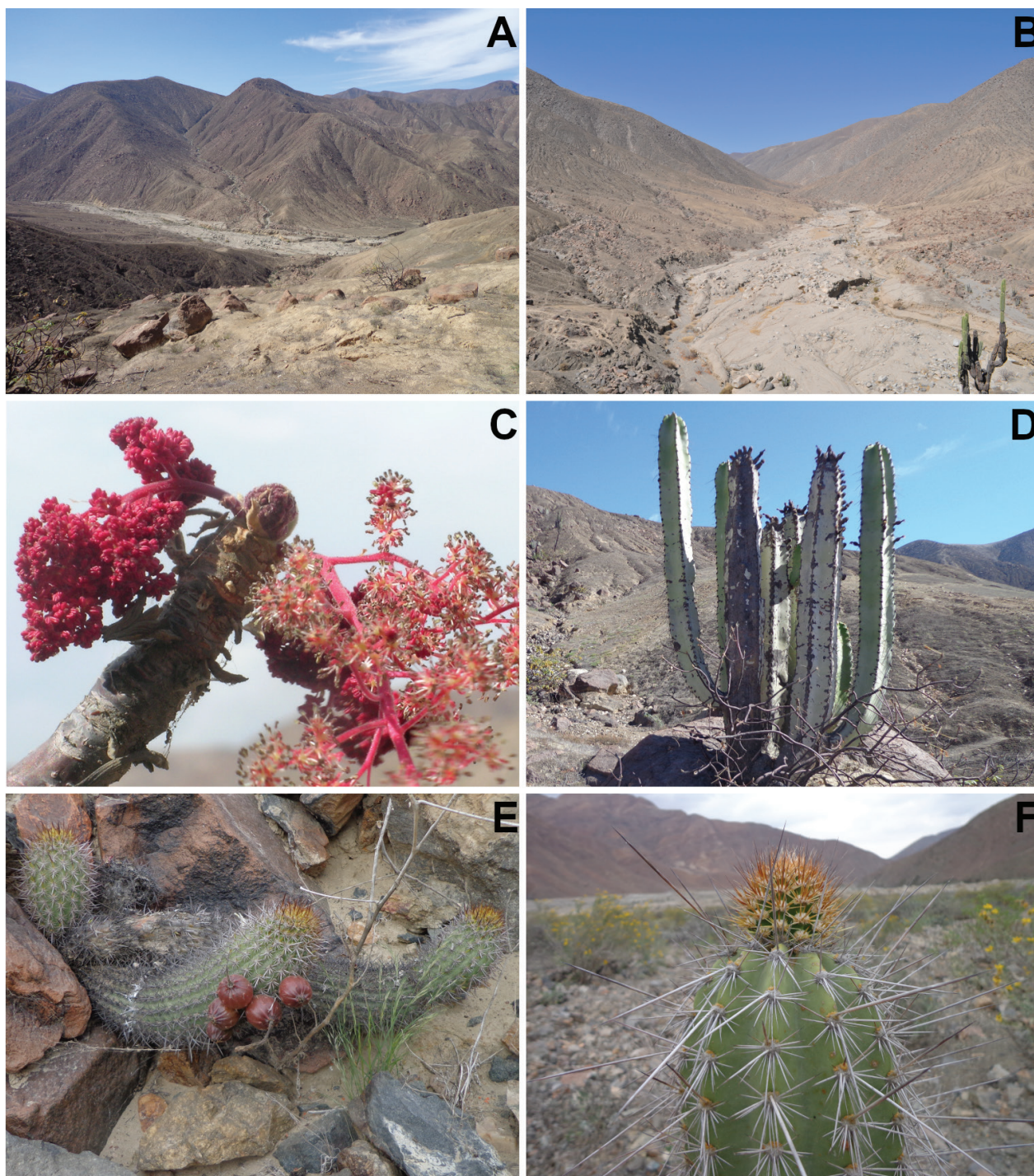
Figure 2. Landscapes in La Bolivar (images **A** and **B**) and representative species. **C.** *Orthopterygium huaucui*; **D.** *Neoraimondia arequipensis*; **E.** *Cleistocactus acanthurus*; **F.** *Armatocereus procerus*.

Herbarium (National History Museum of the San Marcos National University). Since conditions of extreme aridity did not always allow the collection of complete material for herbarium deposition, we also chose to register species using photographic material where possible.

Based on the quantitative survey in 2014 and several site visits between 2014–2019 (allowing us to record specimens within and outside of the survey plots) we assembled a list of species and morphospecies for the two locations. We used the morphospecies concept on collections that were difficult to identify at species level, but otherwise had morphological

characters that unequivocally differed from all the other material already identified in our study. We followed APG IV (Angiosperm Phylogeny Group 2016), scientific names and authorship were confirmed by consulting The Plant List (2013). Growth form followed Pérez-Harguindeguy et al. (2013) and was determined in the field and by consulting TROPICOS (Missouri Botanical Garden 2020). Each species was assigned to an herbaceous, shrub, stem succulent and climber growth form. Elevation range and region were also determined by consulting TROPICOS (Missouri Botanical Garden 2020), by following the geographic
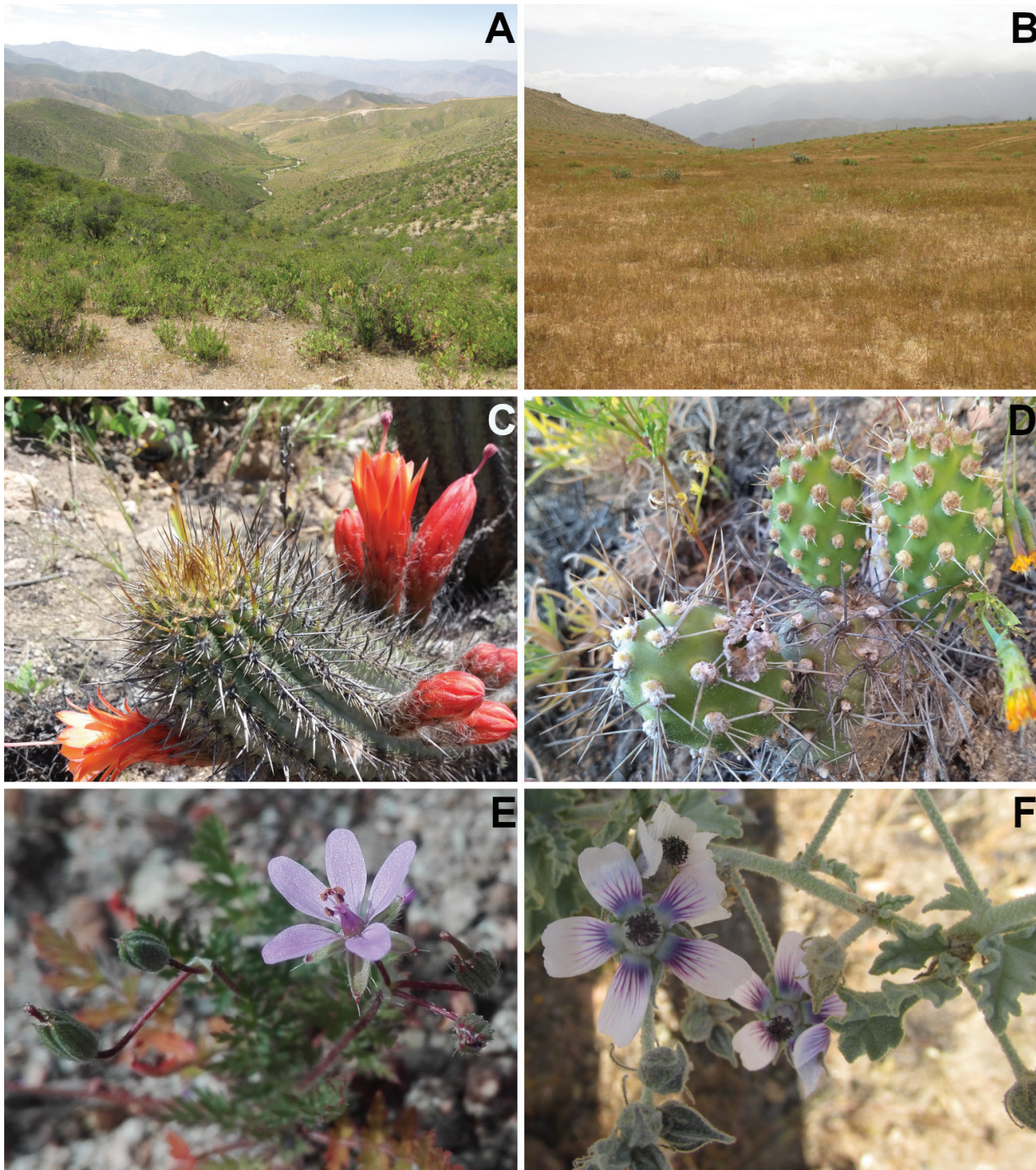
Figure 3. Landscapes in Huancacasa (images **A** and **B**) and representative species: **C.** *Cleistocactus hystrix*; **D.** *Cumulopuntia sphaerica*; **E.** *Erodium cicutarium*; **F.** *Tarasa operculata*.

regionalization of Brako and Zarucchi (1993) and contrasted with published literature for Peru. International and national conservation status followed IUCN (2020) and Ministerio de Agricultura y Riego (2006), respectively. Endemism assessment followed León et al. (2006) and was restricted to Peru. We considered records to be new for Ica, when they had not been reported previously in the region by Brako and Zarucchi (1993), León et al. (2006), Whaley et al (2019), or any other published work citing voucher specimens from Ica. An additional group of species was considered as potential new records since their taxonomic status is

not yet fully confirmed (specimens tentatively labeled as aff. or cf., pending collection and revision of additional material). This latter group was excluded from further analyses, except for *Oldenlandia* as it represents a new genus for Ica.

Data analysis

To assess if the plots in our study captured a representative sample of the vegetation in each locality, we pooled plot species presence/absence data per locality. We calculated

species accumulation curves (SAC) for each locality, for up to 30 sampling units (plots) using sample-based (incidence-raw data) rarefaction and extrapolation with the *iNEXT* function in the iNEXT package (Hsieh et al. 2020). To calculate species richness and Shannon Wiener α-diversity (Moreno 2001) we used only species that occurred within plots. Species abundances were used to compare vegetation between plots within each of the localities and between localities through Non-Metric Multidimensional Scaling (NMDS), and one-way Similarity (ANOSIM) analyses using the Bray-Curtis index. We used the Mann-Whitney U non-parametric test to determine if there were any differences in species richness and abundance between localities. To assess the potential influence of selected environmental variables (Suppl. material 1) on community composition, we fitted them onto the NMDS ordination plot using the *envfit* function in vegan (Oksanen et al. 2019). To relate elevation with species richness and abundance we used linear regression analyses. We plotted rank-abundance curves (Magurran 2004) for each location, and identified the most important species, species with the highest frequency (i.e. present in more than 65% of the plots) and those whose abundance and relative abundance was greater than average values. All analyses were performed using PAST (Hammer et al. 2001) and the R programming environment (R Core Team 2019). Plot floristic data used in the analyses are available on Figshare (Linares-Palomino et al. 2021).

Results

Sample completeness

The total estimated species pool based on Chao's species estimator in Huancacasa was 57 species (95% confidence interval estimated between 48 and 88 species), which was lower than in La Bolivar with 78 species (95% confidence interval estimated between 56 and 141 species). Species accumulation curves for both habitats (Figure 4) illustrate similar rates of plant species accumulation (based on overlapping 95% confidence intervals). Although accumulation curves were not fully asymptotic, the number of plant species recorded for Huancacasa was 77% of the Chao estimator value. In La Bolivar, however, only 55% of the Chao estimator value was reached.

Floristic Catalogue based on qualitative plant surveys

Our floristic survey recorded 215 species and morphospecies from both localities. From this, we present data based on 202 species that were identified at least to genus level (Suppl. material 2, 198 identified to species level and 14 to genus level). 87 species were recorded in La Bolivar (Suppl. material 3) and 136 species in Huancacasa (Suppl. material 4), with 21 species in common. The combined surveys included 141 genera and 44 families (see details for each locality in Table 1). In total, 196 species (97%) were angiosperms
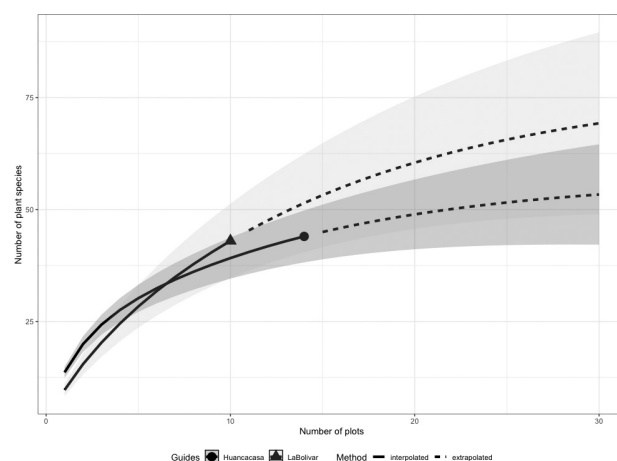
Figure 4. Species accumulation curves for Huancacasa and La Bolivar.

(24 monocots, 172 dicots), five ferns (*Adiantum poiretii*, *Astrolepis sinuata*, *Cheilanthes mollis*, *Pellaea ternifolia* and *Ophioglossum* sp.) and one gymnosperm (*Ephedra americana*). *Asteraceae* (43 species), *Poaceae* (19 species), *Solanaceae* (19 species), *Cactaceae* (11 species), *Amaranthaceae* (9 species), *Verbenaceae* (9 species), *Malvaceae* (8 species), *Fabaceae* (7 species) and *Euphorbiaceae* (5 species) were the most species rich families and included among all 64.4% of all species; other families contributed between one and four species (see details for each locality in Table 1). The most species rich genera with five species each were *Solanum* (*Solanaceae*: *S.* cf. *bukasovii*, *S. chilense*, *S. corneliomulleri*, *S. excisirhombeum* and *S. peruvianum*) and *Nolana* (*Solanaceae*: *N. humifusa*, *N. laxa*, *N. weberbaueri*, *N. thinophila* and *N. weissiana*). Other genera had between one and four species (see details for each locality in Table 1).

We recorded 31 species considered endemic to Peru and 18 considered under some form of threat by national or IUCN standards (see details for each locality in Table 1). *Solanaceae*, *Cactaceae* and *Asteraceae* included 54.8% of all endemics. In terms of growth forms, we recorded 142 terrestrial herbs (70.29%), 47 shrubs (23.27%), 11 stem succulents or cacti (5.45%) and two climbers (0.99%) (Table 1). Based on their known distribution, we recorded 10 coastal species (4.95%), 69 Andean-coastal species (34.15%), 69 Andean species (34.15%), 9 Andean-Amazonian species (4.45%), and 18 cosmopolitan species (18.91%). We could not define distribution for 27 taxa (13.36%) at genus level or with uncertain taxonomic identification (cf. and aff.) (Table 1).

83 species and three families (*Ophioglossaceae*, *Pteridaceae* and *Rosaceae*), are presented as new departmental records for Ica, including six additional species that are considered as potential new records (Table 1). The new records belong to 72 genera and 31 families. *Asteraceae* (24 species), *Poaceae* (8 species) and *Solanaceae* (5 species) contributed to most of the new records. Eight of the new records for Ica are Peruvian endemics already recorded in other regions in Peru (*Onoseris minima*, *Senecio tovari*, *Apodanthera weberbaueri*, *Jatropha macrantha*, *Nasa chenopodiifolia*, *Cistanthe weberbaueri*, *Nolana laxa* and *N. weissiana*). Three species are considered to be under threat according to national legislation (*Cnidoscolus basiacanthus*, *Jatropha macrantha* and

Table 1. Floristic summary based on qualitative and quantitative plant surveys. Species number in the richest families and genera are shown in brackets after family and genus name.

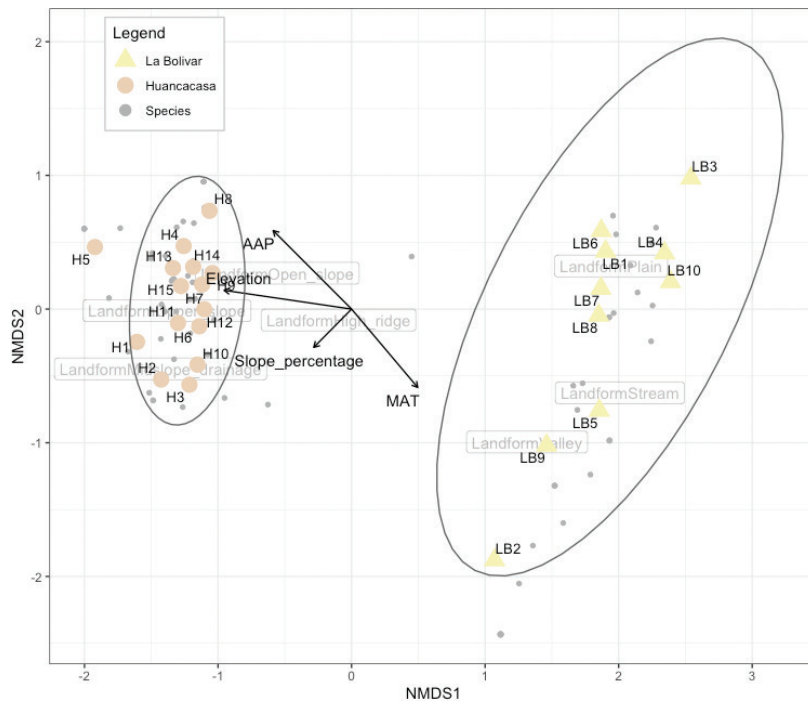|	La Bolivar	Huancacasa	Total
Number of species	87	136	202
Number of families	29	40	44
Number of genera	72	106	141
New records	26	66	78
Most species rich families	*Asteraceae* (15), *Solanaceae* (13), *Poaceae* (7), *Cactaceae* (5), *Amaranthaceae* (5), *Euphorbiaceae* (5)	*Asteraceae* (35), *Poaceae* (13), *Cactaceae* (7), *Solanaceae* (7), *Amaranthaceae* (5), *Malvaceae* (5), *Fabaceae* (5)	*Asteraceae* (43), *Poaceae* (19), *Solanaceae* (19), *Cactaceae* (11), *Amaranthaceae* (9), *Verbenaceae* (9), *Malvaceae* (8), *Fabaceae* (7), *Euphorbiaceae* (5)
Most species rich genera	*Nolana* (4), *Exodeconus* (3)	*Solanum* (3), *Eragrostis* (3), *Fuertesimalva* (3), *Erodium* (3), *Baccharis* (3), *Conyza* (3), *Gnaphalium* (3), *Senecio* (3)	*Solanum* (5), *Nolana* (5)
Endemic to Peru	21	11	31
Threatened	9	10	18
Potential new records	0	6	5
Growth form			
Stem succulent (cactus)	5	7	11
Herbaceous	63	94	142
Shrub	19	33	47
Climber	0	2	2
Region			
Coastal	8	2	10
Andean	23	52	69
Coastal-Andean	35	41	69
Andean-Amazonian	4	7	9
Cosmopolitan (widespread on three regions)	12	12	18

Kageneckia lanceolata), and one according to IUCN (*Kageneckia lanceolata*, Suppl. material 2).

Community structure based on quantitative data

The Shannon-Wiener α diversity index for Huancacasa was 2.658 bit/ind. and 2.649 bit/ind. for La Bolivar. Both localities differed in terms of species composition as shown by the two separate groups in the NMDS ordina-tion plot (Figure 5) and the ANOSIM results indicating higher dissimilarity ($R = 0.9788$, $p < 0.0001$).

The Mann-Whitney U test confirmed that there were significant differences between localities in terms of species richness ($w = 119.5$, $p = 0.014$, Figure 6a) and abundances ($w = 133$, $p = 0.0006$, Figure 6b), with the highest values of these parameters in Huancacasa. The regression analysis for species richness (Figure 7a) and abundance (Figure 7b) against elevation was significant, showing an increasing trend of both parameters with elevation.

Figure 5. NMDS ordination for plots in Huancacasa and La Bolivar. Stress = 0.07, ellipses are 95% of the confidence interval around the centroid of each group. Continuous environmental variables (elevation, slope, MAT = mean annual temperature, AAP = annual accumulated precipitation) and factors (landform) are overlaid.

As shown by the rank-abundance curves (Figure 8), the species with the highest mean abundance (± standard error) values in Huancacasa were *Junellia fasciculata* (45.3 ± 10.5 individuals/plot), *Grindelia brachystephana* (35.1 ± 9.7), *Clinanthus incarum* (33.4 ± 10.7) and *Cleistocactus hystrix* (15.5 ± 0.4). They were followed by *Atriplex rotundifolia* (7.7 ± 3.5 individuals/plot), *Cumulopuntia sphaerica* (7.3 ± 2.8) and *Erodium cicutarium* (7.3 ± 2.6). These species represented 75% of all individuals (Suppl. material 5). The most abundant species in La Bolivar (Suppl. material 6) was the shrub *Orthopterygium huaucui* (20.3 ± 13.2 individuals/plot), followed by *Neoraimondia arequipensis* (12.1 ± 2.8), *Presliophytum incanum* (9.5 ± 6.8), *Cleistocactus acanthurus* (9.2 ± 2.9) and *Armatocereus procerus* (5.9 ± 1.8).

Growth form composition showed that both localities are represented mainly by shrub and herb species, followed by stem succulent (cacti) species. Climbers were
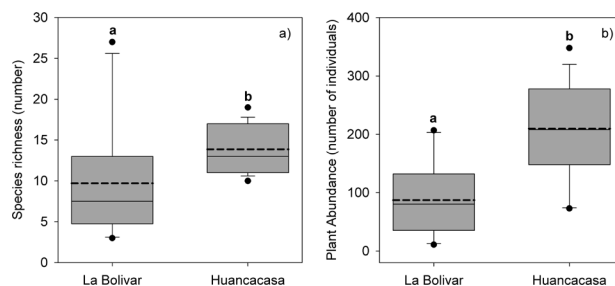

Figure 6. Boxplots showing differences between localities in species richness (**a**) and plant abundances (**b**).

registered only in Huancacasa. The relative abundance of growth forms showed that the cacti growth form was most abundant at La Bolivar (37.05%), followed by shrubs and herbs (Table 2). Conversely, in Huancacasa cacti had lower relative abundance (11.31%) and were replaced by
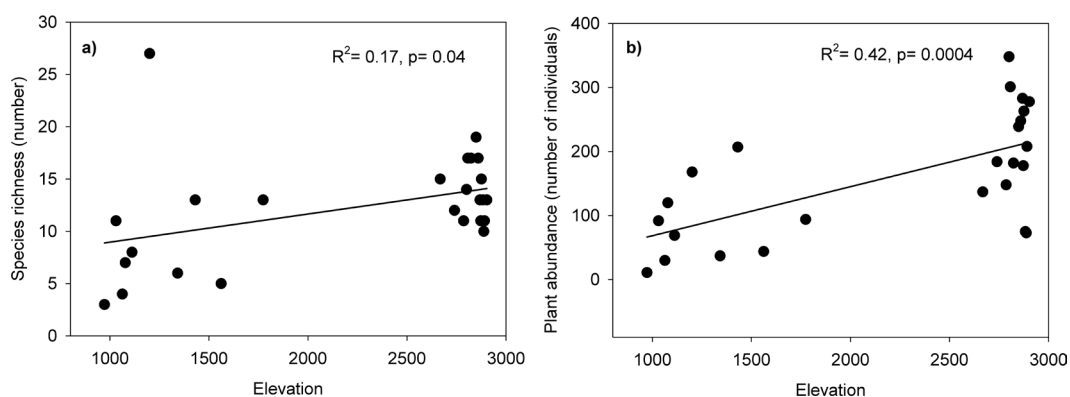
Figure 7. Regression analyses between species richness and elevation (**a**) and plant abundances and elevation (**b**).
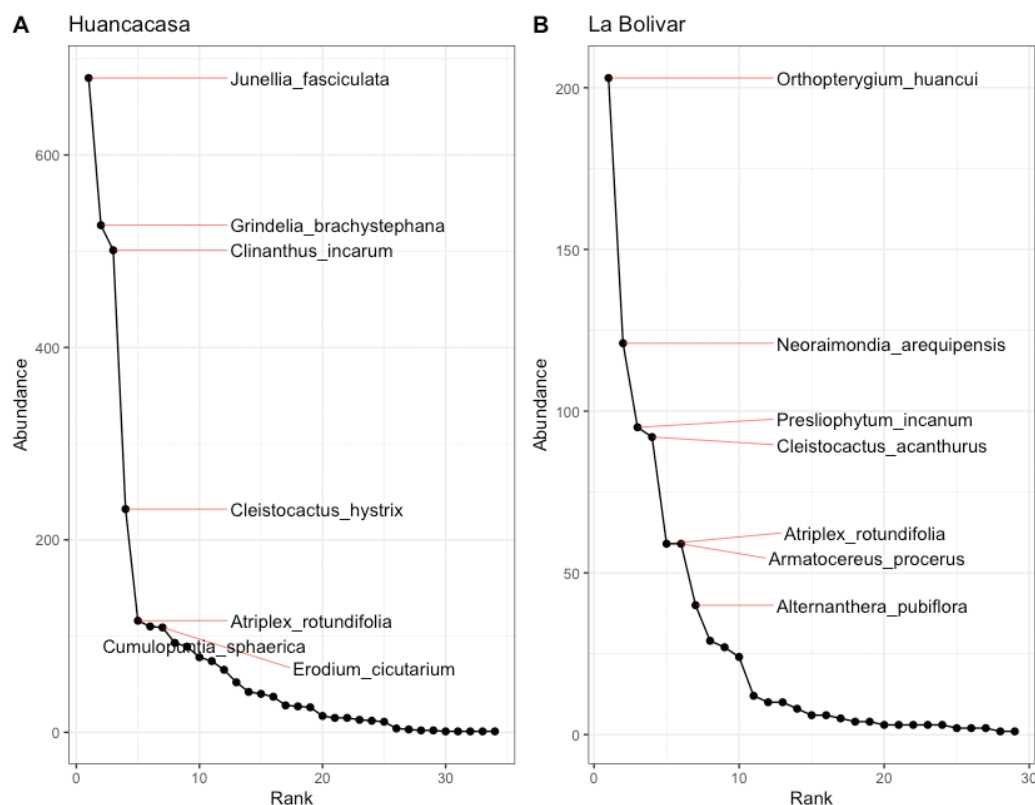
Figure 8. Rank-abundance curves for Huancacasa and La Bolivar, note the different scales in y-axes.

Table 2. Diversity and growth form composition at Huancacasa and La Bolivar based on the quantitative survey conducted in 2014.

	La Bolivar (740–1,790 m a.s.l)	Huancacasa (2,600–3,000 m a.s.l.)
Endemic to Peru	7	3
Threatened	5	3
Region		
Coastal	2	0
Andean	5	8
Coastal-Andean	15	6
Andean-Amazonian	1	2
Cosmopolitan (widespread on three regions)	2	5
Mean richness (spp./plot) ± se	9.7 ± 1.8	13.87 ± 0.70
Mean abundance (ind./plot) ± se	87.2 ± 16.3	209.67 ± 20.82
Shannon-wiener (bit/ind.)	2.649	2.658
Growth form		
Cactus species (%) *	(5) 17.86	(2) 5.88
Cactus cover (%)	37.05	11.31
Herbs species (%) *	(13) 46.43	(19) 55.88
Herbs cover (%)	28.66	39.9
Shrub species (%) *	(10) 35.71	(12) 35.29
Shrub cover (%)	34.29	48.3
Climber (%)	0	(1) 2.94
Climber cover (%)	0	0.5

* Species number in parentheses.

shrubs species as the most abundant (48.30%) growth form (Table 2).

Elevation (R^2 = 0.93, p = 0.0009), mean annual temperature (R^2 = 0.59, p = 0.0009), annual precipitation (R^2 = 0.69, p = 0.0009) and landform (R^2 = 0.47, p = 0.037) were significantly related to the NMDS ordination differentiating both localities, whereas slope was not significant (R^2 = 0.16, p = 0.13). Plain, Stream and Valley landforms were more common in La Bolivar, while Open Slope, Upper Slope, High Ridge and Midslope drainage characterized Huancacasa (Figure 5).

Discussion

Our research reinforces the need to increase exploration and documentation of the vegetation along the dry western slopes of the Andes (with an emphasis on the transition zones from the deserts in the coastal lowlands to the Puna highlands). Particularly we found that: (1) there is an important number of species inhabiting the western slopes of the Andes, many of them endemics (2) there is a different floristic composition between localities and, (3) species richness and abundance increase as elevation rises.

An overview of the desert flora of the western Andes slopes

Between both sampled localities a total of 215 species and morphospecies were recorded. This represents 19.4% of the 501 species mentioned by Whaley et al. (2019), which are also included in other floristic studies of the Ica department (León et al. 1997; Ostolaza 1998; Roque and Cano 1999; Cano et al. 2005; Orellana 2011; Cárdenas 2015). A total of 83 (41.01%) species found in our study have not been recorded hitherto for the Ica department (mainly of the *Asteraceae, Poaceae* and *Solanaceae* families). Additionally, six species are considered as potential new records (we

provide ecological and distribution notes for selected species in Suppl. material 7). A possible explanation of these new records could be due to the lower sampling efforts of the pre-montane and Andean areas in the department in comparison to the threatened lomas formations. In fact, several authors had found the species recorded as new in this study in adjoining departments for coastal fog oases or lomas and Andean vegetation (Brako and Zarucchi 1993; Arakaki and Cano 2003; Leon et al. 2004; Dillon et al. 2011; Montesinos et al. 2015a, 2015b). For example, of the new records, 55.42% have been reported in other Peruvian departments of the Andean region above 1,500 m a.s.l. Another 25.3% of these species are distributed along the Coastal and Andean regions at elevations above sea level and only *Euphorbia micromera* and *Nolana weissiana* have been reported in the coastal region at elevations between 0 to 1,000 m a.s.l. Of the remaining species, *Erodium moschatum, Portulaca pilosa, Cleome chilensis* and *Dicliptera montana*, are found in the Andean-Amazon region (Brako and Zarucchi 1993), while *Heterosperma diversifolium, Gnaphalium dombeyanum, Philibertia solanoides, Stellaria ovata* and *Porophyllum ruderale* are considered cosmopolitan (that is, distributed across the three regions). These broad distribution patterns of species along the Andean altitudinal gradient were also evident in the other species recorded in both study locations.

Of the 202 species listed in our study, 15.3% are endemic, the locality of La Bolivar having the highest number of endemic species. Most of our new endemic records for Ica are northern extensions of the Arequipa and Moquegua departments (e.g. *Onoseris minima, Cistanthe weberbaueri, Nolana weissiana*), but some were previously recorded in northern Andean Peru (e.g. *Apodanthera weberbaueri*). For most of these endemics, little more than their taxonomy and locality are known. We only have plot data for populations of *Senecio tovari* and *Nasa chenopodiifolia*, and show that they are locally extremely rare, both having been collected only in Huancacasa, the former species in five of the 15 plots (with 1 or 5 individuals), and the latter

species in only one of ten plots (1 individual). We also increased the number of known localities for *Nolana laxa* (from four in Lima to an additional locality in Ica) and *Nolana weissiana* (from two in Arequipa to one locality in Ica). According to Knapp et al. (2006), *Nolana weberbaueri* had not been collected since 1910. We recorded this endemic species in Ica within La Bolivar, unfortunately it was outside our plots so we cannot provide better information on population characteristics. Overall, our data suggest that most of these endemic species seem to have small local populations, restricted to extremely dry habitats along the Pacific coast and the western Andean slopes, a pattern already reported for the species in the lomas formations (Dillon et al. 2009).

According to the geographic regionalization in Peru, more than 74% of the recorded species are distributed both in the coastal or Andean region. This concurs with Sarmiento (1975) who linked these dry western slopes of the Central Andes to both the desert (coastal region) and the Puna (Andean region). On the other hand, Rundel et al. (2007) suggested they had closer affinities with the Puna vegetation (Andean region). This is supported by the 34.2% of species found in our study that have been reported to have Andean distribution, with some species occurring above 4,500 m a.s.l. as in the case of *Gnaphalium polium* and *Adiantum poiretii*. Another 34.2% of the recorded species was found to have coastal-Andean distribution (500 m a.s.l. to above 4,500 m a.s.l.), with some species extending well into the lower coastal region (below 500 m a.s.l.), like *Galinsoga parviflora* and *Bidens pilosa* (Rodríguez et al. 2016) which are found at sea level.

Changes in the desert flora along the elevation gradient

La Bolivar, located in the lower western Andes slope (740–1,790 m a.s.l.) differed markedly in its species composition to Huancacasa, located in the higher western Andes slope (2,600–3,000 m a.s.l.). For instance, La Bolivar harbor more coastal species than Huancacasa; conversely, Huancacasa has more species restricted to the Andean region than La Bolivar, and both localities share an important number of species coming from both the coastal and Andean regions. These results can be explained by the elevational differences between both localities (approximately 900 m) (Ruhm et al. 2020) through changes in mean annual temperature, annual precipitation, and landform characteristics, as we found in this study.

Both localities had *Asteraceae*, *Solanaceae*, *Cactaceae*, *Malvaceae* and *Fabaceae* as the most species rich families, following the general dominance patterns reported in previous studies (Gentry 1982; Whaley et al. 2010a, 2019). These families contain species adapted to xeric environments and steppe communities. Huancacasa had a number of species-rich genera coming from different families. Conversely, in La Bolivar only the genera *Exodeconus* and *Nolana* (both *Solanaceae*) were noted for their species

numbers. This is in accordance with a pattern documented by Arroyo et al. (1988) for the northern Chilean Andes, where fewer species per genus were reported as aridity increased. Species such as Nolana can survive harsh conditions and stands out as the most widespread genus found from northern Peru to southern Chile and in interior Andean sites (Dillon et al. 2009).

We found significant differences in species richness and abundance between localities, with the Huancacasa plots showing higher values in both parameters. These results coincide with observed reductions in species richness and total plant cover in harsh habitats. This is explained by the decreased productivity mainly limited by abiotic factors (Arroyo et al. 1988). For instance, Huancacasa has an annual precipitation that is six-fold that of La Bolivar, providing better plant growth conditions and thus increasing the number of individuals per species. Furthermore, both localities differ in their dominant growth form. Cacti growth form tended to dominate in La Bolivar (i.e. *Neoraimondia arequipensis* and *Armatocereus procerus*) followed by shrubs (i.e. *Orthopterygium huaucui*). These growth forms have stress-resistant strategies (through a combination of ecophysiological features, Jones 1992; Larcher 2003; Carvajal et al. 2015, 2017) allowing them to gain prominence over other growth forms as herbs in this harsh Andean habitat. For instance, we highlight the presence of *Presliophytum incanum*, a stinging nettle with high drought tolerance and endemic to Peru (Whaley et al. 2010a). Cacti species are particularly adapted to extreme aridity (Ward 2016), additionally some species as *Orthopterygium huaucui* function as a nurse species for the cacti, facilitating the establishment of *Cleistocactus acanthurus*, *Neoraimondia arequipensis* and *Melocactus peruvianus* (Novoa and Vega 2013). In contrast, Huancacasa is dominated by seasonal shrubs and herbaceous species (*Junellia fasciculata*, *Grindelia brachystephana* and *Clinanthus incanum*), and only one cactus (*Cumulopuntia sphaerica*).

Comparing our results to a floristic presence-absence matrix of vegetation surveys in Chile and Peru in coastal to Andean environments (Ruhm et al. 2020), these authors recognized three main groups of floristic affinities: North Chilean Coastal Desert, North Chilean Andean Desert and Peruvian Desert. Despite the clear local floristic differences reported between our study sites, at wider geographical scales they show strong links to and are nested within the Peruvian desert group. For instance, the highest percentage of species that Huancacasa shared with any of the other locations was with the southwest Andean part of Peru (Ilo river watershed in Moquegua department), with La Bolivar (in this study) and in the extreme south of Peru (Tacna department) (30%, 20% and 13% of the total species number in Huancacasa, respectively). La Bolivar also shared a significant number of its species with the Ilo river watershed (28%), Huancacasa (25%) and with Tacna (24%). In contrast, the highest percentage of shared species with sites in the desert and Andes of Chile were usually below 8% of the recorded species in Huancacasa and La Bolivar. Our results concur well with the pattern

of distinct desert plant communities reported by Ruhm et al. (2020) and reflect the high levels of endemism reported here and for the Atacama and Peruvian desert communities (Rundel et al. 1991; Moat et al. 2021).

Conclusion

Overall, our results indicate that more than 74% of the species recorded in this study are typical of coastal-Andean ecosystems. Furthermore, they suggest that the Andean slopes of the department of Ica are harboring an important percentage of the diversity of the dry western slopes of the Andes along the coast to highlands transition, including endemic and threatened species. Whaley et al. (2019) estimated the regional flora of Ica to be between 550 to 650 vascular plant species. The new records we report here bring the flora of Ica to 583 species, well within this range. Additional surveys and collections may reveal more about the distribution of species that are considered endemic for some departments, extending their range, and updating their conservation status. The quantitative data reported here show that several species were local or regionally rare, suggesting that a revision of their national or international threat assessment category is needed. This is especially relevant for the island-like vegetation patches that characterize the lomas, cactus and scrub habitats within the Ica desert, each of which can hold unique plant assemblages (Rundel et al. 1991). Furthermore, the interface between the deserts in the coastal lowlands to the Puna highlands, where our study area was situated, is an area that seems to have been subjected to similar ecological divergence and ecogeographical isolation factors as reported for coastal deserts further south (Ruhm et al. 2020). These conditions, the scant floristic and vegetation studies in these habitats, and the number of remaining unidentified material (which we have been unable to adequately sample and identify despite ongoing visits to our study area) and species that are awaiting taxonomic confirmation included

as cf. and aff. suggest that there are several taxa that will be added in the future.

Data availability

Plot-based species abundance data have been deposited at Figshare and are publicly available (https://doi.org/10.25573/data.13624055.v3). All other data used and mentioned in the manuscript are provided as Suppl. materials 1–7.

Author contributions

R.L.P designed the study, N.V conducted the field sampling, R.L.P and A.M.H performed the statistical analyses, A.M.H led the writing, while all authors critically revised the manuscript.

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Supplementary material

Supplementary material 1
Plot characteristics in the study area (coordinates are in the WGS-84 system).
Link: https://doi.org/10.3897/VCS.68006.suppl1

Supplementary material 2
List of species found in the western slopes of the Andes of Ica.
Link: https://doi.org/10.3897/VCS.68006.suppl2

Supplementary material 3
La Bolivar Floristic Catalogue with most common species records.
Link: https://doi.org/10.3897/VCS.68006.suppl3

Supplementary material 4
Huancacasa Floristic Catalogue with most common species records.
Link: https://doi.org/10.3897/VCS.68006.suppl4

Supplementary material 5
Mean plot abundance (± se), frequency, and relative abundance of species in Huancacasa (15 plots).
Link: https://doi.org/10.3897/VCS.68006.suppl5

Supplementary material 6
Mean plot abundance (± se), frequency, and relative abundance of species in La Bolivar (10 plots).
Link: https://doi.org/10.3897/VCS.68006.suppl6

Supplementary material 7
Notes on the ecology and distribution of the main new records for the Ica department, Peru.
Link: https://doi.org/10.3897/VCS.68006.suppl7