



Spatial and temporal variation of the vegetation of the semiarid Puna in a pastoral system in the Pozuelos Biosphere Reserve

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Abstract This study aimed to analyze the spatial and temporal variation of the vegetation in the northern Argentine Puna, utilizing both field sampling and remote-sensing tools. The study was performed within the Pozuelos Biosphere Reserve (Jujuy province, Argentina), which aims to generate socio-economic development compatible with biodiversity conservation. Our study was designed to analyze the dynamics of the Puna vegetation at local scale and assess and monitor the seasonal (dry and wet seasons), interannual, and spatial

variation of the vegetation cover, biomass, dominant species, and vegetation indices. Ten vegetation units (with differences in composition, cover, and high and low stratum biomass) were identified at our study site. The diversity of these vegetation units correlated with geomorphology and soil type. In the dry season, the vegetation unit with greatest vegetation cover and biomass was the *Festuca chrysophylla* grassland, whereas in the wet season, the units with greatest cover and biomass were vegas (peatlands) and short grasslands. The *Festuca chrysophylla* grasslands and short grasslands were located in areas with clay soils, except peatlands, associated with valleys and coarse-texture soils. The vegetation indices used (NDVI, SAVI, and MSAVI2) were able to differentiate functional types of vegetation and showed a good statistical fit with cover values. Our results suggest that the integrated utilization of remote-sensing tools and field surveys improves the assessment of the Puna vegetation and would allow a periodic monitoring at production unit scale taking into account its spatial and temporal variation.

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Introduction

The Puna or Altiplano is a high mountain plateau located at 3500 m above sea level in the Central Andes region, with cold climate, strong solar radiation, low

atmospheric humidity, and wide thermal amplitude (Aceituno 1996). In Argentina, the Puna extends over the northwestern part of the country, and the main activity of the rural areas is the herding of llamas (*Lama glama*) and sheep (*Ovis aries*) (Göbel 2001; Yacobaccio 2007; Lamas 2012; Wawrzyk and Vilá 2013). Together with vicuñas (*Vicugna vicugna*), a wild South American camelid, these livestock species are the main regional herbivores (Arzamendia et al. 2006; Vilá 2012; Arzamendia et al. 2014; Rojo 2017). The herding systems in the region are primarily based on the natural vegetation, whose main plant communities are shrub steppes. Peatlands, a local type of mountain wetlands known as “vegas” or “bofedales”, are also present in areas with higher soil moisture (Ruthsatz and Movia 1975; Cabrera 1976; Caziani and Derlindati 1999; Ruthsatz 2012). A key aspect when herders define livestock movements throughout the grazing sites is the existing heterogeneity of vegetation communities along the landscape (Göbel 2001). Several issues such as the land degradation throughout the drier sector of the Puna region have emerged in the last years (Navone et al. 2006). One of the main reasons pointed out as a cause of this land degradation is overgrazing, but evidence to confirm this correlation is scarce (Genin et al. 1995; Buttolph, and Coppock 2013). One of the barriers to understand the effect of grazing in the Puna region is the lack of basic information of the vegetation dynamics at local scale (Genin et al. 1995).

Like most drylands, the Puna shows wide intra- and inter-annual climate variability with sequences of dry and humid cycles (Aceituno 1996). Additionally, during the past 100 years, this region has suffered significant climatic changes, characterized by a persistent warming trend and an increase in the elevation of the 0 °C isotherm (Morales et al. 2012).

The natural heterogeneity of geological, geomorphic, and soil characteristics is known as geodiversity and has been proposed as an important feature that evidences the complexity of natural systems (Gray 2005; Stavi et al. 2018). Regarding this issue, in the Pozuelos Basin, Jujuy, Argentina, Cendrero et al. (1993) found an altitudinal range in which lower altitude areas present more developed soil and higher vegetation cover. In this basin, a plan for improvement of sheep was implemented during the 1960s, with the introduction of new breeds. One of the results of this plan was an increase in the number of sheep in relation to that of llamas, with the consequent increase in the risk of land degradation, as

the former leave the soil unprotected (Cendrero et al. 1993). However, little research was done about the impact of this plan on the natural vegetation. Ref. "Gray 2005" is cited in the body but its bibliographic information is missing. Kindly provide its bibliographic information in the list. Gray M. 2005. Geodiversity and geoconservation: what, why, and how?. *Geodiversity & geoconservation*, 22 (3): 4-12.

Previous studies describing the vegetation of the Argentine Puna have been focused on its composition and cover (Cabrera 1957; Cabrera 1968; Ruthsatz and Movia 1975; Cabrera and Willink 1983; Castañeda and González 1991; Bonaventura et al. 1995), and the current knowledge regarding both its ecological (Arzamendia et al. 2006; Arzamendia et al. 2008, Talamo et al. 2010) and systematic aspects (Ospina González et al. 2013, 2016) is scarce and fragmentary. Few studies have been conducted at a scale that can provide data which contribute to the development of rangeland management strategies and few detailed maps of the vegetation community distribution in the area are available (Ruthsatz and Movia 1975; Cendrero et al. 1993). Attributes such as cover and biomass of the natural vegetation, soil characteristics, and vegetation indices (such as NDVI and SAVI) have not been thoroughly analyzed in the semiarid Puna of Argentina. Most reference values for the Puna vegetation are from Bolivia, where species composition and local environmental conditions are different from those in Argentina (Navarro 1993; Genin et al. 1995; Alzérreca et al. 2001; Genin and Alzérreca 2006; Muñoz García et al. 2013).

The rough geomorphology and harsh climatic conditions of the Puna impose severe limitations on field studies, especially those that require intense monitoring and sampling over large areas. In this context, vegetation indices, which are remote-sensing tools, have been extensively used to assess the vegetation in drylands worldwide (Jackson and Huete 1991; Bannari et al. 1995; Sonnenschein et al. 2011; Xue and Su 2017). However, in the Argentine Puna, remote-sensing tools have been used only at a large scale, to study the regional physiognomic distribution and vegetation productivity in the Puna region of Salta and Jujuy Provinces (Baldassini et al. 2012), but not to study the vegetation at the local scale. To conduct local-scale research, remote sensing together with field data may allow complementing the characterization of different plant communities defined by their structural attributes

(Gould 2000). In Peru, the Normalized Difference Vegetation Index (NDVI) has been implemented to analyze the vegetation trends in “bofedales” at a more precise scale (Mazzarino and Finn 2016), but the wetter environment of the Peruvian Puna as compared with the Argentine Puna hinders the possibility of result comparisons between these two regions. In Bolivia, Genin and Alzerreca (1995) also implemented the NDVI to analyze the vegetation, using NOAA-AVHRR images. This constituted one of the first attempts at integrating remote sensing and fieldwork while focusing on rangeland management in the region. The use of remote-sensing tools, especially of vegetation indices, in the Puna is challenging due to the difficulties associated with determining the characteristics of dryland vegetation and the influence of soil brightness on the final results (Bannari et al. 1995).

Based on all the above, the aim of the present study was to analyze the spatial and temporal heterogeneity of the vegetation of the Argentine semiarid Puna by utilizing structural attributes (aboveground biomass and cover) and by relating them with vegetation indices. In this context, we wondered whether the spatial variability and species composition of vegetation units vary according to geomorphological environments and local soil characteristics and whether these differences are variable between years and/or seasons. To answer these questions, we conducted detailed vegetation surveys across the north of the Pozuelos Biosphere Reserve and complemented them by remote-sensing assessments. We also evaluated remote-sensing vegetation indices at a finer scale of spatial resolution and tested the hypothesis that these indices may allow us to differentiate among vegetation units as precisely as field data.

Materials and methods

Study area

This study was conducted in the Pozuelos Biosphere Reserve, located in the Argentine Puna, in Jujuy Province, at 3700–4000 m above sea level, covering approximately 14,000 ha (Fig. 1). The reserve extends over an endorheic basin, with a central depression and a permanent lake (which is the core area) flanked by two north-to-south ridges. The reserve forms part of the UNESCO-MAB initiative that aims to generate socio-economic development compatible with conservation

(UNESCO-MAB Biosphere Reserve Directory). In this Reserve, the main rural activity is the herding of sheep and llama on the natural vegetation.

The study site was located at an altitudinal gradient through the following morphodynamic environments of the reserve: western sierras (main massif and fluvial valley), piedmont and paleo-lake (as defined by lithology, superficial deposits, and plant cover), which constitutes the buffer and transition area of the reserve, where pastoral activities are allowed (Cendrero et al. 1993). Local climatic conditions are cold, dry, and with a wide diurnal temperature range due to the high altitude and the low moisture content of the air. Average annual temperature is 7.7 °C, and the mean annual precipitation is 375 mm, concentrated primarily in the summer wet season (Buitrago 2000).

Along the western edge of the study area, steep mountain slopes include an area of rough terrain composed of rocks and shallow soils. The general slope within the study area is oriented towards the East, where the Santa Catalina River flows. The study site is part of the Puna Ecoregion, specifically the Semiarid Puna Complex (Morello et al. 2012), formerly phytogeographically classified as Dry Puna (Cabrera 1971; Cabrera 1976), where the dominant plant formation is shrub-steppe. However, the distribution pattern of shrubs and grasses is not homogeneous. Additionally, the vegetation distribution in this site has been influenced by anthropogenic activities, mainly grazing (Cendrero et al. 1993).

The vegetation communities of the Puna usually present two vegetation strata: a high stratum of shrubs and tussock grasses and a low stratum of short dicotyledonous herbs, graminoids, and grasses (Cabrera 1957; Ruthsatz and Movia 1975; Arzamendia et al. 2006). Typical vegetation species are represented by the “tolilla” (*Fabiana densa*) and “chijua” (*Baccharis boliviensis*) shrubs. Near the water courses, a shrub of the genus *Parastrephia*, the “tola”, becomes more frequent. The moist areas around the springs in the upper parts of many streams are covered by permanently green meadows, called “vegas” (Cendrero et al. 1993). In the study area, ten herder families and their livestock (mainly llamas and sheep) share the habitat with vicuñas. The herders use a transhumant pastoral strategy with livestock displacement within the study area during the wet (December to May) and dry (May to November) seasons. In the mountains of the western sierras, each family grazes approximately a mean of 350 sheep and

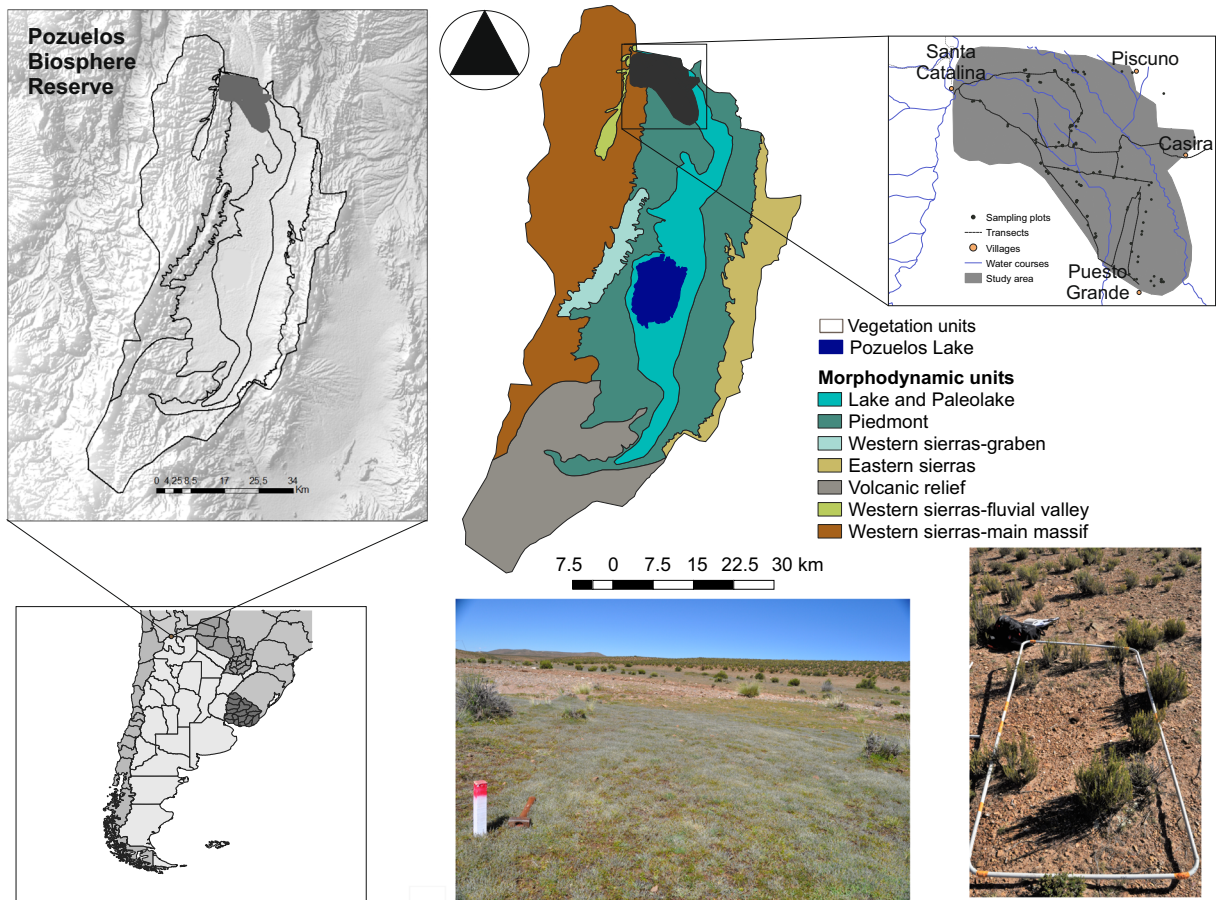


Fig. 1 Location of the study area in northwestern Jujuy Province, northern Argentina. Illustration of the sampling design and location of the cover sampling plots in the study site and photographs

of one of the vegetation units (peatlands) and a 2×1 -m sampling plot in the *Baccharis boliviensis* and *Fabiana densa* steppe

30 llamas, which coexist with 120 vicuñas, whereas in the piedmont and paleo-lake, the families graze herds of approximately a mean of 700 sheep and 250 llamas, which coexist with 900 vicuñas. These abundances make up a mean animal stock during the period analyzed equivalent to 1.19 sheep per ha (minimum: 0.62 in the mountains of the western sierras, maximum: 2.06 in the flat areas of the piedmont and paleo-lake) (Rojo 2017). Livestock management practices did not differ among the herders. In the study area, a management project of wild vicuña live shearing has been in action since 2012 (Arzamendia et al. 2014).

Vegetation sampling and data collection

Fieldwork was conducted during the dry (September 2012, 2013, and 2014) and wet (April 2013 and February 2014) seasons. The fieldwork of 2013 was carried

out in April and not in February due to the intense rainstorms and the river flood event occurred in that summer. The annual rains recorded in the wet season (November–April) in the city of La Quiaca, which is at a linear distance of 50 km from the town of Santa Catalina and 40 km from the study area, were 456.8 mm in 2013 and 270 mm in 2014 (Servicio Meteorológico Nacional).

To achieve a representative sampling, we used a random stratified sampling design. Sites were stratified along an altitudinal gradient within the morphodynamic environments (western sierras, piedmont, and paleo-lake) and represented all the vegetation patch types (or vegetation units) within their classification in an area of 10,569.26 ha. We surveyed ten vegetation units, distinguished by their physiognomy and dominant plant species (Matteucci and Colma 1982), utilizing a set of sampling points

(n = 46), which were georeferenced with a GPS Garmin E-Trex 20 (Fig. 1). Based on these points, we produced a supervised classification (maximum likelihood) of Landsat OLI 8 (Jan-02-2014) band combinations (Tso and Mather 2009) to obtain a preliminary extent of each unit. The final spatial extent of each vegetation unit was defined through a visual interpretation based on fieldwork and satellite images.

At least five georeferenced cover sampling plots (2 m × 1 m rectangles) were placed in each vegetation unit. Plots were marked to allow for repeat measurements. The physiognomic properties estimated were the maximum and the mean height (cm) of the vegetation and the cover (%) of the herbaceous plants and/or grasses and shrub layers. Two layers were defined: a high stratum, composed of shrubs, open tussock grasses and plants < 2 m and > 0.10 m tall, and a low stratum, defined by the presence of short grasses, graminoids, and dicotyledonous herbs < 0.10 m tall. Total, low-stratum and high-stratum cover were calculated through visual estimation, classifying cover into 10 categories, each of 10%, ranging between 0 and 100 (Matteucci and Colma 1982). A floristic survey comprising all vascular plant species present in the sampling plots was performed and voucher specimens were collected and deposited in the JUA herbarium (Universidad Nacional de Jujuy, Jujuy, Argentina).

To determine biomass, plant biomass sampling plots (0.5 m²; 1 m × 0.5 m) were located near plant cover sampling plots and the plants classified into low- and high-stratum species and harvested separately. Then, each individual of the high stratum was identified and all above-ground biomass within the plots was removed (Sala and Austin 2000). A total of 121 biomass sampling plots were assessed in the dry season and 75 in the wet season. Samples were dried at 60 °C to achieve a dry weight. The samples were weighted using a precision balance accurate to 0.1 g. Biomass data were expressed as kg/ha.

Superficial soil was also sampled to analyze certain physical and chemical properties, such as texture (Bouyoucos 1927), pH, electrical conductivity, and total organic matter (Walkley 1947). Ref. "Bouyoucos 1927" is cited in the body but its bibliographic information is missing. Kindly provide its bibliographic information in the list. Bouyoucos, J. (1927). The hydrometer as a new method for the mechanical analysis of soils. *Soil Science*, 23, 343–352.

Vegetation indices

Two optic satellite images Landsat OLI 8, from the wet and dry seasons, respectively, obtained through the Global Visualization (GloVis) Viewer (U.S. Dept. of the Interior, U.S. Geological Survey, Reston, VA, USA) were used for remote sensing and determination of vegetation indices. The dates of the acquisition of the images were Jan-02-2014 and Sept-15-2014. The images were corrected to surface reflectance with the Semiautomatic classification tool of QGIS (Quantum GIS Development Team 2009) and projected onto POSGAR 2007–Argentina 3, EPGS: 5345. Ref. "Quantum GIS Development Team, 2016" is cited in the body but its bibliographic information is missing. Kindly provide its bibliographic information in the list. Quantum GIS -QGIS- Development Team. (2009). *QGIS Geographic Information System*. Open Source Geospatial Foundation. URL <http://qgis.org>

The following four vegetation indices were calculated in 47 of the georeferenced sampling plots: (i) the Normalized Difference Vegetation Index (NDVI), because it is widely used and has been previously implemented in the region (Rouse et al. 1974), in accordance with Eq. (1); (ii) the Soil Adjusted Vegetation Index (SAVI) (Huete 1988), which considers the influence of soil reflectance on NDVI and is generated through Eq. (2) with two correction factors related to the vegetation cover (0.5 and 0.75 for intermediate and low vegetation density, respectively); and (iii) the Modified Soil Adjusted Vegetation Index (MSAVI2) (Qi et al. 1994a, b), obtained through Eq. (3).

$$NDVI = (NIR - RED) / (NIR + RED) \tag{1}$$

$$SAVI = (NIR - RED) / (NIR + RED + L) \times (1 + L) \tag{2}$$

$$MSAVI2 = (2 \times NIR + 1 - \sqrt{(2 \times NIR + 1)^2 - 8 \times (NIR - RED)}) / 2 \tag{3}$$

In Eq. 2, L is the adjustment factor for the influence of soil brightness, whose value depends on vegetation density. In this study, we chose a value of 0.75 (because 0.5 is recommended for intermediate vegetation cover and 1 for very low vegetation cover).

All the vegetation indices were calculated using the QGIS raster calculator tool.

To analyze the relationship between plant cover, biomass, and vegetation indices, we used the images taken during the same year in which we sampled the vegetation in the field. But, as the February images (field measures) were covered with clouds, we used the January image (Jan-02-2014). As Landsat 7 images had an SLC-off effect in 2013, most field points could not be used, so the correlation between plant cover/biomass and vegetation indices was estimated for wet season of 2014.

Data analysis

The data were analyzed using the R software (R Core Team 2015). The plots were made using the *ggplot2* package. The variation in the aboveground biomass (kg of dry weight, kg/ha) of the low stratum was analyzed using a two-way ANOVA, in which factors were *season-year* (four levels: wet season 2013, dry season 2013, wet season 2014, and dry season 2014) and *vegetation unit* (10 vegetation units). We considered the factor season + year instead of season and year individually because we found differences in the biomass recorded during the wet season. To identify which levels of the factor season + year had significant influence on the biomass of the vegetation units, we conducted Tukey's honestly significant difference (HSD) post hoc test for multiple comparisons (Crawley 2007), using the R package *agricolae*. Due to the interactions found, to determine possible differences among vegetation units during the dry and wet seasons and within the wet season, we used a one-way ANOVA. The biomass of the high stratum was analyzed using a three-factor ANOVA (in which factors were year, season, and vegetation unit) and differences between seasons were analyzed using a one-way ANOVA.

The vegetation cover of both strata was analyzed using a three-factor ANOVA (in which factors were season, year, and vegetation units) and differences among vegetation units within each season were analyzed with a one-way ANOVA (in which the factor was the vegetation unit). The comparison was made using Tukey's HSD post hoc test.

Biomass values of both strata were expressed as log-transformed (natural log, ln) to accomplish normality and homoscedasticity assumptions. Cover values (percentages) were transformed to arcsine, using

$\text{asin}(\sqrt{\text{cover}})$ after expressing them as proportion (cover value(%)/100), following McDonald (2014) to accomplish parametric assumptions.

To analyze whether the vegetation indices showed differences among them and between seasons, they were analyzed using a two-way ANOVA (in which factors were season, with two levels (wet and dry), and vegetation index, with four levels (NDVI, SAVI-0.5, SAVI-0.75, and MSAVI2). The values of the vegetation indices were log-transformed to accomplish normality and homoscedasticity assumptions. To identify how vegetation indices were able to identify vegetation units, we used a two-ANOVA for each index (in which factors were season and vegetation units). The comparison was made using Tukey's HSD post hoc test.

Then, to identify the relation between the structural variables and each vegetation index, we used ordinary least squares regressions. We evaluated the vegetation indices in 24 sampling plots where we recorded aboveground biomass and cover in 2014.

Results

Spatial distribution and species composition of vegetation units

We identified ten vegetation units according to their composition, physiognomy, and spatial distribution on the landscape (Fig. 2). The species composition and soil characteristics of the vegetation units are detailed in Tables 1 and 2. In the massif of the western sierras and piedmont, we identified three vegetation units dominated by *Baccharis boliviensis*, whereas in steep sloped areas, the high stratum was co-dominated with *Fabiana densa* and *Jarava ichu*. In the piedmont, which presents shallow soils, with a high content of rock fragments within the topsoil, the high stratum was dominated by *B. boliviensis* alone.

In the paleo-lake and piedmont units, *Festuca chrysophylla* grasslands were located in depressions with fine textured soils, whereas *Parastrephia quadrangularis* steppes were identified in flat areas, on silty clay loam and wet season high moisture soils, where temporary floods occur (Fig. 2). We also found a transition area with both species characterized as a unit. The most extensive unit in loamy soil with less than 40% rock content soils was the *Tetraglochin cristatum* steppes, located along flat areas near the Santa

Catalina River, presenting several transitions with adjacent units (*F. chrysophylla*, *B. boliviensis*, and *P. quadrangularis*). Short grasslands with only low-stratum species were present in flat areas and with varying patch sizes. We also found several transition areas with *F. chrysophylla* grasslands and *T. cristatum* steppes.

The riparian vegetation presented the highest spatial heterogeneity in its composition and dominant species (Table 1) and was present in sandy soils with frequent sand dunes. The spatial pattern of this vegetation unit consisted of patches of diverse area and was influenced by the presence of temporary river branches that remove soil and vegetation biomass, especially during the wet season. Patches were dominated by species like *B. boliviensis*, *T. cristatum*, *J. ichu*, *Ocyroe armata*, and *Cenchrus chilensis*.

The peatlands were located in hollows and valleys, in soils with high moisture content, often including surface water, especially during the wet season. The surface water displayed differential runoff velocities, depending on the rain intensity. High-stratum species were almost absent, except for some individuals of *F. chrysophylla*.

The low-stratum typical species were *Aristida antoniana* and *Bouteloua simplex*, with higher species diversity in the units with soils with high moisture content (Tables 1 and 2).

All soil samples covering the ten vegetation units had low salinity content (lower than 2 dS/m), were moderately/slightly acid (pH range 5.51–6.26), and showed a wide textural gradient along the landscape (Table 2).

Structural attributes of vegetation units

Total plant cover showed a high degree of correlation (Pearson's correlation = 0.91, $p < 0.0001$, $t: 25.38$) with the low-stratum cover, which is the one that contributed the most to total variation. The three-factor ANOVA of the low-stratum cover revealed significant differences among vegetation units and seasons, with no interactions between the factors ($F_{(39,100)} = 6.7$, $p < 0.0001$). The low-stratum cover was higher during the wet season (average wet season: 55.18%, dry season: 41.98%, $F_{(1,138)} = 9.86$, $p < 0.01$). In the dry season, the *F. chrysophylla* grasslands were the units that showed the highest cover values (mean 68.75%, $F_{(9,67)} = 11.41$, $p < 0.0001$), whereas in the wet season, peatlands (mean

82.5%), *F. chrysophylla* grasslands (mean 80.83%), and short grasslands (mean 78.33%) were the units that showed the highest cover values ($F_{(9,53)} = 15.21$, $p < 0.0001$). In both seasons, the lowest cover values were found in the vegetation units dominated by *B. boliviensis* in the riparian and steep slope areas (Fig. 3).

The results of the low-stratum biomass analysis showed a significant effect related to the year, season, and vegetation unit ($F_{(39,100)} = 7.15$, $p < 0.0001$), with significant interactions. The interaction between year and season can be explained by differences in the slope of the increase (between the dry and the wet season) by year, which showed the highest values at the most productive units (peatlands, *F. chrysophylla* grasslands, *P. quadrangularis*, and *F. chrysophylla* shrub-grass steppe and short grasslands) in 2014 (Fig. 4).

During the dry season, *F. chrysophylla* grasslands showed the highest biomass (mean 608.40 kg/ha, $F_{(9,67)} = 7.998$, $p < 0.0001$, Fig. 3), whereas during the wet season of 2013, there were marginally significant differences among vegetation units ($F_{(9,28)} = 2.32$, $p = 0.05$). In the wet season, peatlands showed the highest mean value (1128.55 kg/ha in 2013 and 3075.55 kg/ha in 2014) and dispersion of the data, followed by *F. chrysophylla* grasslands (1009.6 kg/ha) in 2013 and short grasslands (mean 1337.03 kg/ha) in 2014 ($F_{(9,15)} = 4.083$, $p < 0.01$).

The high-stratum cover showed no differences between seasons and years, but varied with vegetation units ($p < 0.001$, $F_{(35,83)} = 2.236$) and showed no interaction among the factors. The high-stratum cover of *P. quadrangularis* steppe was the highest ($p > 0.001$, $F_{(8,110)} = 9.144$), followed by the mixed *P. quadrangularis* and *F. chrysophylla* grass-shrub steppe and riparian vegetation (mean Pq: 35.42%, Pq + Fc: 32.73%, Rveg: 30.37%) (Fig. 5). High-stratum species were absent in short grasslands and appeared in peatlands in a low proportion.

Similarly to that observed for the cover, the high-stratum biomass showed differences only within units ($p < 0.0001$, $F_{(24,75)} = 3.825$), which allowed us to gather the data in a one-way ANOVA ($p > 0.01$, $F_{(17,82)} = 3.907$). The high stratum of riparian vegetation, mostly *Ocyroe armata*, which are tall woody shrubs, showed the highest standing biomass (mean: 20996.3 kg/ha) (Fig. 6), with more than three-fold higher biomass than the other units.

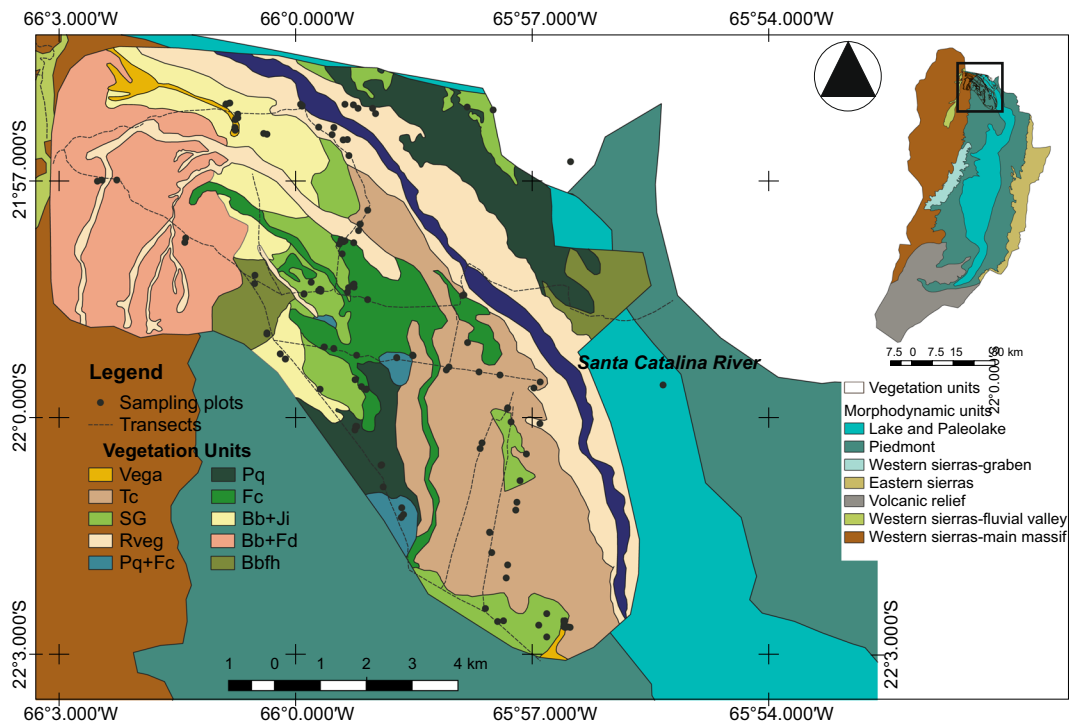


Fig. 2 Spatial distribution of the vegetation units in the study area, and their localization within the morphodynamic environments of the Pozuelos Basin (Cendrero et al. 1993). Bb + Ji: *Baccharis boliviensis* and *Jarava ichu* steppe. Bb + Fd: *B. boliviensis* and *Fabiana densa* steppe. Bbfh: *B. boliviensis* steppe in foothills. Tc:

Tetraglochin cristatum steppe. Fc: *Festuca chrysophylla* grassland. Rveg: Riparian vegetation. SG: short grassland. Pq + Fc: *Parastrephia quadrangularis* and *F. chrysophylla* steppe. Pq: *P. quadrangularis* steppe. Vega: peatlands

Application of vegetation indices in the study site

The analysis of the four different vegetation indices chosen showed differences between seasons and index, with no interactions between them (vegetation index and season) ($F_{(7,360)} = 45.84$, $p < 0.0001$). The NDVI showed the highest values during both the dry and wet seasons, and the soil-adjusted indices SAVI ($L = 0.5$), SAVI ($L = 0.75$) and MSAVI2 had a similar response: they differentiated between seasons but showed similar trends.

The NDVI and SAVI ($L = 0.5$) were compared by vegetation unit in the dry and wet seasons (Fig. 7). The greatest differences between seasons and vegetation indices were found in the vegetation units that presented the highest cover values (Fc, SG, Pq, Pq + Fc, and peatlands). Both indices showed the lowest values in the riparian and mountain slope areas. NDVI showed the best ability to differentiate vegetation units in the dry season, whereas SAVI was better in the wet season.

A significant relation was found between the low-stratum cover and vegetation indices during the wet season of 2014 (Fig. 8, Table 3). Wider differences between NDVI and the other indices were found in the high-cover vegetation units. MSAVI 2 and SAVI ($L = 0.75$) showed similar linear equations. No significant relationship was found between the indices and plant biomass ($p < 0.05$).

Discussion

In this study, we identified ten different vegetation units in the northern Pozuelos Reserve Basin, in the Argentine Puna, and characterized them by their spatial distribution composition, aboveground biomass, and cover by stratum, associated with geomorphological and edaphic components. We also presented the composition and structural variables of the plants (cover and biomass), reflected by vegetation indices derived from satellite image data. An effort was made to correlate the

Table 1 Vegetation units and species list organized by stratum

Vegetation unit	Acronym	High-stratum species	Low-stratum species
<i>Baccharis boliviensis</i> and <i>Jarava ichu</i> steppe	Bb + Ji	<i>Adesmia</i> (R.E. Fr.) <i>erinacea</i> Phil., <i>Baccharis boliviensis</i> (Wed.) Cabrera, <i>Jarava ichu</i> Ruiz y Pav. <i>ichu</i> Phil., <i>Parastrephia quadrangularis</i> (Meyen) Cabrera, <i>Tetraglochin cristatum</i> (Britton) Rothm.	<i>Aristida antoniana</i> Steud ex Döll, <i>Bouteloua simplex</i> Lag., <i>Mathueniopsis</i> sp. Speg., <i>Eleocharis</i> sp.
<i>B. boliviensis</i> and <i>Fabiana densa</i> steppe	Bb + Fd	<i>A. erinacea</i> , <i>B. boliviensis</i> , <i>Fabiana densa</i> J. Rémy, <i>Astragalus garbancillo</i> Cav.	<i>A. antoniana</i> , <i>B. simplex</i> , <i>Dichondra argentea</i> Hum. & Bomp. ex Willd., <i>Dalea boliviana</i> Britton, <i>Nasella arcuata</i> (R.E. Fr.) Torres, <i>Nasella novari</i> (R.E. Fr.) Torres, Unidentified Portulacaceae
<i>B. boliviensis</i> steppe in foothills	Bbth	<i>B. boliviensis</i> , <i>J. ichu</i> , <i>A. erinacea</i>	<i>A. antoniana</i> , <i>A. asplundii</i> , <i>B. simplex</i> Lag., <i>Hypseocharis pimpinellifolia</i> J. Remy, <i>Muhlebergia fastigiata</i> (J. Presl) Henrard
<i>Tetraglochin cristatum</i> steppe	Tc	<i>Ephedra breana</i> Phil., <i>Festuca chrysophylla</i> Phil., <i>J. ichu</i> , <i>P. quadrangularis</i> , <i>T. cristatum</i> .	<i>Azorella</i> sp., <i>A. antoniana</i> , <i>A. asplundii</i> , <i>B. simplex</i> , <i>Cardionema</i> (R.E. Fr.) <i>burkartii</i> Subils, <i>Eleocharis</i> sp., unidentified Fabaceae, <i>Hypochoeris meyeniana</i> (Walp.) Benth & Hook. f. ex. Griseb, <i>H. pimpinellifolia</i> , <i>N. arcuata</i> , unidentified Portulacaceae, unidentified Plantaginaceae
<i>Festuca chrysophylla</i> grassland	Fc	<i>F. chrysophylla</i> , <i>Deyeuxia</i> sp., <i>P. quadrangularis</i> , <i>T. cristatum</i>	<i>Azorella</i> sp., <i>A. antoniana</i> , <i>Distichlis humilis</i> Phil, unidentified Fabaceae, <i>M. fastigiata</i> , <i>H. pimpinellifolia</i> , <i>N. arcuata</i> , <i>N. novari</i> , unidentified Plantaginaceae, <i>Tarasa</i> sp., <i>Trifolium amabile</i> Kunth
Riparian vegetation	Rveg	<i>Cortaderia</i> sp., <i>Colletia spinosissima</i> Gmel., <i>B. boliviensis</i> , <i>Baccharis incarum</i> Wedd., <i>Solanum boliviense</i> (R.E. Fr.) Dunal, <i>T. cristatum</i> With patches of <i>Ocyroe armata</i> (Wedd.) Bonifacio and patches of <i>Cenchrus chilensis</i> (E. Desv.) Morrone	<i>A. antoniana</i> , <i>A. asplundii</i> , <i>B. simplex</i> , <i>C. burkartii</i> , <i>H. meyeniana</i> , <i>H. pimpinellifolia</i> , unidentified Portulacaceae, unidentified Plantaginaceae, <i>Poa</i> sp., <i>Portulaca</i> (R.E. Fr.) <i>rotundifolia</i> , <i>Tarasa</i> sp., <i>Juncus</i> sp.
<i>Parastrephia quadrangularis</i> and <i>Festuca chrysophylla</i> steppe	Pq + Fe	<i>P. quadrangularis</i> , <i>Deyeuxia</i> sp., <i>F. chrysophylla</i> , <i>T. cristatum</i> .	<i>Azorella</i> sp., <i>A. antoniana</i> , <i>A. asplundii</i> , <i>B. simplex</i> , <i>C. burkartii</i> , <i>D. humilis</i> , <i>H. pimpinellifolia</i> , <i>M. fastigiata</i> , <i>N. arcuata</i> , <i>N. novari</i> , unidentified Plantaginaceae, <i>Tarasa</i> sp., <i>T. amabile</i>
<i>P. quadrangularis</i> steppe	Pq	<i>Festuca</i> (R.E. Fr.) <i>orthophylla</i> Philg (= <i>F. chrysophylla</i>), <i>Ospina</i> González et al. 2013), <i>P. quadrangularis</i> , <i>Parastrephia lucida</i> (Meyen) Cabrera, <i>T. cristatum</i> .	<i>A. antoniana</i> , <i>A. asplundii</i> , <i>B. simplex</i> , <i>D. humilis</i> , <i>Eleocharis</i> sp., unidentified Fabaceae, <i>H. meyeniana</i> , <i>H. pimpinellifolia</i> , <i>M. fastigiata</i> , <i>N. arcuata</i> , <i>N. novari</i> , unidentified Plantaginaceae, <i>Tarasa</i> sp., <i>T. amabile</i>
Short grasslands	SG		<i>Azorella</i> sp., <i>A. antoniana</i> , <i>A. asplundii</i> , <i>B. simplex</i> , <i>C. burkartii</i> , <i>D. humilis</i> , <i>Eleocharis</i> sp., unidentified Fabaceae, <i>H. meyeniana</i> , <i>H. pimpinellifolia</i> , <i>M. fastigiata</i> , <i>N. arcuata</i> , <i>N. novari</i> , unidentified Portulacaceae, <i>Portulaca</i> (R.E. Fr.) <i>rotundifolia</i> , <i>T. amabile</i>
Vega	Vega	<i>P. quadrangularis</i> , <i>Festuca chrysophylla</i> Phil., <i>Deyeuxia</i> sp.	<i>A. antoniana</i> , <i>A. asplundii</i> , <i>B. simplex</i> , <i>D. humilis</i> , <i>Eleocharis</i> sp, unidentified Fabaceae, <i>H. meyeniana</i> , <i>H. pimpinellifolia</i> , <i>Lachemilla pinnata</i> (Ruiz y Pav.) Rothm. <i>M. fastigiata</i> , Unidentified Plantaginaceae, <i>T. amabile</i>

Table 2 Soil physical and chemical properties (mean ± SD) of vegetation units (by acronym): pH, electrical conductivity (EC), total organic matter (TOM, in %), and texture, n/d: no data

Vegetation unit	pH	EC (μS/cm)	TOM	Coarse fragments (%)	Sand %	Silt %	Clay %	Textural class
Bb + Ji	6.05 ± 0.18	525.52 ± 604.2	3.06	14.47	57.90	30.10	12.00	Gravelly sandy loam
Bb + Fd	6.22 ± 0.02	86.42						n/d
Bbfh	6.02 ± 0.54	187.4						n/d
Tc	5.71 ± 0.09	467.05 ± 591.6	3.83		52.90	37.20	9.90	Sandy loam/ Loam
Fc	5.37 ± 0.44	1040.75 ± 414.25	4.02		21.80	39.20	39.00	Clay loam/ Clay
Rveg	6.33 ± 0.24	572.65 ± 207.18	1.06 ± 0.13	86.42	n/d		6.90	Sandy loam
Pq + Fc	5.65 ± 0.11	1113.47 ± 630.1	4.69 ± 0.67	467.05	3.83	5.69	45.10	Clay
Pq	5.68 ± 0.41	551.60 ± 428.2	n/d	1040.75	4.02	–	38.70	Silty clay/ Silty clay loam
SG	6.26 ± 0.64	860.68 ± 607.91	1.75 ± 0.26	377.53	0.96		9.10	Sandy loam
Vega	5.70 ± 0.33	908.80 ± 806.2	2.87	5.27	74.00	14.70	11.30	Sandy loam

indices and field data to demonstrate the utility of these vegetation indices as one of the primary information sources to monitor vegetation communities. We found that cover was well reflected by the indices and that they can be used to map a scarcely studied area.

Our results showed that our study site is primarily composed of native species and are further evidence of the hypothesis that highlands are less susceptible to non-native species invasions (Sakai et al. 2001; Pauchard and Alaback 2004; Muñoz and Bonacic 2006). We also

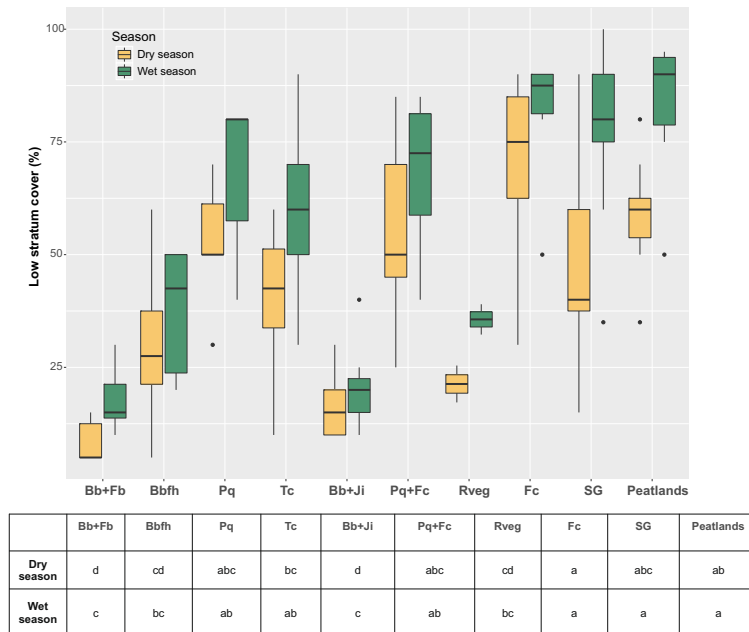
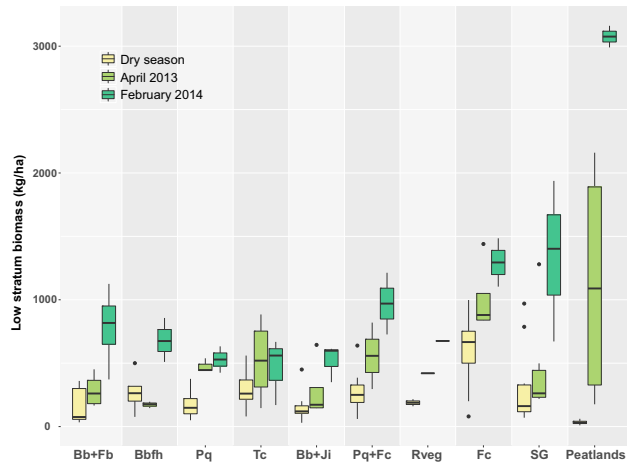


Fig. 3 Low-stratum cover (%) of vegetation units in the dry and wet seasons. The horizontal thick lines show the median values, whereas the bottom and top lines of the boxes represent the 25th and 75th percentiles, respectively. In the bottom table, the different letters indicate significant differences among vegetation units for each season. Bb + Ji: *Baccharis boliviensis* and *Jarava ichu* steppe. Bb + Fd: *B. boliviensis* and *Fabiana densa* steppe. Bbfh:

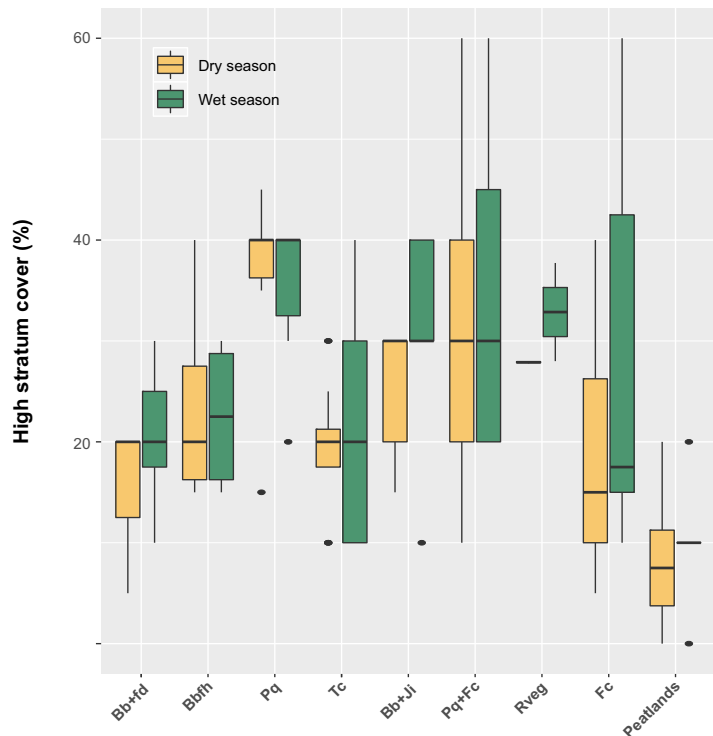
B. boliviensis steppe in foothills. Tc: *Tetraglochin cristatum* steppe. Fc: *Festuca chrysophylla* grassland. Rveg: Riparian vegetation. SG: short grassland. Pq + Fc: *Parastrephia quadrangularis* and *F. chrysophylla* steppe. Pq: *P. quadrangularis* steppe. Vega: peatlands. Different letters indicate significant differences ($p < 0.05$) among vegetation units (one-way ANOVA, factor: season)

Fig. 4 Low-stratum biomass for vegetation units during the dry and wet seasons, respectively. Bb + Ji: *Baccharis boliviensis* and *Jarava ichu* steppe. Bb + Fd: *B. boliviensis* and *Fabiana densa* steppe. Bbfb: *B. boliviensis* steppe in foothills. Tc: *Tetraglochin cristatum* steppe. Fc: *Festuca chrysophylla* grassland. Rveg: Riparian vegetation. SG: short grassland. Pq + Fc: *Parastrephia quadrangularis* and *F. chrysophylla* steppe. Pq: *P. quadrangularis* steppe. Vega: peatlands



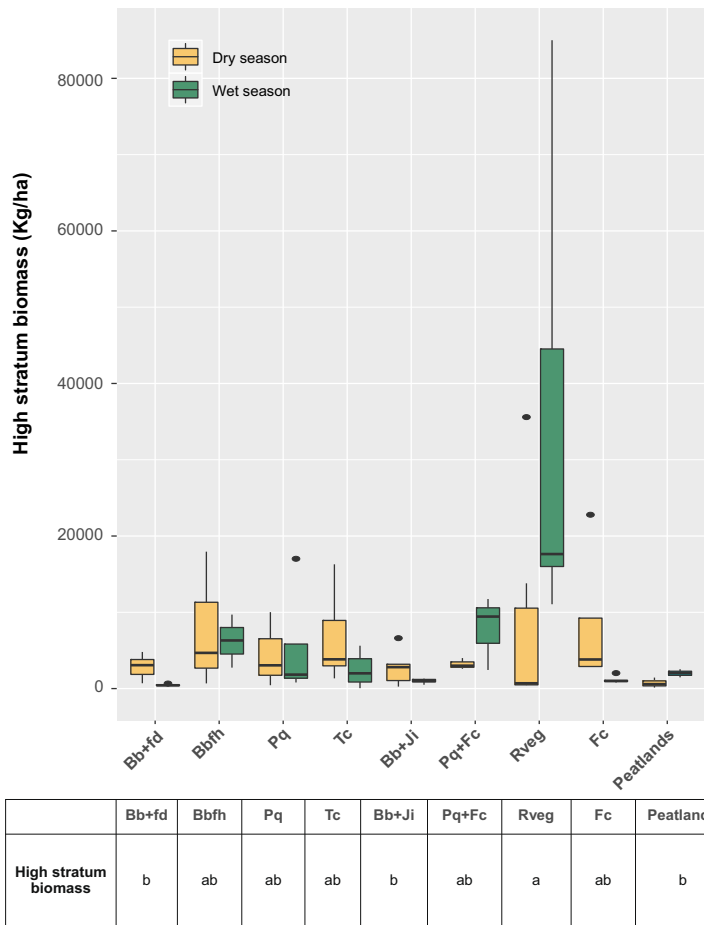
	Bb+Fb	Bbfb	Pq	Tc	Bb+Ji	Pq+Fc	Rveg	Fc	SG	Peatlands
Dry season	b	ab	ab	ab	ab	ab	ab	a	ab	c
Wet season 2013	ab	b	ab	ab	ab	ab	ab	a	ab	ab
Wet season 2014	b	b	b	b	b	ab	b	ab	ab	a

Fig. 5 High-stratum cover of vegetation units. The horizontal thick lines show the median values, whereas the bottom and top lines of the boxes represent the 25th and 75th percentiles, respectively. In the bottom table, the different letters indicate significant differences among vegetation units by season. Bb + Ji: *Baccharis boliviensis* and *Jarava ichu* steppe. Bb + Fd: *B. boliviensis* and *Fabiana densa* steppe. Bbfb: *B. boliviensis* steppe in foothills. Tc: *Tetraglochin cristatum* steppe. Fc: *Festuca chrysophylla* grassland. Rveg: Riparian vegetation. SG: short grassland. Pq + Fc: *Parastrephia quadrangularis* and *F. chrysophylla* steppe. Pq: *P. quadrangularis* steppe. Vega: peatlands



	Bb+fd	Bbfb	Pq	Tc	Bb+Ji	Pq+Fc	Rveg	Fc	Peatlands
High stratum cover	c	abc	a	bc	abc	ab	abc	bcd	d

Fig. 6 High-stratum biomass of vegetation units. The horizontal thick lines show the median values, whereas the bottom and top lines of the boxes represent the 25th and 75th percentiles, respectively. In the bottom table, the different letters indicate significant differences among vegetation units by season. Bb + Ji: *Baccharis boliviensis* and *Jarava ichu* steppe. Bb + Fd: *B. boliviensis* and *Fabiana densa* steppe. Bbfb: *B. boliviensis* steppe in foothills. Tc: *Tetraglochin cristatum* steppe. Fc: *Festuca chrysophylla* grassland. Rveg: Riparian vegetation. SG: short grassland. Pq + Fc: *Parastrephia quadrangularis* and *F. chrysophylla* steppe. Pq: *P. quadrangularis* steppe. Vega: peatlands



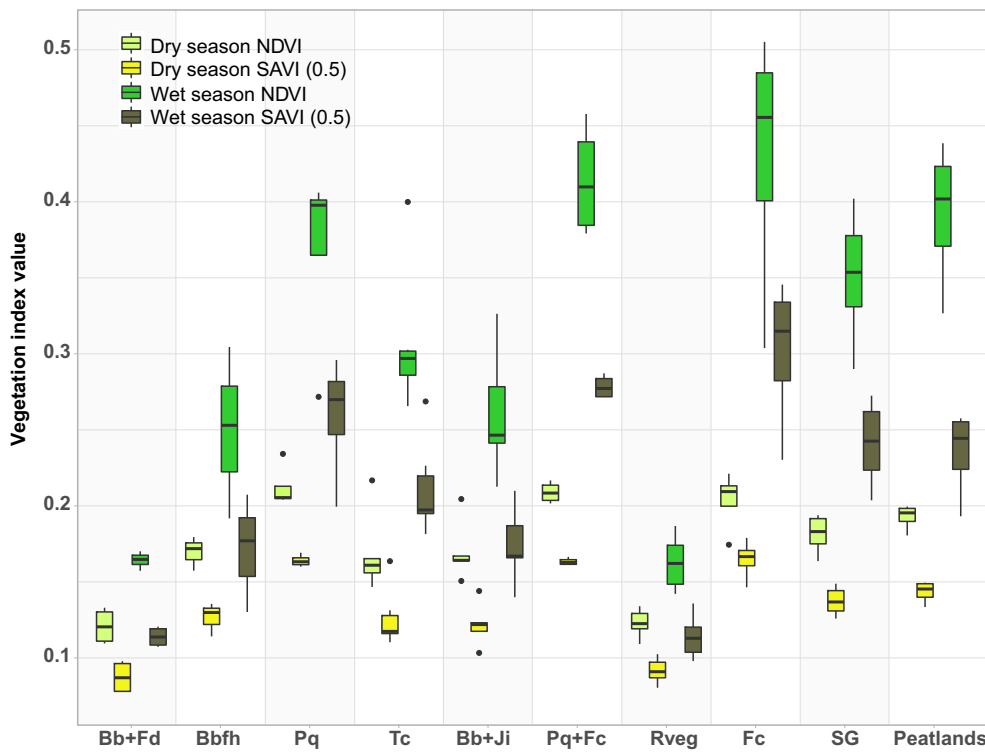
found a lower number of species than that described by Cabrera (1957), which could indicate a decrease in biodiversity, but with no evidence of soil chemical degradation considering pH and EC, a fact that agrees with previous studies (Bonaventura et al. 1995).

In agreement with previous publications (Ruthsatz and Movia 1975, Bonaventura et al. 1995), the spatial pattern of the vegetation showed assemblages related to the topography, soil, and water availability in a gradient from the sierras to the paleo-lake, which are components of the morphodynamic environments (Cendrero et al. 1993).

In the piedmont and western sierras, the typical steppes were dominated by *Baccharis boliviensis*, *Fabiana densa*, *Parastrephia lepidophylla*, and *Tetraglochin cristatum* (as described by Cabrera 1957, Ruthsatz and Movia 1975, and Bonaventura et al. 1995), covering large areas of the study area. In the paleo-lake and piedmont, the vegetation communities were formed by perennial shrubs and grasses localized in the plains

and gentle slopes and were composed of *B. boliviensis* and *Jarava ichu* mix steppe, *F. chrysophylla* grasslands, *P. quadrangularis*, and *F. chrysophylla* shrub-grass steppe and short grasslands. In the semiarid Argentine Puna, these grassland communities are less studied (Bonaventura et al. 1995) and have been cited as edaphic communities (Cabrera 1957).

Our biomass results are in agreement with the ranges published in a regional assessment of primary productivity of the northern Puna of Argentina (Baldassini et al. 2012), in which the most productive vegetation was the dense grass steppe. Our aboveground biomass records are also consistent with those published for the southern Bolivian Puna (Genin and Alzérrecá 2006), but we found narrower ranges of variation within the same vegetation units. The values of vegetation cover also agree with those obtained in a southern site of the Pozuelos Basin (Bonaventura et al. 1995; Arzamendia et al. 2006; Arzamendia and Vilá 2015). Data of the



Vegetation index	Season	Bb+Fd	Bbfb	Pq	Tc	Bb+Ji	Pq+Fc	Rveg	Fc	SG	Peatlands
NDVI	Wet season	c	b	a	ab	b	a	c	a	ab	a
	Dry season	d	c	a	abc	bc	a	d	ab	abc	abc
SAVI 0.5	Wet season	d	c	ab	bc	c	ab	d	a	ab	abc
	Dry season	c	b	a	b	b	a	c	a	ab	ab

Fig. 7 Vegetation indices (NDVI and SAVI ($L = 0.5$)) by vegetation unit and season in 2014. The horizontal thick lines show the median values, whereas the bottom and top lines of the boxes represent the 25th and 75th percentiles, respectively. Bb + Fd: *Baccharis boliviensis* and *Fabiana densa* steppe. Bbfb: *Baccharis boliviensis* steppe in foothills. Pq: *Parastrephia quadrangularis* steppe. Tc: *Tetraglochin cristatum* steppe. Bb + Ji: *Baccharis boliviensis* and *Jarava ichu* steppe. Pq + Fc: *Parastrephia*

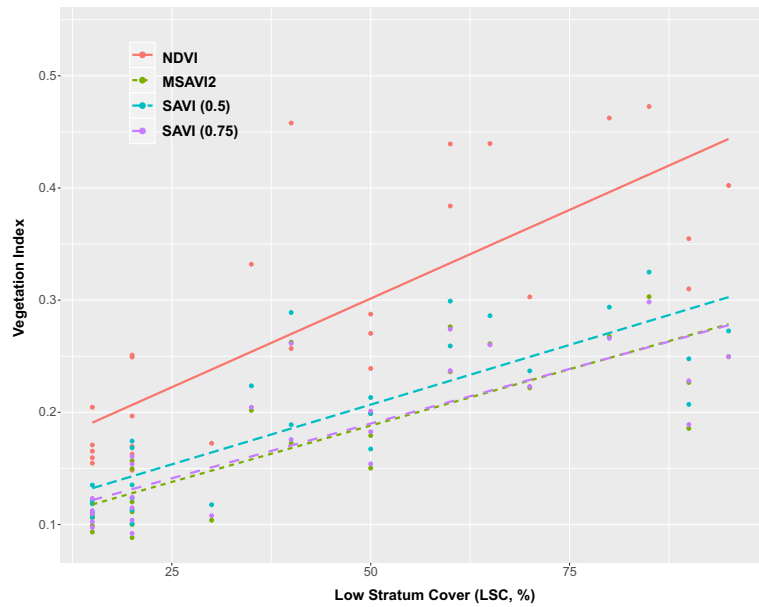
quadrangularis and *Festuca chrysophylla* steppe. Rveg: Riparian vegetation. Fc: *Festuca chrysophylla* grassland. SG: short grassland. Vega: peatlands. In the bottom table: different letters indicate significant differences ($p < 0.05$) among vegetation units (one-way ANOVA for each season and vegetation index). Satellite image information: Landsat OLI 8, acquisition date: Jan-02-2014 and Sept-15-2014, Path: 232, Row: 75

biomass of most of the vegetation units described in our study are here reported for the first time.

The peatlands (or “vegas”) found on sandy soils showed higher values of cover and biomass in the wet season and notable differences with the surrounding vegetation units. They really work as an “oasis” in the semi-desert. Studies on Andean wetlands have pointed out that the groundwater dynamic is the main driver of peatlands (Squeo et al. 2006; Ruthsatz 2012; Cooper et al. 2019). The widest difference in biomass between the wet and dry season was probably caused by a high grazing pressure by sheep, especially during

the dry season. This vegetation unit is considered a key resource within Andean grazing systems (Squeo et al. 2006; Buttolph and Coppock 2013). Symptoms of peatlands degradation have been mentioned in various sites of the Puna region, and overgrazing has been pointed out as one of the causes (Navone et al. 2006; Squeo et al. 2006). However, the cause-effect of this degradation is difficult to assess because the groundwater trends play a major contribution to the dynamics and imply a larger spatial and temporal scale of the functioning of this vegetation unit. Since natural and anthropic causes can be interplaying, further research

Fig. 8 Linear regression results between vegetation indices and low-stratum cover (LSC) for the wet season of 2014



is needed to understand the processes occurring in the vegas (Squeo et al. 2006; Tchilinguirian and Olivera 2012; Cooper et al. 2019).

The *F. chrysophylla* grasslands, locally known as “chillaguales”, had high vegetation cover and low stratum biomass across both seasons. This vegetation unit is preferred by herders to lead livestock (especially sheep) to graze in the dry season. The shrub *T. cristatum*, locally known as “cangia”, has been recorded as a dominating species in one vegetation unit, and was present in most of the piedmont vegetation units, where grazing pressure was high as has been indicated as an indicator of overgrazing. These results are consistent with those of other studies in Peru (Catorci et al. 2013) as well as in other areas of the reserve (Arzamendia et al. 2006).

As the high stratum showed no differences between the dry and wet season and the low stratum was heavily influenced by the rains, they are both important as environmental indicators for the management of the area

and must thus be analyzed separately but in an integrated way. The low stratum is probably an accurate proxy to detect seasonal variation and forage availability and is threatened by overgrazing, which also increases soil erosion. Our methodology is thus useful to identify areas that can be vulnerable and areas that allow moderate and intensive pastoral use, which may help to achieve a better distribution of livestock, according to the land carrying capacity. High-stratum species (tussock grasses and shrubs) showed no significant time variation between years and seasons and played a major role in providing permanent soil cover when the low-stratum cover was low or absent. In addition, high-stratum species can be foraged by livestock and wild vicuñas during dry periods, although they are not the species preferred by these herbivores (Borgnia et al. 2006, Arzamendia et al. 2006; Arzamendia and Vilá 2015). The harvest of shrubs and tussock grasses by herders as firewood and rural constructions can have high impact in some areas, triggering land degradation processes caused by low

Table 3 Summary information of linear regressions between vegetation indices and low-stratum cover (LSC) for the wet season of 2014

Equation	<i>F</i> value	<i>p</i> value	Adj. <i>R</i> squared
NDVI = 0.143 + 0.003 LSC	$F_{(1,25)} = 40.64$	< 0.0001	0.604
MSAVI2 = 0.088 + 0.002 LSC	$F_{(1,25)} = 50.90$	< 0.0001	0.657
SAVI(0.5) = 0.100 + 0.002 LSC	$F_{(1,25)} = 50.23$	< 0.0001	0.654
SAVI (0.75) = 0.092 + 0.002 LSC	$F_{(1,25)} = 51.61$	< 0.0001	0.661

vegetation cover and the effect of wind and water erosion (Navone et al. 2006). This effect was also observed by Cendrero et al. (1993), who pointed out that the acquisition of firewood from “tolares” (*P. quadrangularis*), which provide biomass for the small cities of the Puna, is deteriorating the system.

The vegetation indices analyzed were able to detect seasonal and spatial variation in the vegetation. The sensitivity of the method with the indices as proxies was lower than that detected in the field. In the field, we determined ten units, whereas the indices (NDVI in the dry season and SAVI in the wet season), in their best detections, determined six units. However, the ones grouped together have common features related to structural attributes and are differentiated from the others, so they are very useful indicators.

The lowest values of vegetation indices grouped the shrubland communities, whereas the highest values grouped the grasslands. The mean values of all the indices used were higher than those reported in other drylands of Argentina (Verón and Paruelo 2010; Goirán et al. 2012; Buzzi et al. 2017), as well as higher than those obtained in the Bolivian Puna (Genin et al. 1995). Our study site is one of the richest areas for pastures in the Puna (Cabrera 1957; Bonaventura et al. 1995; Paz et al. 2011). Therefore, it is not surprising to find vegetation cover higher than 50% in the wet season, especially in the piedmont and paleo-lake areas. The NDVI showed higher values than the other indices, probably associated with the soil brightness, and, in accordance with that reported by Qi et al. (1994a), these differences were greater in the most productive vegetation units. All the vegetation indices showed a good fit to low stratum cover, which means that they were able to detect the spatial and temporal differences in forage availability. These results show a higher fit to cover than those obtained in a different basin of the Puna from Jujuy province (Maggi and Ponienman 2018) and in Patagonian drylands (Gaitán et al. 2013).

Our results suggest that the development of an adequate environmental monitoring in northern Argentine Puna has to consider geomorphological features, climate conditions, and herbivory as key elements that influence vegetation dynamics. Also, even if vegetation is scarce, the knowledge of vegetation dynamics can be relevant to understand arid land processes (Thomas 2011), particularly those associated with land degradation (Tchilinguirian and Olivera 2012). Field assessment of vegetation

strata, biomass, and cover are important to evaluate forage availability and changes in composition. Vegetation indices can also be appropriate to identify ranges of cover and temporal variability in wider areas. In this work, we propose a combined assessment at local scale, based on geomorphology, remote sensing, and field data of structural variables of vegetation. For instance, vegetation units with similar cover, biomass, and vegetation indices values can be differentiated by geomorphology, such as the case of *B. boliviensis* and *F. densa* steppes (low biomass and cover, mountain hills), which can be differentiated from riparian vegetation (low biomass and cover, paleo-lake), or the case of the units in the piedmont and paleo-lake areas, which are located in different classes of soils and have different vegetation indices values.

The combined sources of information used in the present study showed that the use of indices can be reliable. This information, which had not yet been published, is important to develop proper management strategies of wide areas of the Puna rangelands in northern Argentina.

Conclusions

In the study area, ten different units of plant communities with differential attributes were identified. Vegetation units that occupy small areas in relation to others can be much more productive in terms of cover and biomass and can be effectively detected by satellite indices. The low stratum is much more reactive to environmental water conditions and is a determining source of grazing. The high stratum does not show such variations and is the rescue forage for herbivores in dry seasons. Grasslands (dominated by tall and short grasses) should also be considered essential to rangelands in the region, as they provide a significant amount of forage and protection against land degradation. Considering the high heterogeneity of the region, deeper studies on grazing with enclosures and deferred grazing would be needed to improve our understanding of the system.

To establish robust conservation and management measures, our data must be shared with the peasant communities living in the area to combine these findings with traditional local practices to obtain management

decisions based both on good science and on traditional knowledge.

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