Sheep grazing differentially affects the canopy attributes and functional diversity of shrubs and perennial grasses in arid rangelands

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Abstract We analysed how changes in community attributes promoted by domestic grazing are reflected on functional traits in canopies of shrubs and perennial grasses in rangelands of the Patagonian Monte. We selected four sites across a gradient of grazing pressure and assessed (i) changes in plant cover, and species richness and diversity and (ii) changes in functional traits (community weighted mean: CWM, functional diversity and redundancy) related to plant growth (leaf N concentration, height of the plant, and specific leaf area-SLA) in shrub and perennial grass canopies. Shrub cover decreased and species and functional diversity increased with increasing grazing pressure. Nonsignificant changes were found in shrub species richness and functional redundancy across the grazing gradient. Positive relationships were found between shrub species diversity and CWM of SLA, and leaf N, while CWM-height was not related to grazing pressure. Perennial grass cover decreased steadily with grazing pressure, while species richness decreased significantly at high grazing pressure. Perennial grass diversity, functional diversity and redundancy of functional plant traits, and CWM-height increased at intermediate grazing pressure, while the inverse pattern was observed for CWM of SLA and leaf N. These results highlighted that species diversity was the community attribute that best reflected functional changes induced by grazing pressure in shrub and perennial grass canopies in these rangelands. We concluded that shrubs persist under high grazing pressure increasing species and functional diversity of relevant plant traits, while perennial grass canopies were only able to persist under intermediate grazing pressure.

Keywords Community weighted mean · Functional redundancy · Patagonian Monte · Species diversity · Species richness

Introduction

Plant diversity conservation is crucial for the maintenance of ecosystem processes such as primary productivity and nutrient cycling (Naeem et al. 1999; Díaz and Cabido 2001). The contribution of individual
plant species to ecosystem processes may vary considerably among and within ecosystems (Grime 1998; Naeem et al. 1999) and depends mainly on plant attributes related to growth rates, biomass production, and organic matter inputs to the soil (Naeem et al. 1999). These processes are modulated by the combination of the environment and the type and intensity of disturbances (Lambers et al. 2006).

Arid and semiarid ecosystems cover more than 37% of the land surface of the earth and are considered vulnerable to desertification (Maestre et al. 2012). Shrubs and grasses are the most conspicuous growth forms in these ecosystems (Noy Meir 1973; Aguiar and Sala 1999). Canopy and chemical traits in shrubs allow them to avoid or tolerate desiccation, while perennial grasses are mainly represented by species avoiding drought (Aerts and Chapin 2000; Bertiller et al. 2004; Díaz and Cabido 2001). The most common land use in arid ecosystems is domestic grazing (Defossé et al. 1990; Laity 2008). Domestic grazers direct and/or indirect affect plant relative abundance with important impacts on community structure and functioning (Milchunas and Lauenroth 1993; Bisigato et al. 2009). A central topic that has been addressed in several studies is the relationship between diversity and ecosystem functioning. A common pattern emerging from some of these studies is that species diversity varies with disturbance intensity following a hump-shaped or unimodal distribution (Rosenzweig and Abramsky 1993; Willig and Presley 2018). Accordingly, a moderate grazing pressure may improve plant diversity through the consumption of dominant species affecting indirectly plant competitive relationships and thus enhancing plant species complementary in the community (Connell 1978; Tilman 1982). However, in arid environments, increased domestic grazing could increase plant mortality and eventually cause a steadily decrease in species richness (Huston and Huston 1994; Proulx and Mazumder 1998) indicating that the humped-shape pattern is not common in most of these ecosystems (Willig and Presley 2018).

In the Patagonian Monte, domestic sheep grazing was introduced at the end of the nineteenth century triggering changes in plant communities (Defosse and Robberecht 1987). The most conspicuous changes induced by grazing are related to the decrease of preferred plant species cover such as perennial grasses and some tall shrubs with high N concentration and scarce structural and chemical defences, and their replacement by others with morpho-physiological defences against herbivory (Reynolds et al. 1997; Bisigato et al. 2009). Thus, the effect of selective grazing on plant species richness and diversity depends on the balance between local species extinction and colonization rates (Glenn and Collins 1992; Olff and Ritchie 1998). Beyond species changes, the loss of particular functions is the main threat to ecosystem processes and services. Several studies recognized that plant diversity effects on community processes would depend on functional traits of individual species and their interactions, instead of the effects induced by the amount of species in the community (Díaz and Cabido 2001). Functional traits are plant morpho-physio-phenological attributes impacting on species fitness and ecosystem functioning (Grime 1998; Violle et al. 2007).

Effects of changes in plant species traits on ecosystem processes may be explained by the mass-ratio (Grime 1998; Violle et al. 2007; de Bello et al. 2010), the niche differentiation hypotheses (Loreau et al. 2001) and the redundancy hypothesis (Ehrlich and Walker 1998), among others. The mass-ratio hypothesis states that environmental conditions select viable species traits favourable to plant establishment and persistence in a particular ecosystem (sensu habitat filtering, Díaz et al. 1998). Also, traits of dominant species may be used to predict changes in ecosystem properties such as biomass production or nutrient cycling (Garnier et al. 2004; Vile et al. 2006) directly related to ecosystem services like fodder production or soil fertility (Díaz et al. 2007). In this context, the community weighted mean index quantifies the mean values of selected functional traits at community level (Garnier et al. 2004; Violle et al. 2007). The niche differentiation hypothesis states that species with contrasted functional traits can optimize the use of ecosystem resources by complementarity in their use (i.e. resource use differs across scales of space and time) (Hooper et al. 2005; Gross et al. 2007; Kang et al. 2015). Several indices using species trait distribution in canopies were proposed to capture functional diversity and consequently the effect of resource complementarity on ecosystem processes (Lepš et al. 2006; Díaz et al. 2007; Valencia et al. 2015). The redundancy hypothesis proposes the existence of functional compensation through different species performing similar functions within the
community (Walker 1992). Accordingly, some species may improve the ecosystem stability, enhancing ecosystem “resilience”. In this sense, the loss of a few ecologically unique species is expected to have a larger ecological impact than the loss of species sharing very similar functional traits (Barbet-Massin and Jetz 2015). A priori, these hypotheses may appear to be opposite, but they may simultaneously act determining changes in the structure and function of plant communities. Accordingly, these issues are relevant in relation to land management generally seeking to maintain systems within stable states providing desirable and predictable ecosystem services (Chillo et al. 2011).

Plant traits related to seed dispersal, seedling establishment, light capture, and chemical and/or structural defences against biotic and abiotic factors (such as seed mass, plant height, specific leaf area: SLA, N concentration in leaves) are usually used to summarize the main trade-offs defining plant life histories and plant effects on ecosystems processes (e.g. primary production and nutrient cycling) across worldwide environmental gradients (Westoby 1998; Bertiller et al. 2006; Jardim and Batalha 2008). However, there are few studies linking changes in canopy and functional diversity of plant communities induced by disturbances in arid and semiarid ecosystems (e.g. de Bello et al. 2006; Gross et al. 2013). There is an overriding need to perform studies on this issue in order to have a more integrative view of the complexity of disturbance effects on arid ecosystems (Lavorel et al. 2013). Understanding this complexity is necessary for responsible management of Earth’s ecosystems and the diverse biota they contain under changing climatic conditions. Our aim was to analyse changes in community attributes (plant cover, species richness and species diversity) and functional traits (assessed by the community weighted mean, functional diversity and redundancy) induced by grazing pressure in canopies of the two main growth forms (shrubs and perennial grasses) in arid rangelands of the Patagonian Monte. We asked (i) how changes in community attributes promoted by domestic grazing reflect on shrub and perennial grass canopies functional traits, and (ii) whether the cover, species richness and species diversity of these growth forms are intrinsic community attributes synthesizing functional properties of plant canopies in arid rangelands.

Methods

Study area and sites

We selected a study area in the austral Monte Phytogeographic Province of Argentina (Patagonian Monte) dominated by the typical open shrubland of Larrea divaricata, and perennial grasses of Nassella and Pappostipa genus (León et al. 1998). Mean annual temperature is 13 °C and mean annual precipitation is 188 mm with high interannual variation (Barros and Rivero 1982). Plant canopy covers less than 40% of the soil and presents a random patchy structure consisting of patches formed by shrub clumps encircled by perennial grasses and isolated individuals of grasses or shrubs colonizing bare soil areas (Bisigato and Bertiller 1997; Mazzarino et al. 1998). Continuous grazing with Merino sheep, for producing fine wool, was introduced at the beginning of the twentieth century with mean stocking rate ranging from 0.11 to 0.14 sheep ha\(^{-1}\) (including juveniles and adults) up to nowadays. Sheep management has been conducted in ranches of about 10,000 ha typically organized in 4 equal paddocks sharing a unique permanent watering point keeping sheep in the same paddock throughout the year. This management led to the formation of extended piospheres (1500–4000 m) surrounding watering points (Lange 1969) since these points may temporally hold high stocking densities impacting on plant community structure and soil properties (Bisigato and Bertiller 1997; Bertiller et al. 2002; Ares et al. 2003; Bisigato et al. 2005, 2009; Pazos et al. 2007; Larreguy et al. 2017; Bär Lamas et al. 2013). Our study was conducted at four sites, two located at La Esperanza research area and the other two at La Elvira research area (both ca. 10,000 ha) distant 118 km from each other. Sites within each research area were separated between 1800 and 3800 m from each other, located far and near from the watering point. Both research areas are submitted to different managements. La Elvira is actually under grazing management with a stocking rate of ca. 0.11 sheep ha\(^{-1}\) and La Esperanza has been grazed with the same stocking rate up to 2008, when all domestic herbivores were removed. After the removal of sheep, the population of the wild herbivore Lama guanicoe (guanaco) increased, reaching ca. 0.1 animal ha\(^{-1}\) (Escobar et al. 2004; FNP 2013). These sites had a similar vegetation type (shrubland of Larrea divaricata and...
grass species of *Poa*, *Nassella* and *Pappostipa* genus), soil condition (sandy to loamy sandy soil texture), and topography (flat landscape) but different signs of grazing disturbance (Fig. 1, Table 1). These sites represent a typical gradient of grazing disturbance in the Patagonian Monte characterized by decreasing total, perennial grass and in some cases shrub cover, reduction of shrub patch size (Instituto Nacional de Tecnología Agropecuaria 1990; Bisigato and Bertiller 1997; León et al. 1998; Bertiller et al. 2002; Pazos et al. 2007, 2010; Bisigato et al. 2008; Rossi and Ares 2012; Larreguy et al. 2017) and increased faeces density (Bár Lamas et al. 2013; Larreguy et al. 2017) with increasing grazing disturbance (Fig. 1). Faeces counting’s are usually used as an index of grazing pressure (Lange and Willcocks 1978) directly related to grazing disturbance (van der Graaf et al. 2006; Pazos et al. 2007; Bertiller and Ares 2008).

Community attributes (cover, species richness and diversity of shrubs and perennial grasses)

Within each site, we delimited a representative area of 3 ha (150 m × 200 m) and assessed species composition and cover of shrubs and perennial grasses in four randomly 25 m long transects (separated at least 15 m

![Image of geographical location and grazing pressure](image_url)
from each other) in autumn 2010. Using the intercept line method (Muller-Dombois and Ellenberg 1974), we estimated the percentage of soil covered by growth form (shrubs and perennial grasses) intercepted in each transect according to Bisigato and Bertiller (1997), affecting the length of the segment intercepted by each plant by your percentage of internal coverage:  

\[
\text{Growth form cover(\%)}_j = \left( \frac{\sum_{i=1}^{S_j} l_{ij} * C_{ij}}{l_t} \right) * 100
\]

where \( l = \) length in metres intercepted by each plant of each species \( i \) in community \( j \), \( S_j \) is the number of intercepted plant of each species in the community \( j \), \( C_{ij} = \) percentage of internal coverage of each plant of each species, \( l_t = \) total length of the transect in metres.

We used the number of species and cover at each transect as a surrogate for species richness and species abundance of perennial grasses and shrubs. Also, we calculated the Simpson’s index of diversity (SD\( j \); Botta-Dukát 2005) by growth form as:

\[
\text{SD}_j = 1 - \sum_{i=1}^{S_j} P_{ij}^2
\]

where \( P_{ij} \) is the abundance (expressed as cover proportion) of the species \( i \) in the community \( j \) (i.e. cover of species \( i/ \) total of covers of all the species for each growth form), and \( S_j \) is the number of species in the community \( j \). Simpson’s index of diversity varies between zero and one, indicating the highest value greater diversity of species within the growth form.

Plant traits

We selected three modal size individuals (most frequent canopy diameter and height) of each shrub and perennial grass species per site and we registered the plant height excluding reproductive structures in case of being present (Laughlin et al. 2010) in summer 2010–2011. We collected fully expanded green leaves of three branches of the external plant crown (sun and partially shaded leaves) of each shrub individual and three tillers of each perennial grass plant. We followed standardized protocols to assess N concentration and specific leaf area (SLA) in green leaves (Coombs et al. 1985; Cornelissen et al. 2003).

Functional indices

We calculated three complementary functional indices for each plant trait (plant height, N concentration and SLA in green leaves) in shrubs and perennial grasses and site: the community weighted mean (CWM\( j \)), the functional diversity (FD\( j \)) and the functional redundancy (FR\( j \)) index. CWM\( j \) assesses the mean trait value weighted by the abundance of each species at the plant community representing the selected site (Violle et al. 2007; Valencia et al. 2015):

| Table 1 | Grazing disturbance levels based on the comparison between the perennial grass cover at each site and those reported in other areas of the Patagonian Monte |
|---------------------------------|---------------------------------|---------------------------------|
| **Perennial grass cover (%)**   | **References**                  | **Sites of this study**         |
| Site excluded from domestic herbivores for 12 years | 5.8–7.2 | Pazos et al. (2007) |
|                                 |                                 | Carrera and Bertiller (2013)    |
|                                 |                                 | Larreguy et al. (2012)          | – |
| Sites with low grazing disturbance (> 3000 m far from the watering point) | 4.8–5.4 | Bisigato and Bertiller (1997) |
|                                 |                                 | Prieto et al. (2011)            | Site 1 |
| Sites with moderate grazing disturbance (c.a. 1000 m far from the watering point) | 1–2.5 | Bisigato and Bertiller (1997) |
|                                 |                                 | Bisigato et al. (2008)          | Site 2 |
| Sites with high grazing disturbance (< 300 m from the watering point) | < 0.9 | Bisigato and Bertiller (1997) |
|                                 |                                 | Prieto et al. (2011)            | Sites 3 and 4 |
|                                 |                                 | Larreguy et al. (2012)          |
|                                 |                                 | Carrera and Bertiller (2013)    |
CWM_j = \sum_{i} p_{ij} T_{ij}

where in the community j, the proportional abundance of species i is represented as \( p_{ij} \), and the mean trait value of species i in community j is \( T_{ij} \), and \( S_j \) is the number of species in the community j.

FD quantifies the trait dispersion degree within the plant community, and it is comparable to the trait variance distribution weighted by the relative abundance of each species. \( F D_j \) was estimated by the Rao’s quadratic entropy, commonly used in trait-based ecological studies using the Macro excel file (“Funct-Div.xls”) (Lepš et al. 2006):

\[
FD_j = \sum_{i=1}^{S_j} \sum_{x=1}^{S_j} d_{ij} p_{ij} p_{xj}
\]

where \( S_j \) is the number of species in the community j, \( p_i \) and \( p_x \) are the proportions of species i, and x in the community j, and \( d_{ij} \) is the dissimilarity of species in the community j. Dissimilarity is expressed as 1 minus the overlapping in the trait among pairs of species scaled between zero (no dissimilarity, e.g. dissimilarity of each species to itself) and one (maximum dissimilarity) (for more details see Lepš et al. 2006).

FR quantifies the overrepresentation of species with similar functional traits within the community (Mouillot et al. 2014). In accordance with de Bello et al. (2007), \( F R_j \) is the part of the species diversity in the community that is not explained by \( F D_j \). Therefore, \( F R \) was calculated as

\[
FR_j = SD_j \ - \ FD_j
\]

We also calculated the mean \( F D_j \) and \( F R_j \) values of all traits per growth form (shrubs and perennial grasses) at each site (community j).

Statistical analyses

Linear and nonlinear regression analyses were used to quantify the relationship between community traits (plant cover, species richness and diversity), functional indices (CWM, FD, FR) of shrub and perennial grass traits and grazing pressure. For practical reasons and based on previous studies in the area (e.g. Bár Lamas et al. 2013), we used the variable values of each transect as independent observational units but it should be noted that the four transects of each site have the same explanatory variable (i.e. number of faeces). We selected the best least squares fit (lowest \( p \) value and highest \( r^2 \) value) between a linear and a nonlinear saturation function depending on the shape of the variable response. Pearson correlation analyses (normal distribution of data) were used to assess the relationship between community traits (species richness, cover and diversity) and functional indices. Note that some variables, such as species diversity and functional diversity may be for mathematical reasons correlated. SPSS software was used to perform statistical analyses (Norusis 1997). The significance level used throughout this study was \( p \leq 0.05 \).

Results

Shrub canopy

Shrub cover was reduced with increasing grazing pressure, while species richness was not significantly related to grazing pressure. Species diversity of shrubs increased steadily with increasing grazing pressure (Fig. 2).

The community weighted mean of plant height (CWM-height) of shrubs did not significantly vary across the grazing pressure gradient, while the CWM of N (CWM-N) and specific leaf area (CWM-SLA) of this growth form increased with increasing grazing pressure (Fig. 3a). Functional diversity of plant height (FD-height), SLA (FD-SLA), leaf N (FD-leaf N) and mean value of FD traits in shrub canopy significantly increased with increasing grazing pressure, while functional redundancy (FR) of these traits was not significantly related to grazing pressure (Fig. 3b).

Shrub species richness was positively associated with FR-height, FR-leaf N and mean-FR. Shrub cover was only negatively associated with CWM-leaf N, and the Simpson diversity index of shrubs was positively related to all indexes except for CWM-height and FR-height (Table 2a).

Perennial grass canopy

The cover of perennial grasses decreased steadily (from 4.2 to 0.1%) with grazing pressure, while the perennial grass species richness only decreased under high grazing pressure. Species diversity of perennial grasses peaked at intermediate grazing pressure and then decreased with higher grazing pressure (Fig. 4).
CWM-height peaked at intermediate grazing pressure, while CWM-N and CWM-SLA showed the inverse pattern (Fig. 5a). FD-height and mean value of FD traits of perennial grasses increased with increased grazing pressure, while FD-leaf N peaked at intermediate grazing pressure and then decreased with higher grazing pressure. FD-SLA did not vary across grazing pressure gradient. FR in perennial grass traits except for leaf N (no variation with grazing pressure) increased up to intermediate grazing pressure and then decreased under higher grazing pressure (Fig. 5b).

Species richness of perennial grasses was not significantly correlated to any functional index. Perennial grass cover was negatively related to CWM-height, FD-leaf N and FR-SLA, and positively associated with CWM-SLA. Simpson diversity index of perennial grasses was positively correlated to all indexes except for CWM-SLA and CWM-leaf N (Table 2b).

Discussion

In this study, we analysed trends in traditional community traits such as species richness, diversity and cover along with functional indices based on plant height, SLA, and leaf N in shrub and perennial grass canopies in arid rangelands of the Patagonian Monte. Although this study included only one grazing gradient, the selected sites were representative of sites with low (Bisigato and Bertiller 1997; Prieto et al. 2011; Larreguy et al. 2017), moderate (Bisigato and Bertiller 1997; Bisigato et al. 2008; Larreguy et al. 2017) and high (Bisigato and Bertiller 1997; Prieto et al. 2011; Larreguy et al. 2012, 2017) grazing disturbance described for the Patagonian Monte. Shrubs and perennial grasses are the dominant growth forms in most arid ecosystems of the world and the plant traits selected in this study are relevant descriptors that capture basic processes in plant functioning (Westoby et al. 1999; Díaz and Cabido 2001; Lepsˇ et al. 2006; Bá r Lamas et al. 2019). Low values of these traits in plant canopies are usually associated with xeromorphic attributes induced either by natural or anthropic disturbances (Díaz et al. 2007).

Our results showed that grazing pressure affected differentially canopy and functional attributes (assessed by functional indices) of shrub and perennial grass canopies. Functional diversity and species diversity can be positively or negatively correlated, or uncorrelated, depending on the environmental conditions and disturbance type and intensity (Díaz and Cabido 2001; Song et al. 2014). We found that grazing pressure led to increasing species and functional diversity of shrub canopies without significant changes in species richness and functional redundancy along with a moderate reduction of canopy cover.
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![Graphical representation of plant height, SLA, and leaf N under different grazing pressures.](image)

**a**
- CWM-plant height (cm)
  - FD-plant height
  - FR-plant height

**CWM-SLA (mm² mg⁻¹)**
- FD-SLA
- FR-SLA

**CWM-leaf N (mg g⁻¹)**
- FD-leaf N
- FR-leaf N

**Grazing pressure (faeces m⁻²)**
- Mean FD
- Mean FR

**Regression equations and their significance levels:**

- **CWM-plant height (cm)**
  - $y = 0.12x + 76.66, r^2 = 0.10, p = 0.23$
  - $y = 0.01x + 3.27, r^2 = 0.28, p = 0.04$
  - $y = 5.06x^{0.23}, r^2 = 0.63, p < 0.01$

- **CWM-SLA (mm² mg⁻¹)**
  - $y = -2.52e^{-6}x^2 + 0.01x - 0.04, r^2 = 0.82, p < 0.01$
  - $y = -2.72e^{-6}x^2 - 6.27e^{-6}x + 0.03, r^2 = 0.09, p = 0.54$
  - $y = -2.11e^{-6}x^2 + 0.001x + 0.02, r^2 = 0.23, p = 0.18$
  - $y = -4.29e^{-6}x^2 + 0.001x + 0.02, r^2 = 0.23, p = 0.18$
  - $y = -2.03e^{-6}x^2 + 0.01x - 0.01, r^2 = 0.83, p < 0.01$
  - $y = -1.21/x + 0.08, r^2 = 0.21, p = 0.07$

- **CWM-leaf N (mg g⁻¹)**
  - $y = 0.12x + 76.66, r^2 = 0.10, p = 0.23$
  - $y = 0.01x + 3.27, r^2 = 0.28, p = 0.04$
  - $y = 5.06x^{0.23}, r^2 = 0.63, p < 0.01$

- **Mean FD**
  - $y = -2.22e^{-6}x^2 + 0.01x - 0.03, r^2 = 0.82, p < 0.01$
  - $y = -3.16e^{-6}x + 0.001x + 0.02, r^2 = 0.23, p = 0.18$

- **Mean FR**
  - $y = -2.11e^{-6}x^2 + 0.001x + 0.02, r^2 = 0.23, p = 0.18$
(63.2% reduction in cover between both extremes of the grazing gradient). Increasing shrub species diversity across the grazing pressure gradient indicated more evenly contribution of species to the shrub canopy cover consistently with changes in individual species abundance reported in other arid ecosystems disturbed by sheep grazing (Milchunas and Lauenroth).

**Table 2** Correlation coefficients ($r$) between community attributes (species richness, cover, species diversity) and functional indices (community weighted mean: CWM, functional diversity: FD, functional redundancy: FR) of height, SLA and leaf N in shrub and perennial grass canopies.

| Index          | (a) Shrub canopy                  | (b) Perennial grass canopy              |
|----------------|-----------------------------------|----------------------------------------|
|                | Species richness | Cover | Species diversity | Species richness | Cover | Species diversity |
| CWM-height     | -0.02              | -0.47 | 0.14             | 0.22             | -0.51** | 0.73**            |
| CWM-SLA        | 0.38               | -0.03 | 0.56*            | 0.36             | 0.85**  | -0.47             |
| CWM-leaf N     | -0.01              | -0.55*| 0.68**           | 0.22             | 0.13    | -0.18             |
| FD-height      | 0.35               | 0.39  | 0.99**           | 0.07             | -0.45   | 0.92**            |
| FD-SLA         | 0.43               | -0.39 | 0.99**           | 0.02             | -0.21   | 0.81**            |
| FD-leaf N      | 0.34               | -0.40 | 0.99**           | -0.07            | 0.54*   | 0.91**            |
| Mean-FD        | 0.37               | -0.39 | 0.99**           | 0.002            | -0.43   | 0.94**            |
| FR-height      | 0.76**             | 0.37  | 0.12             | 0.14             | -0.27   | 0.73**            |
| FR-SLA         | 0.28               | 0.004 | 0.75**           | 0.17             | -0.48*  | 0.68**            |
| FR-leaf N      | 0.69**             | -0.01 | 0.74**           | 0.38             | -0.03   | 0.62**            |
| Mean-FR        | 0.66**             | 0.09  | 0.70**           | 0.26             | -0.34   | 0.80**            |

Bold values denote statistical significance at the $p < 0.05$ level

* $p < 0.01$, *$p \leq 0.05$

\[
y = 6.54e^{-0.03x}, r^2=0.89, p<0.01
\]

\[
y = -0.0002x^2+0.02x+4.46, r^2=0.71, p< 0.01
\]
a  \( y = -0.002x^2+0.50x-1.76, r^2=0.83, p<0.01 \)

\[ y = 0.0003x^2-0.07x+8.50, r^2=0.85, p< \]

\[ y =0.001x^2-0.18x+20.60, r^2=0.53, p<0.01 \]

b  \( y = -4.87/x+0.45, r^2 = 0.28, p=0.03 \)

\[ y =-2.66e^{-0.05}x^2+0.01x-0.08, r^2=0.58, p<0.01 \]

\[ y = -0.002x^2+0.50x-1.76, r^2=0.83, p<0.01 \]

\[ y =0.001x^2-0.18x+20.60, r^2=0.53, p= 0.01 \]

\[ y =-3.89e^{-0.05}x^2+0.01x-0.18, r^2=0.77, p< 0.01 \]

\[ y =-1.85e^{-0.05}x^2+0.003x+0.05, r^2=0.31, p= 0.09 \]

\[ y =-3.18/x+0.40, r^2 = 0.07, p=0.18 \]

\[ y = -2.66e^{-0.05}x^2+0.01x-0.08, r^2=0.58, p< 0.01 \]
Increasing values of these traits with increasing grazing disturbance could be attributable to compensatory growth in preferred shrub species after tissue removal by grazers (McNaughton 1984; Cooper et al. 2003). New growth tissues usually have higher SLA and N concentration than mature tissues (Lattanzi et al. 2004). Moreover, shrubs could also colonize by seeds denuded soil gaps in the most degraded sites (Bisigato and Bertiller 1997). Young plants usually show higher leaf N concentration and SLA than adult ones (Coley and Barone 1996). However, the lack of variation in CWM-height of shrub canopy with grazing disturbance did not support this assertion. Since then, we do not expect that differences in CWM of SLA and leaf N may be attributable to shrub colonization and probably they were the consequence of regrowth after defoliation. Moreover, shrub canopies were capable to persist under high grazing pressure increasing functional diversity in relevant plant traits related to plant growth (Westoby et al. 1999) while maintaining low values of functional redundancy. These findings highlighted the ability of shrub canopies to resist grazing disturbances through (i) increased species diversity and functional diversity in relevant traits which allow to maintain a differential use of resources in space and/or time enhancing the complementarity in resource use among them (Loreau et al. 2001; Hooper et al. 2005; Gross et al. 2007; Cornwell and Ackerly 2009; Valencia et al. 2015) and (ii) a high ability to replace tissues lost by defoliation.

In contrast to shrub canopies, increasing grazing pressure led to a high reduction of the cover of perennial grass canopies probably due to a direct effect of tissues removal by grazers. However, this cover reduction was not followed by decreasing perennial grass species richness being this firstly noticeable under high grazing pressure. Moreover, perennial grass diversity depicted a hump-shaped curve across the grazing disturbance gradient in accordance with the pattern predicted by the well-known hypothesis of intermediate disturbance (Connell 1978; Miller et al. 2011). These results would indicate that tissue removal by grazers firstly affected the cover leading to a more even species cover contribution to grass canopy and subsequently reduced species richness and diversity probably by cover reduction and loss of highly preferred grass species. The CWM-height of perennial grasses followed the same pattern as that of species diversity across the grazing pressure gradient, while the inverse pattern was observed for CWM of SLA and N concentration in leaves. This could be attributable to direct or indirect effects of grazing on perennial grass species abundance, local extinction, and replacement. Grazing pressure reduces the cover of highly preferred grass species such as *Poa ligularis* and *Nassella tenuis*, while the tallest grass *Pappostipa speciosa* frequently increases the absolute or relative cover (Pazos et al. 2007). However, this latter may not counteract the reduction of total perennial grass cover under high grazing disturbance. At intermediate grazing pressure with presence of the three-dominant grass species, *P. speciosa* may be not grazed and grazers may firstly graze this species when the abundance of the highly preferred species become scarce at high grazing pressure. Moreover, some highly preferred grass species may be clumped under the protection of well-defended shrub canopies. These tussocks are not only protected from grazers but also may grow taller due to the shelter and shading effect of shrub canopies (Westoby et al. 2002; Bertiller et al. 2004; Vesk et al. 2004; Fynn 2012). Patterns in CWM of SLA and N supported this assumption since *P. speciosa* has the lowest SLA and N concentration in green leaves among the three-grass species (Carrera et al. 2000, 2009). However, under high grazing pressure the fragmentation of shrub patches induced by grazing (Bisigato and Bertiller 1997) could expose these tussocks to grazers reducing the height and increasing the SLA and leaf N due to tissues regrowth.

Functional diversity and redundancy of perennial grass traits followed similar patterns than that of species diversity across the grazing pressure gradient. High functional diversity in grass canopies at intermediate grazing pressure may be associated with differential use of resources in space and/or time.
enhancing species complementarity in their use (Valencia et al. 2015). High leaf trait diversity indicates the occurrence of contrasting leaf strategies (Westoby et al. 2002) in co-occurring species. This may have strong positive effects on ecosystem processes, such as productivity and decomposition, maintaining and improving dryland multifunctionality (Gross et al. 2007; Cornwell and Ackerly 2009; Valencia et al. 2015). However, this canopy state may have low resilience and increasing grazing pressure may lead to species losses and to perennial grass canopies states difficult to revert. The loss of functional redundancy is consistent with existing views on the intensification of land use as one of the main drivers of species loss worldwide, through the simplification of ecosystem structure (Pimm and Raven 2000; Laliberté et al. 2010). The fact that functional redundancy enhances resilience is particularly important for land-use regulation and ecosystem management, given that redundancy tends to decrease with high land-use intensity (Pillar et al. 2013).

In conclusion, our results highlighted the ability of shrub canopies to hold up to grazing disturbance through the increase in species diversity and functional diversity and probably the replacement of tissues lost by defoliation. In contrast, perennial grass canopies were able to hold up intermediate grazing disturbances by increasing functional diversity, functional redundancy. This canopy state may be identified as a resilience threshold since at higher grazing pressure perennial grass canopies lost their ability to compensate grazing impacts shifting to perennial grass canopies states difficult to revert. Thus, understanding functional changes on main components of plant canopies under grazing disturbance is crucial because land-use change is expected to be the most important driver of changes in biodiversity worldwide for this century (Laliberté et al. 2013).

Management tools monitoring functional variables are key factors for the maintenance and conservation of perennial grass and shrub functions in rangelands (Pillar et al. 2013). Grazing pressure increased the functionality of shrub canopies across the whole gradient and that of perennial grass canopies up to mid intensities. Our study indicated that among the community and functional traits analysed, species diversity could be used as an indicator of functional canopy responses to sheep grazing at the Patagonian Monte rangelands. Thus, in order to prevent degradation by grazing, species diversity could be used to monitor the rangeland conservation function by identifying resilience thresholds beyond which the community loses functional and canopy components (Grime 1998; Bisigato et al. 2008). In this sense, functional responses of vegetation to grazing disturbance in arid ecosystems will depend on the level of disturbance caused by grazing pressure on perennial grass species which are the most directly affected by grazing and on shrub canopies that could act as refuges for perennial grasses.

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