



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.

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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 et al. 2007). 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 complementarity 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 (Defossé 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; Olf 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 held 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 (Bär 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

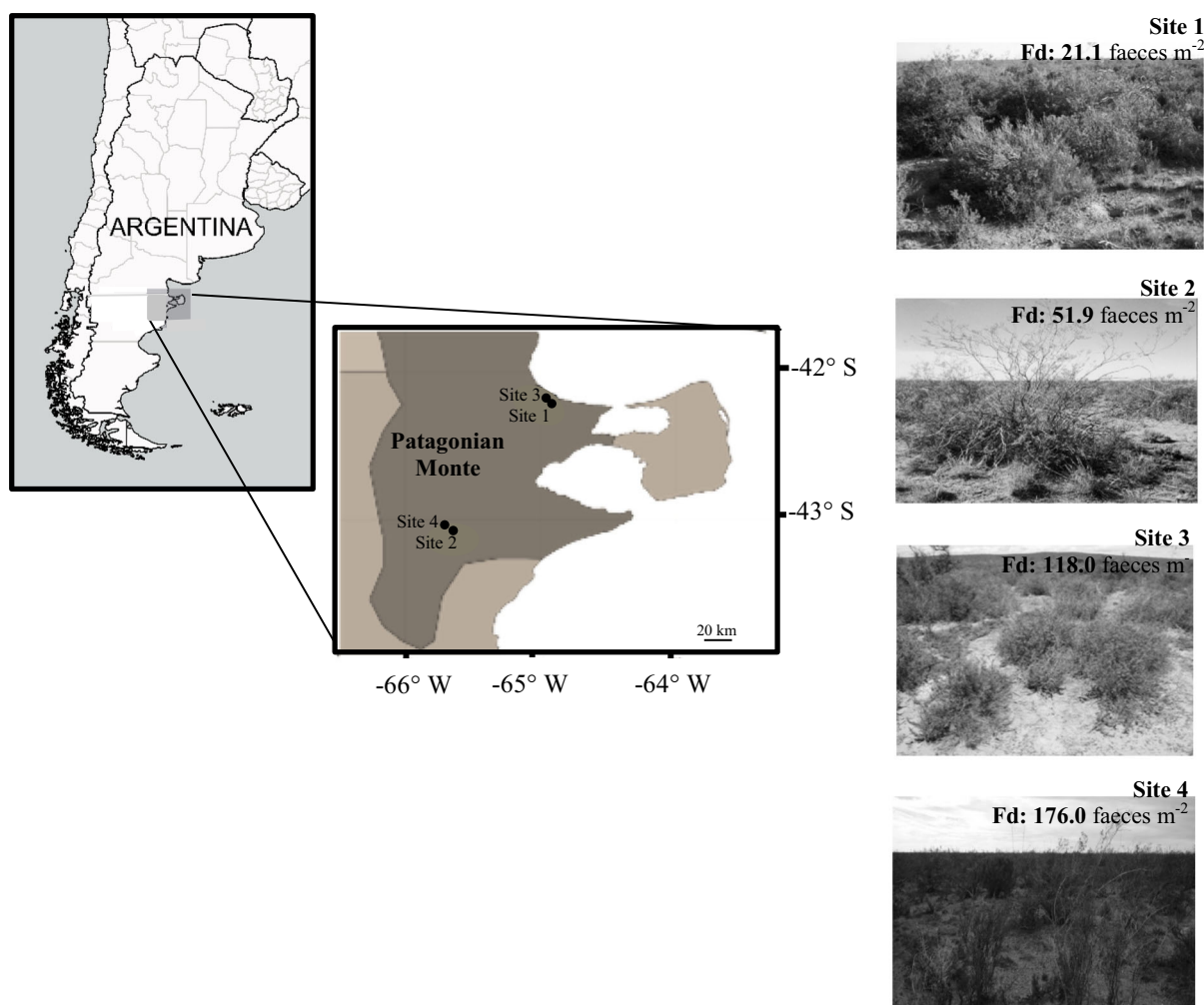


Fig. 1 Geographical location and grazing pressure (Fd: faeces density reported in Bär Lamas et al. 2013; Larreguy et al. 2017) of the four study sites in the Patagonian Monte (site 1: 42° 12' 16.40" S, 64° 58' 54.90" W, 21.1 faeces m⁻²; site 2: 43° 08'

11.74" S, 65° 42' 49.79" W, 51.9 faeces m⁻²; site 3: 42° 11' 27.35" S, 64° 59' 32.15" W, 118.0 faeces m⁻²; site 4: 43° 06' 15.70" S, 65° 43' 47.70" W, 176.0 faeces m⁻²)

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) Larreguy et al. (2012) Carrera and Bertiller (2013)	Sites 3 and 4

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:

$$\text{Growth form cover}(\%)_j = \left(\frac{\sum_{i=1}^{S_j} l_j * C_{ij}}{lt_j} \right) * 100$$

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, lt = 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:

$$SD_j = 1 - \sum_{i=1}^{S_j} p_{ij}^2$$

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):

$$\text{CWM}_j = \sum_i^{S_j} p_{ij} T_{ij}$$

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. FD_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):

$$\text{FD}_j = \sum_{i=1}^{S_j} \sum_{x=1}^{S_j} d_{ixj} p_{ij} p_{xj}$$

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_{ixj} 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), FR_j is the part of the species diversity in the community that is not explained by FD_j . Therefore, FR was calculated as

$$\text{FR}_j = \text{SD}_j - \text{FD}_j$$

We also calculated the mean FD_j and FR_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. Bär 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).

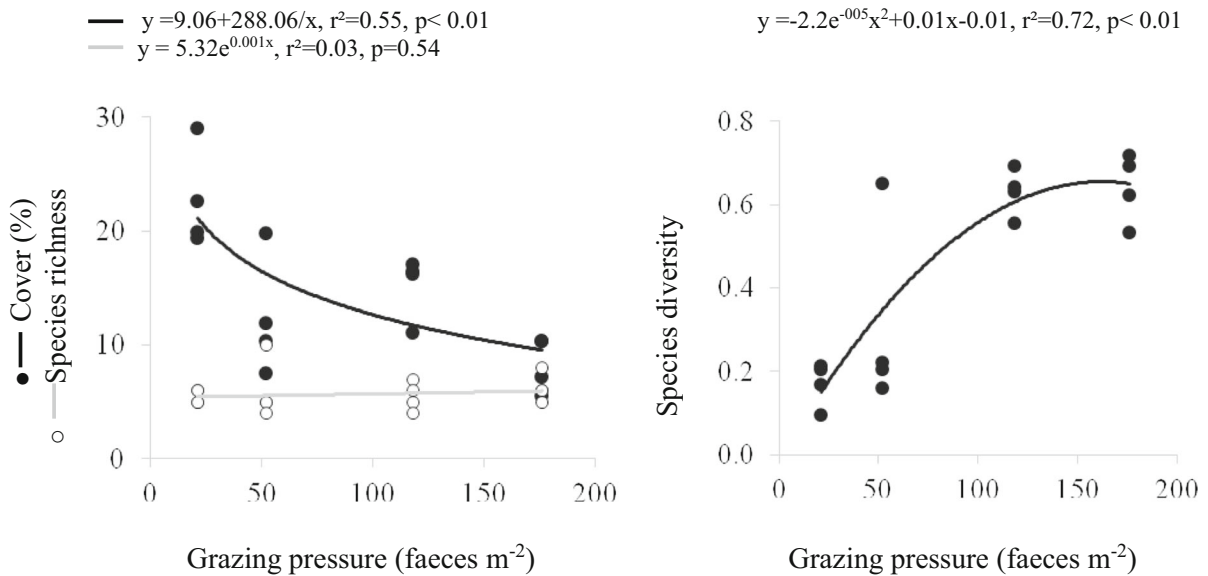


Fig. 2 Relationship between plant cover, species richness, species diversity of shrub canopy and grazing pressure (faeces m⁻²)

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 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; Lepš et al. 2006; Bär 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

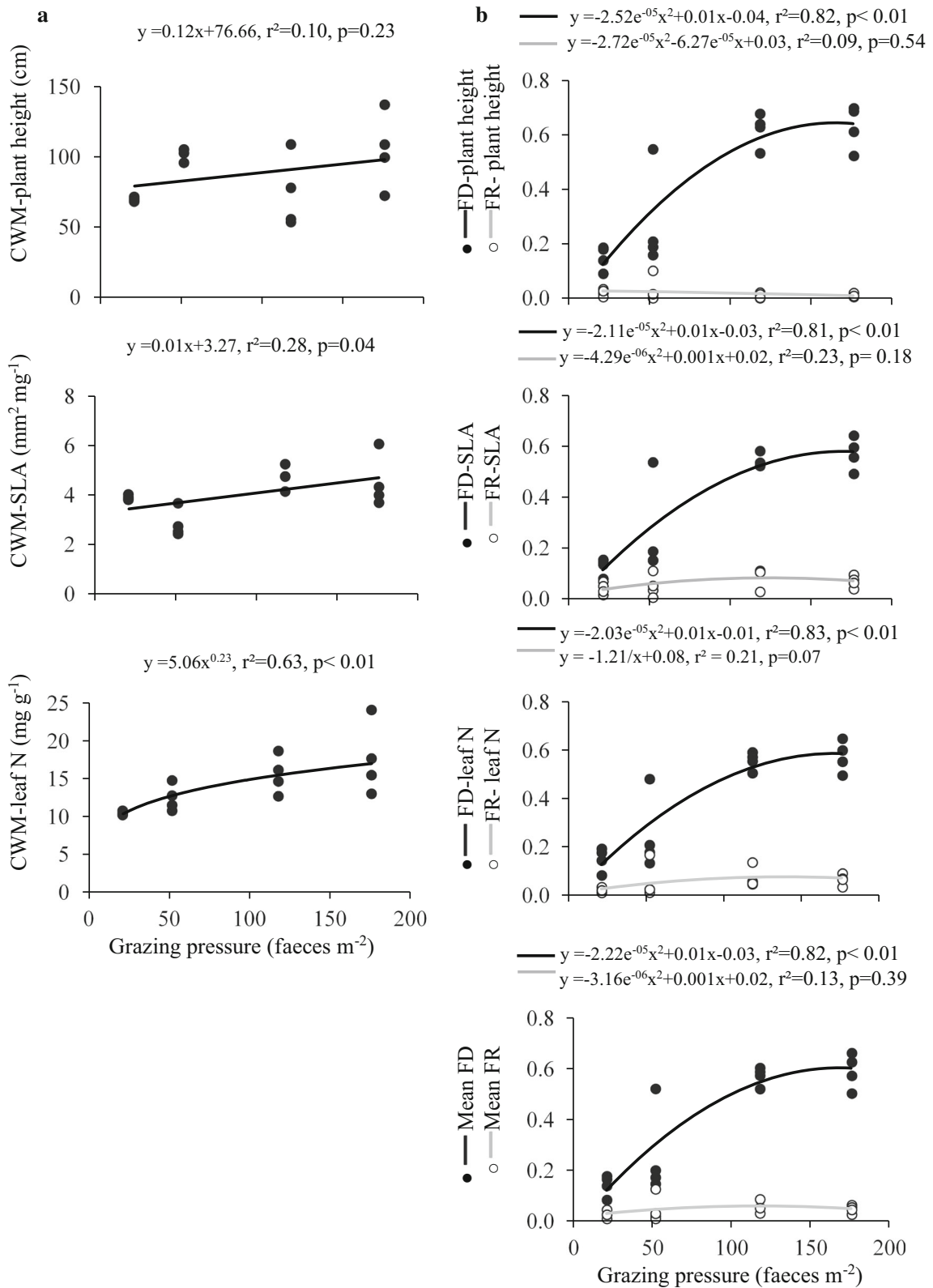


Fig. 3 Relationship between **a** community weighted mean (CWM) of plant height, specific leaf area (SLA) and N concentration in green leaves of shrub canopy and grazing pressure (faeces m⁻²); and **b** functional diversity (FD) and redundancy (FR) of shrub canopy and grazing pressure (faeces m⁻²)

(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* ≤ 0.05

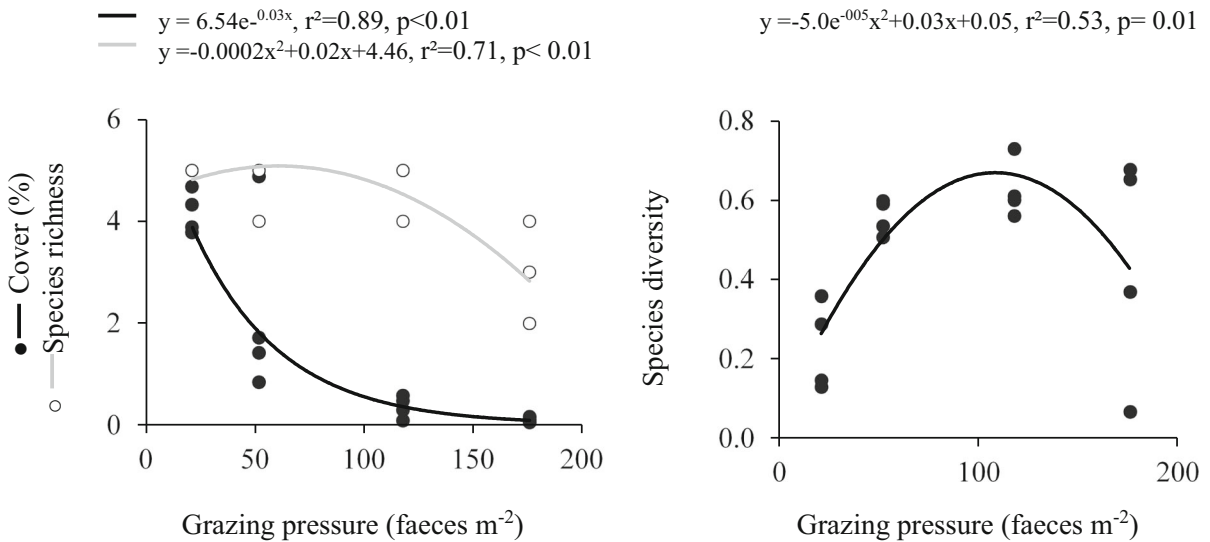
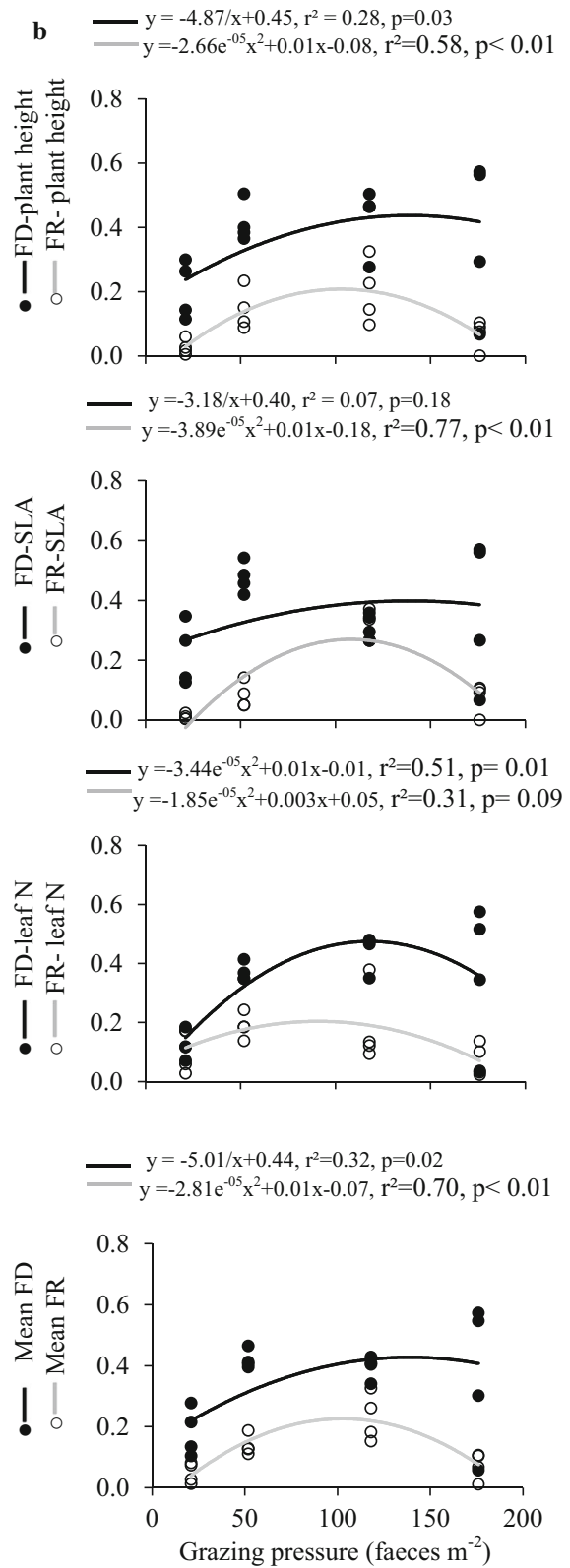
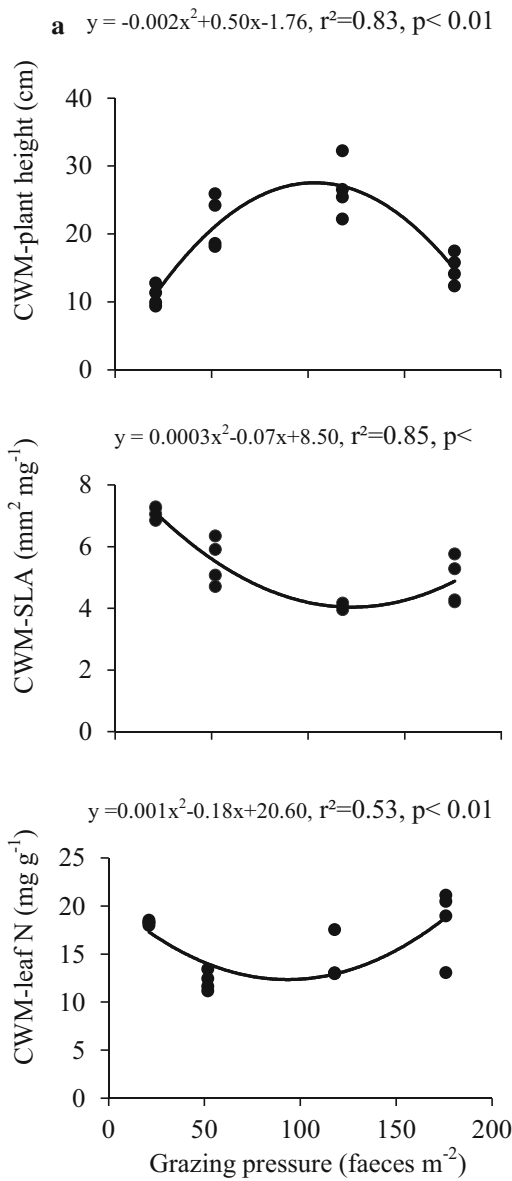


Fig. 4 Relationship between plant cover, species richness, species diversity of perennial grass canopy and grazing pressure (faeces m⁻²)



◀ **Fig. 5** Relationship between **a** community weighted mean (CWM) of plant height, specific leaf area (SLA) and N concentration in green leaves of perennial grass canopy and grazing pressure (faeces m^{-2}); and **b** functional diversity (FD) and redundancy (FR) of perennial grass canopy and grazing pressure (faeces m^{-2})

1993; Westoby et al. 2002). Contrary to our expectation, this trend in species diversity was associated with increasing community weighted mean (CWM) values of SLA, and leaf N in shrub canopies.

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 species 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; Veski 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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References

- Aerts R, Chapin FS (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv Ecol Res* 30:1–67. [https://doi.org/10.1016/S0065-2504\(08\)60016-1](https://doi.org/10.1016/S0065-2504(08)60016-1)
- Aguilar MR, Sala OE (1999) Patch structure, dynamics and implications for the functioning of arid ecosystems. *TREE* 14:273–277. [https://doi.org/10.1016/S0169-5347\(99\)01612-2](https://doi.org/10.1016/S0169-5347(99)01612-2)
- Ares JO, Bertiller MB, Bisigato A (2003) Modeling and measurement of structural changes at a landscape scale in dryland areas. *Environ Model Assess* 8:1–13. <https://doi.org/10.1023/A:1022499815527>
- Bär Lamas MI, Carrera AL, Bertiller MB (2019) Plant traits related to leaf decomposition processes in arid ecosystems of northern Patagonia. *J Plant Ecol* 12:216–227. <https://doi.org/10.1093/jpe/rty012>
- Bär Lamas MI, Larreguy C, Carrera AL, Bertiller MB (2013) Changes in plant cover and functional traits induced by grazing in the arid Patagonian Monte. *Acta Oecol* 51:66–73. <https://doi.org/10.1016/j.actao.2013.06.002>
- Barbet-Massin M, Jetz W (2015) The effect of range changes on the functional turnover, structure and diversity of bird assemblages under future climate scenarios. *Glob Change Biol* 21:2917–2928. <https://doi.org/10.1111/gcb.12905>
- Barros V, Rivero MM (1982) Mapas de probabilidad de precipitación en la Provincia del Chubut. *Contribución Nro 54*. Centro Nacional Patagónico, Puerto Madryn
- Bertiller MB, Ares JO (2008) Sheep spatial grazing strategies at the arid Patagonian Monte, Argentina. *Rangel Ecol Manag* 61:38–47. <https://doi.org/10.2111/07-130.1>
- Bertiller MB, Ares JO, Bisigato AJ (2002) Multi-scale indicators of land degradation in the Patagonian Monte,

- Argentina. *J Environ Manag* 30:704–715. <https://doi.org/10.1007/s00267-002-2725-4>
- Bertiller MB, Bisigato AJ, Carrera AL, del Valle HF (2004) Estructura de la vegetación y funcionamiento de los ecosistemas del Monte Chubutense. *Bol Soc Argent Bot* 39:139–158
- Bertiller MB, Mazzarino MJ, Carrera AL, Diehl P, Satti P et al (2006) Leaf strategies and soil N across a regional humidity gradient in Patagonia. *Oecologia* 148:612–624. <https://doi.org/10.1007/s00442-006-0401-8>
- Bisigato AJ, Bertiller MB (1997) Grazing effects on patchy dryland vegetation in northern Patagonia. *J Arid Environ* 36:639–653. <https://doi.org/10.1006/jare.1996.0247>
- Bisigato AJ, Bertiller MB, Ares JO, Pazos GE (2005) Effect of grazing on plant patterns in arid ecosystems of Patagonian Monte. *Ecography* 28:561–572. <https://doi.org/10.1111/j.2005.0906-7590.04170.x>
- Bisigato AJ, López Laphitz R, Carrera AL (2008) Non-linear relationships between grazing pressure and conservation of soil resources in Patagonian Monte shrublands. *J Arid Environ* 72:1464–1475. <https://doi.org/10.1016/j.jaridenv.2008.02.016>
- Bisigato AJ, Villagra PE, Ares JO, Rossi BE (2009) Vegetation heterogeneity in Monte Desert ecosystems: a multi-scale approach linking patterns and processes. *J Arid Environ* 73:182–191. <https://doi.org/10.1016/j.jaridenv.2008.09.001>
- Botta-Dukát Z (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *J Veg Sci* 16:533–540. <https://doi.org/10.1111/j.1654-1103.2005.tb02393.x>
- Carrera AL, Bertiller MB (2013) Combined effects of leaf litter and soil microsite on decomposition process in arid rangelands. *J Environ Manag* 114:505–511. <https://doi.org/10.1016/j.jenvman.2012.10.059>
- Carrera AL, Sain CL, Bertiller MB (2000) Patterns of nitrogen conservation in shrubs and grasses in the Patagonian Monte, Argentina. *Plant Soil* 224:185–193. <https://doi.org/10.1023/A:1004841917272>
- Carrera AL, Mazzarino MJ, Bertiller MB, del Valle HF, Carretero EM (2009) Plant impacts on nitrogen and carbon cycling in the Monte Phytogeographical Province, Argentina. *J Arid Environ* 73:192–201. <https://doi.org/10.1016/j.jaridenv.2008.09.016>
- Chillo V, Anand M, Ojeda RA (2011) Assessing the use of functional diversity as a measure of ecological resilience in arid rangelands. *Ecosystems* 14:1168–1177. <https://doi.org/10.1007/s10021-011-9475-1>
- Coley PD, Barone JA (1996) Herbivory and plant defenses in tropical forests. *Annu Rev Ecol Syst* 27:305–335. <https://doi.org/10.1146/annurev.ecolsys.27.1.305>
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310
- Coombs J, Hind G, Leegood RC, Tienszen LL, Vonshsk A (1985) Analytical techniques. In: Coombs J, Hall DO, Long SP, Scurlock JMO (eds) *Techniques in bioproduktivty and photosynthesis*. Pergamon Press, New York, pp 219–228
- Cooper SM, Owens MK, Spalinger DE, Ginnett TF (2003) The architecture of shrubs after defoliation and the subsequent feeding behavior of browsers. *Oikos* 100:387–393. <https://doi.org/10.1034/j.1600-0706.2003.11792.x>
- Comelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N et al (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Austral J Bot* 51:335–380. <https://doi.org/10.1071/BT02124>
- Cornwell WK, Ackerly DD (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecol Monogr* 79:109–126. <https://doi.org/10.1890/07-1134.1>
- de Bello F, Lepš J, Sebastià MT (2006) Variations in species and functional plant diversity along climatic and grazing gradients. *Ecography* 29:801–810. <https://doi.org/10.1111/j.2006.0906-7590.04683.x>
- de Bello FD, Lepš J, Lavorel S, Moretti M (2007) Importance of species abundance for assessment of trait composition: an example based on pollinator communities. *Community Ecol* 8:163–170. <https://doi.org/10.1556/ComEc.8.2007.2.3>
- de Bello F, Lavergne S, Meynard CN, Lepš J, Thuiller W (2010) The partitioning of diversity: showing Theseus a way out of the labyrinth. *J Veg Sci* 21:992–1000. <https://doi.org/10.1111/j.1654-1103.2010.01195.x>
- Defossé GE, Robberecht R (1987) Patagonia: range management at the End of the World. *Rangelands* 9:106–109
- Defossé GE, Bertiller MB, Ares JO (1990) Above-ground phytomass dynamics in grassland steppe of Patagonia, Argentina. *J Range Manag* 43:157–160. <https://doi.org/10.2307/3899036>
- Díaz S, Cabido M (2001) Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol Evol* 16:646–655. [https://doi.org/10.1016/S0169-5347\(01\)02283-2](https://doi.org/10.1016/S0169-5347(01)02283-2)
- Díaz S, Cabido M, Casanoves F (1998) Plant functional traits and environmental filters at a regional scale. *J Veg Sci* 9:113–122. <https://doi.org/10.2307/3237229>
- Díaz S, Lavorel S, McIntyre SUE, Falczuk V, Casanoves F et al (2007) Plant trait responses to grazing—a global synthesis. *Glob Chang Biol* 13:313–341. <https://doi.org/10.1111/j.1365-2486.2006.01288.x>
- Ehrlich P, Walker B (1998) Rivets and redundancy. *Bioscience* 48:387–388
- Escobar JM, Degorgue G, Llanos E (2004) Inventario, Evaluación y Planificación del uso de Pastizales Naturales. Establecimiento La Esperanza. Fundación Patagonia Natural (FPN). World Land Trust (WLT). Instituto Nacional de Tecnología Agropecuaria. Centro Regional Patagonia Sur. Estación Experimental Agropecuaria Chubut (44 pp.) FNP-Fundación Patagonia Natural (2013) Available at: <https://www.patagonianatural.org>. Accessed Dec 2013
- Fynn RW (2012) Functional resource heterogeneity increases livestock and rangeland productivity. *Rangel Ecol Manag* 65:319–329. <https://doi.org/10.2111/REM-D-11-00141.1>
- Garnier E, Cortez J, Billès G, Navas ML, Roumet C et al (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85:2630–2637. <https://doi.org/10.1890/03-0799>
- Glenn SM, Collins SL (1992) Effects of scale and disturbance on rates of immigration and extinction of species in prairies. *Oikos* 63:273–280. <https://doi.org/10.2307/3545388>

- Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J Ecol* 86:902–910. <https://doi.org/10.1046/j.1365-2745.1998.00306.x>
- Gross N, Suding KN, Lavorel S, Roumet C (2007) Complementarity as a mechanism of coexistence between functional groups of grasses. *J Ecol* 95:1296–1305
- Gross N, Börger L, Soriano Morales SI, Bagousse Pinguet L, Quero JL et al (2013) Uncovering multiscale effects of aridity and biotic interactions on the functional structure of Mediterranean shrublands. *J Ecol* 101:637–649. <https://doi.org/10.1111/1365-2745.12063>
- Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P et al (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–35. <https://doi.org/10.1890/04-0922>
- Huston MA, Huston MA (1994) Biological diversity: the coexistence of species. University Press, Cambridge
- Instituto Nacional de Tecnología Agropecuaria (1990) Atlas de suelos de la República Argentina. Band 1. Project PNUD-Argentina 05-019, Buenos Aires, Argentina
- Jardim AVF, Batalha MA (2008) Can we predict dispersal guilds based on the leaf-height-seed scheme in a disjunct cerrado woodland? *Braz J Biol* 68:553–559. <https://doi.org/10.1590/S1519-69842008000300013>
- Kang S, Ma W, Li FY, Zhang Q, Niu J et al (2015) Functional redundancy instead of species redundancy determines community stability in a typical steppe of Inner Mongolia. *PLoS ONE* 10:e0145605. <https://doi.org/10.1371/journal.pone.0145605>
- Laity J (2008) Deserts and desert environments. Wiley-Blackwell Publishes House, Chichester
- Laliberté E, Wells JA, DeClerck F, Metcalfe DJ, Catterall CP et al (2010) Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecol Lett* 13:76–86. <https://doi.org/10.1111/j.1461-0248.2009.01403.x>
- Laliberté E, Norton DA, Scott D (2013) Contrasting effects of productivity and disturbance on plant functional diversity at local and metacommunity scales. *J Veg Sci* 24:834–842. <https://doi.org/10.1111/jvs.12044>
- Lambers H, Chapin FS, Pons TL (2006) Plant physiological ecology. Springer, New York, NY
- Lange RT (1969) The piosphere: sheep track and dung patterns. *J Range Manag* 22:396–400. <https://doi.org/10.2307/3895849>
- Lange RT, Willcocks MC (1978) The relation between sheep-time spent and egesta accumulated within an arid zone paddock. *Aust J Exp Agric* 18:764–767. <https://doi.org/10.1071/EA9780764>
- Larreguy C, Carrera AL, Bertiller MB (2012) Production and turnover rates of shallow fine roots in rangelands of the Patagonian Monte, Argentina. *Ecol Res* 27: 61–68. <https://doi.org/10.1007/s11284-011-0869-5>
- Larreguy C, Carrera AL, Bertiller MB (2017) Reductions of plant cover induced by sheep grazing change the above-ground partition and chemistry of organic C stocks in arid rangelands of Patagonian Monte, Argentina. *J Environ Manag* 199: 139–147. <https://doi.org/10.1016/j.jenvman.2017.04.086>
- Lattanzi FA, Schnyder H, Thornton B (2004) Defoliation effects on carbon and nitrogen substrate import and tissue-bound efflux in leaf growth zones of grasses. *Plant Cell Environ* 27:347–356. <https://doi.org/10.1046/j.1365-3040.2004.01147.x>
- Laughlin DC, Leppert JJ, Moore MM, Hull Sieg C (2010) A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. *Funct Ecol* 24:493–501. <https://doi.org/10.1111/j.1365-2435.2009.01672.x>
- Lavorel S, Storkey J, Bardgett RD, de Bello F, Berg MP et al (2013) A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *J Veg Sci* 24:942–948. <https://doi.org/10.1111/jvs.12083>
- León RJ, Bran D, Collantes M, Paruelo JM, Soriano A (1998) Grandes unidades de vegetación de la Patagonia extra andina. *Ecol Aust* 8:125–144
- Lepš J, de Bello F, Lavorel S, Berman S (2006) Quantifying and interpreting functional diversity of natural communities: practical considerations matter. *Preslia* 78:481–501
- Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP et al (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–808. <https://doi.org/10.1126/science.1064088>
- Maestre FT, Quero JL, Gotelli NJ, Escudero A, Ochoa V et al (2012) Plant species richness and ecosystem multifunctionality in global drylands. *Science* 335:214–218. <https://doi.org/10.1126/science.1215442>
- Mazzarino MJ, Bertiller MB, Schlichter T, Gobbi M (1998) Nutrient cycling in Patagonian ecosystems. *Ecol Aust* 8:167–182
- McNaughton SJ (1984) Grazing lawns: animals in herds, plant form, and coevolution. *Am Nat* 124:863–886. <https://doi.org/10.1086/284321>
- Milchunas DG, Lauenroth WK (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecol Monogr* 63:327–366. <https://doi.org/10.2307/2937150>
- Miller AD, Roxburgh SH, Shea K (2011) How frequency and intensity shape diversity–disturbance relationships. *Proc Natl Acad Sci USA* 108:5643–5648. <https://doi.org/10.1073/pnas.1018594108>
- Mouillot D, Villéger S, Parravicini V, Kulbicki M, Arias-González JE et al (2014) Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proc Natl Acad Sci USA* 111:13757–13762. <https://doi.org/10.1073/pnas.1317625111>
- Mueller-Dombois D, Ellenberg H (1974) Aims and methods of vegetation ecology. Wiley, Hoboken, NY
- Naeem S, Chapin FS, Costanza R, Ehrlich PR, Golley FB et al (1999) Biodiversity and ecosystem functioning: maintaining natural life support processes. *Issues Ecol* 4:1–14
- Norusis MJ (1997) SPSS Base 7.5 for windows users guide. SPSS Inc, Chicago
- Noy-Meir I (1973) Desert ecosystems: environment and producers. *Annu Rev Ecol Syst* 4:25–51. <https://doi.org/10.1146/annurev.es.04.110173.000325>
- Olf H, Ritchie ME (1998) Effects of herbivores on grassland plant diversity. *Trends Ecol Evol* 13:261–265. [https://doi.org/10.1016/S0169-5347\(98\)01364-0](https://doi.org/10.1016/S0169-5347(98)01364-0)
- Pazos GE, Bisigato AJ, Bertiller MB (2007) Abundance and spatial patterning of coexisting perennial grasses in grazed

- shrublands of the Patagonian Monte. *J Arid Environ* 70:316–328. <https://doi.org/10.1016/j.jaridenv.2006.12.025>
- Pazos GE, Ares JO, Bertiller MB (2010) Quantitative assessment of shrub-grass mosaic development in grazed shrublands: an example in the Patagonian Monte (Argentina). *J Arid Environ* 74:998–1002. <https://doi.org/10.1016/j.jaridenv.2009.12.004>
- Pillar VD, Blanco CC, Müller SC, Sosinski EE, Joner F et al (2013) Functional redundancy and stability in plant communities. *J Veg Sci* 24:963–974. <https://doi.org/10.1111/jvs.12047>
- Pimm SL, Raven P (2000) Biodiversity: extinction by numbers. *Nature* 403:843–845. <https://doi.org/10.1038/35002708>
- Prieto LH, Bertiller MB, Carrera AL, Olivera NL (2011) Soil enzyme and microbial activities in a grazing ecosystem of Patagonian Monte, Argentina. *Geoderma* 162:281–287. <https://doi.org/10.1016/j.geoderma.2011.02.011>
- Proulx M, Mazumder A (1998) Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* 79:2581–2592. [https://doi.org/10.1890/0012-9658\(1998\)079\[2581:ROGIOP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2581:ROGIOP]2.0.CO;2)
- Reynolds HL, Hungate BA, Chapin FS, D'Antonio CM (1997) Soil heterogeneity and plant competition in an annual grassland. *Ecology* 78:2076–2090. [https://doi.org/10.1890/0012-9658\(1997\)078\[2076:SHAPCI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[2076:SHAPCI]2.0.CO;2)
- Rosenzweig ML, Abramsky Z (1993) How are diversity and productivity related? In: Ricklefs RD, Schluter D (eds) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, IL, pp 52–65
- Rossi MJ, Ares JO (2012) Depression storage and infiltration effects on overland flow depth-velocity-friction at desert conditions: field plot results and model. *Hydro Earth Syst Sci* 16:3293–3307. <https://doi.org/10.5194/hess-16-3293-2012>
- Song Y, Wang P, Li G, Zhou D (2014) Relationships between functional diversity and ecosystem functioning: a review. *Acta Ecol Sin* 34:85–91. <https://doi.org/10.1016/j.chnaes.2014.01.001>
- Tilman D (1982) *Resource competition and community structure*. Princeton University Press, Princeton, NJ
- Valencia E, Maestre FT, Bagousse-Pinguet L, Quero JL, Tamme R et al (2015) Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands. *New Phytol* 206:660–671. <https://doi.org/10.1111/nph.13268>
- van der Graaf AJ, Stahl J, Klimkowska A, Bakker JP, Drent RH (2006) Surfing on a green wave-how plant growth drives spring migration in the Barnacle Goose *Branta leucopsis*. *ARDEA* 94:567–577
- Vesk P, Leishman M, Westoby M (2004) Simple traits do not predict grazing response in Australian dry shrublands and woodlands. *J Appl Ecol* 41:22–31. <https://doi.org/10.1111/j.1365-2664.2004.00857.x>
- Vile D, Shipley B, Garnier E (2006) Ecosystem productivity can be predicted from potential relative growth rate and species abundance. *Ecol Lett* 9:1061–1067. <https://doi.org/10.1111/j.1461-0248.2006.00958.x>
- Violle C, Navas ML, Vile D, Kazakou E, Fortunel C et al (2007) Let the concept of trait be functional! *Oikos* 116:882–892. <https://doi.org/10.1111/j.10030-1299.2007.15559.x>
- Walker BH (1992) Biodiversity and ecological redundancy. *Conserv Biol* 6:18–23. <https://doi.org/10.1046/j.1523-1739.1992.610018.x>
- Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199:213–227. <https://doi.org/10.1023/A:1004327224729>
- Westoby M, Eldridge D, Freudenberger D (1999) The LHS strategy scheme in relation to grazing and fire. *Proc Int Range Congress* 2:893–896
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annu Rev Ecol Syst* 33:125–159. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150452>
- Willig MR, Presley SJ (2018) Biodiversity and disturbance. *Encycl Anthropocene* 3:45–51

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