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# Original article

# Changes in plant cover and functional traits induced by grazing in the arid Patagonian Monte



M.I. Bär Lamas <sup>a,\*</sup>, C. Larreguy <sup>a</sup>, A.L. Carrera <sup>a,b</sup>, M.B. Bertiller <sup>a,b</sup>

- <sup>a</sup> Centro Nacional Patagónico (CONICET), Unidad de Investigación de Ecología Terrestre, CENPAT, Boulevard Brown 2915, 9120 Puerto Madryn, Chubut, Arcentina
- <sup>b</sup> Universidad Nacional de la Patagonia San Juan Bosco, Boulevard Brown 3700, 9120 Puerto Madryn, Chubut, Argentina

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#### ABSTRACT

Grazing disturbance may affect the structure and functioning of arid rangelands. We analyzed the changes in plant cover and plant functional traits (plant height, SLA, N in green leaves) at the community, morphotype and species level in relation to grazing disturbance in arid ecosystems with more than 100 years of sheep grazing history. We identified two grazing areas and within each area we selected two representative and homogeneous sites located far (low grazing disturbance) and near (high grazing disturbance) from the single permanent watering point. We evaluated the plant cover at community, morphotype (evergreen tall shrubs, deciduous shrubs, dwarf shrubs, perennial herbs and perennial grasses) and species level at each site and randomly selected three individuals of modal size of each species to evaluate at them the selected plants traits. Plant cover was reduced by grazing disturbance at the community level. The cover of perennial grasses and evergreen tall shrubs decreased and that of dwarf shrubs increased with increasing grazing disturbance. Increasing cover of dwarf shrubs did not compensate the cover reduction of the other morphotypes. In contrast, plant height, SLA and N in green leaves were not affected by high grazing disturbance at community level as a consequence of positive and negative changes in these traits at morphotype and species levels induced by high grazing disturbance. We concluded that cover was the trait most affected by high grazing disturbance and positive and negative changes in other traits at plant morphotype or species level did not affect community attributes related to resistance against herbivory.

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# 1. Introduction

Changes in plant species composition and functional traits as responses to disturbances are central topics in basic plant ecology as well as in rangeland management (Niu et al., 2010; Vesk and Westoby, 2001). In the last decades, there has been an ongoing effort to identify plant functional types and traits related to tolerance and avoidance of environmental stresses and how they respond to disturbances for the purpose of predicting vegetation dynamics and ecosystems functioning in changing environments (e.g. Bertiller et al., 2006; Díaz et al., 2007; Vesk and Westoby, 2001; Westoby, 1998). In arid ecosystems, the extreme dry conditions exert a strong selective pressure on plant morphological and life history traits (Bertiller and Bisigato, 1998; Noy Meir, 1973). Most of

these ecosystems are dominated by shrubs and perennial grasses (Whitford, 2002) and have been extensively grazed with domestic herbivores (Defossé et al., 1990). Selective domestic grazing induces strong changes in the relative abundance of plants species with different morpho-physiological traits thus producing important impacts on ecosystem structure and functioning (Bertiller and Bisigato, 1998; Cruz et al., 2010; Díaz et al., 2001; Milchunas and Lauenroth, 1993). The most conspicuous changes induced by domestic grazing are related to the shifting of perennial grasses by long-lived evergreen shrubs and replacements among shrubby species (Bertiller and Bisigato, 1998; Reynolds et al., 1997). Both life forms differ in structural and physiological traits (Bertiller et al., 1991; Carrera et al., 2009; Sala et al., 1989). Shrubs usually produce thick green leaves with large amount of secondary compounds (such as lignin, tannins, or soluble phenolics) protecting them against desiccation, herbivores, pathogens, and radiation effects, while perennial grasses produce leaves of short lifespan, with low protection against abiotic factors and herbivores (Aerts and Chapin, 2000; Campanella and Bertiller, 2008; Carrera et al., 2009).

<sup>\*</sup> Corresponding author. Tel.: +54 280 4451024; fax: +54 280 4451543. *E-mail addresses*: barlamas@cenpat.edu.ar, marlenebarlamas@yahoo.com.ar (M.I. Bär Lamas).

Several plant functional traits were proposed to summarize the major dimensions of variations in plant ecological strategies and to understand the main opportunities and selective forces that shape life histories, architectures, growth allocations, and physiologies of plants (Lambers et al., 2000; Westoby et al., 2002). Among them, specific leaf area (SLA), plant height at maturity and seed size are considered key predictors of the response of species abundance to disturbance. In general, the relative abundance of tall plants with high SLA should decrease while that of short plants with low SLA should increase due to herbivore selection under low or moderate grazing disturbance (Cingolani et al., 2005; Díaz et al., 2001; Westoby et al., 1999). However, selective grazing is not only dependent on plant morphological and functional traits (Day and Detling, 1990; Huntly, 1991) since grazing could also affect these traits (Briske, 1996). This codependency could generate feedback cycles between both vegetation structure and biochemistry, and nutrient cycling and storage (Díaz et al., 2007). Although several studies associated changes in relative abundance of plant species with a set of plant functional traits (Díaz et al., 2004, 2007; Golodets et al., 2009; Vesk and Westoby, 2001), few of them evaluated whether mean values of functional traits of plant species and morphotypes (e.g. plant height, SLA and N concentration in green leaves) would change with disturbance such as that induced by domestic grazing in arid ecosystems (Díaz et al., 2001; Niu et al., 2010; Vesk et al., 2004).

The objective of this study was to analyze the changes in plant cover and plant functional traits (plant height, SLA, N in green leaves) at the community, morphotype and species level in relation to grazing disturbance in arid ecosystems of the Patagonian Monte submitted to sheep grazing for more than 100 years. We hypothesized that grazing disturbance affects plant cover and functional traits (height, SLA and N concentration in green leaves) at community, morphotype and species level. We expected that plant cover, height, SLA and N concentration in green leaves will be reduced at the community level under grazing disturbance. These changes will be the consequence of both changes in the dominance of plant morphotypes (i.e. reduced cover of tall plant morphotypes and/or morphotypes with high SLA and N concentration in green leaves and increased cover of dwarf shrub morphotypes with low SLA and N concentration in green leaves) and changes in functional traits within morphotypes and species (i.e. reduced plant height, SLA, and N concentration in green leaves).

# 2. Materials and methods

#### 2.1. Study site

The study was carried out in northeastern Patagonia (Patagonian Monte). Mean annual temperature is 13 °C and mean annual precipitation is 188 mm (Barros and Rivero, 1982). Soils are a complex of Typic Petrocalcids-Typic Haplocalcids (del Valle, 1998; Soil Survey Staff, 1998). Vegetation corresponds to the shrubland of Larrea divaricata Cav. and Stipa spp., characteristic of the southern portion of the Monte Phytogeographic Province (León et al., 1998). The Patagonian Monte occupies flat landscapes and it is the most homogeneous floristic environment in Patagonian ecosystems (León et al., 1998). In the Patagonian Monte, sheep grazing was introduced at the beginning of the past century and was typically organized in ranches of about 4 paddocks of 2500 ha each sharing a single permanent watering point. This in turn led to the formation of extended piospheres (1500-2000 m) around watering points where the spatial pattern of plants, some traits of plant communities and upper soils are modified by the frequent visit of grazers (Ares et al., 2003; Bertiller et al., 2002; Bisigato and Bertiller, 1997; Bisigato et al., 2005; Carrera et al., 2008; Larreguy et al., 2012). Our study was conducted in two homogeneous (vegetation, soils, and relieve) and representative areas of the Patagonian Monte of about 10.000 ha each: La Elvira (43° 8'52.0"S, 65° 42'49.6"W; 157 m a.s.l.) submitted to sheep grazing with a stoking rate of 0.11–0.14 sheep ha<sup>-1</sup> since the beginning of the last century, and La Esperanza (42° 12'13.7"S, 64° 58'55.6"W; 92 m a.s.l.) that was submitted to the same stocking rate up to the year 2003 when this area was converted to a wildlife refuge and the stocking rate was gradually reduced (0.01 sheep ha<sup>-1</sup> per year) up to the year 2008 when all domestic herbivores were retired. Within each area, we selected one paddock of about 2500 ha with an extended piosphere (Ares et al., 2003) and delimited two sites (3 ha each, minimal area sensu Mueller-Dombois and Ellenberg, 1974) located far (low grazing disturbance) and near (high grazing disturbance) from the single permanent watering point (separated at least 1500 m from each other). Vegetation is characteristic of shrubland of Larrea divaricata Cav. and Stipa spp., relieve is flat (León et al., 1998) and soil texture is sandy or loamy sand at the four sites (Instituto Nacional de Tecnología Agropecuaria, 1990; Rossi and Ares, 2012). Faeces counts and density of sheep paths (Bisigato and Bertiller, 1997; Pazos et al., 2007), vegetation structure assessed by remote sensing (Ares et al., 2003) as well as to reductions in soil organic carbon with increasing grazing (Carrera et al., 2008; Prieto et al., 2011) are usually indicators used to confirm the existence of areas affected by grazing disturbance around watering points (piospheres).

#### 2.2. Indexes of grazing disturbance

We collected 30 soil cores (8 cm diameter and 2 cm depth) from random locations within each site and counted the number of faeces. Additionally, we randomly extracted eight soil samples with a metallic tube (5 cm in diameter, 30 cm depth) to assess soil organic carbon. Soil was air-dried, sieved to 2 mm and analyzed for soil organic carbon by wet combustion (Nelson and Sommers, 1982). Means per site of both attributes were used as indexes of grazing disturbance.

# 2.3. Plant cover

We evaluated the total plant cover and the absolute and relative plant species cover along four randomly located 25-m linear transects by the line intercept method (Mueller-Dombois and Ellenberg, 1974) at each site and area in August 2010. We further assigned each species to one of the following plant morphotypes: evergreen tall shrubs, shrubs more than 30 cm tall with evergreen leaves; deciduous shrubs, shrubs more than 30 cm tall with drought deciduous leaves; dwarf shrubs, shrubs less than 30 cm tall; perennial herbs, plants with leaves that die at the end of the growing season but the living underground stems lay dormant until the next growing season; and perennial grasses (Supplementary material table 1).

# 2.4. Plant traits

We randomly selected three individuals of modal size (most frequent crown diameter and height) of each perennial plant species and registered the plant height excluding the reproductive structures, in the case to be present (Laughlin et al., 2010), at each site and area in summer 2010−2011. The number of three replicates per species and site fulfilled the requirement of a level of accuracy ≤0.15 (Milner and Hughes, 1970). Then, we collected fully expanded young to medium age leaves (Bertiller et al., 2006) from three branches of the external canopy crown (sunny and partially sunny leaves) of each shrub and herb individual, and three tillers of each perennial grass bunch. Collected leaves were air dried and stored at

20 °C for later analysis. We randomly selected three totally expanded leaves per branch of each individual, re-hydrated them up to full expansion and placed each of them on the flat bed of an HP ScanJet ADF scanner and scanned them. Leaf area was calculated from the images obtained by means of the AxioVision 4 program. Then, leaves were oven dried at 60 °C for 48 h and weighed to assess leaf dry mass. We further calculated the mean SLA of each species at each site and area. The rest of the totally expanded green leaves without signs of deterioration (absence of damage by herbivores or pathogens) were oven dried at 60 °C over 48 h. We assessed N concentration by semi-micro Kjeldahl (Coombs et al., 1985) in the leaves of each individual of each species (species level) at each site and area. We calculated the mean of each functional trait for each morphotype (Mt) as:

$$Mt = \left(\sum_{i=1}^{S} trait_i\right) / S$$

where  $trait_i$  is the value of the functional trait (t) of each species (i) in the morphotype M and S is the total number of species in M.

Then, we calculated the weighted mean of each functional trait by site (community) and morphotype by weighting values of functional traits by the relative cover of species in the community and morphotype, respectively (Bernard-Verdier et al., 2012; Bertiller and Ares, 2008) as:

$$Cwt = \sum_{i=1}^{s} p_i * trait_i$$

where Cwt is the weighted mean of the trait (t),  $p_i$  is the relative cover (proportion) of species i in the community (C), trait $_i$  is the value of functional trait (t) of species (i), and S is the total number of species in the community.

$$\mathsf{Mwt} = \sum_{i=1}^{s} p_i * \mathsf{trait}_i$$

where Mwt is the weighted mean of the trait (t),  $p_i$  is the relative cover (proportion) of species i in the morphotype (M), trait $_i$  is the mean value of the functional trait (t) of species (i), and S is the number of species in the morphotype.

# 2.5. Data analysis

We analyzed the significance of differences in mean values of plant cover and functional traits (plant height, SLA and N concentration in green leaves) at the community and morphotype (evergreen tall shrubs, deciduous shrubs, dwarf shrubs, perennial herbs, perennial grasses) levels between sites (low and high grazing disturbance) within each area (La Elvira and La Esperanza) by ANOVA. In those cases in which assumptions of ANOVA were not met, variables were logarithmic transformed (Sokal and Rohlf, 1981). Fisher Least Significant Difference was used for multiple comparisons. We use the log response ratio proposed by Niu et al. (2010) to quantify the changes in abundance and functional traits by plant morphotype (MC), and species (SC) in relation to grazing disturbance: MC or SC = log(H/L) where H and L were the mean relative cover or mean values of plant functional traits of morphotypes or species at sites with high and low grazing disturbance, respectively. Thus, a positive MC or SC value indicates that grazing disturbance led to increased relative cover or mean value of a plant functional trait of a given morphotype or species.

#### 3. Results

# 3.1. Indexes of grazing disturbance

Faeces count was higher and soil organic carbon lower at sites with high than low grazing disturbance at both La Elvira and La Esperanza areas (Table 1).

#### 3.2. Functional traits of plant morphotypes (Mt)

Mean values of functional traits (plant height, SLA and N concentration in green leaves) of plant morphotypes did not vary (p>0.05) between sites with different grazing disturbance at both La Elvira and La Esperanza areas (Table 2).

# 3.3. Total plant cover and weighted means of functional traits at community level (Cwt)

Total plant cover was lower at sites with high than low grazing disturbance at La Elvira ( $F_{1,8}=6.93,\ p=0.04$ ) and La Esperanza ( $F_{1,8}=17.68,\ p<0.01,\ Fig.\ 1a$ ). Community weighted means (Cw) of plant height, SLA and N in green leaves did not vary between sites with high and low grazing disturbance at La Elvira ( $F_{1,8}=1.41,\ p=0.28;\ F_{1,8}=0.11,\ p=0.75;\ F_{1,8}=0.74,\ p=0.42,\ respectively$ ) and at La Esperanza ( $F_{1,8}=0.28,\ p=0.87;\ F_{1,8}=5.16,\ p=0.07;\ F_{1,8}=2.74,\ p=0.15,\ respectively$ ) (Fig. 1b-d, respectively).

# 3.4. Morphotype cover and weighted means of functional traits at morphotype level (Mwt)

The cover of evergreen tall shrubs and perennial grasses was higher at sites with low than high grazing disturbance, while the opposite occurred with dwarf shrubs cover at both areas (Fig. 2a). Morphotype weighted means (Mw) of plant height, SLA, and N concentration in green leaves decreased in perennial grasses while these traits increased in dwarf shrubs at sites with high grazing disturbance at both areas (Fig. 2b–d). Also, Mw of SLA decreased in evergreen tall shrubs with high grazing disturbance at La Esperanza (Fig. 2c).

# 3.5. Changes in plant cover and functional traits of morphotypes (MC) and species (SC) to grazing disturbance

The cover of perennial grasses, perennial herbs and evergreen tall shrubs decreased (negative values) with grazing disturbance while that of dwarf shrubs and deciduous shrubs morphotypes increased (positive values) with grazing disturbance (Fig. 3). Plant height of perennial grasses and evergreen tall shrubs did not change or increased at disturbed sites, while this trait decreased in the rest of morphotypes at disturbed sites (Fig. 3a). The SLA of plant morphotypes decreased at disturbed sites, except SLA of evergreen tall shrubs at La Elvira and of dwarf shrubs at La Esperanza (Fig. 3b). The N concentration in green leaves decreased in all morphotypes,

**Table 1**Mean number of faeces and mean soil organic carbon at sites with low and high grazing disturbance at each area (La Elvira and La Esperanza). Different lowercase letters indicate significant differences between sites at each area.

	Grazing disturbance	Faeces counts (faeces m <sup>-2</sup> )	Soil organic carbon (mg g <sup>-1</sup> )
La Elvira	Low	51.9 b	6.0 a
	High	176.0 a	3.9 b
La Esperanza	Low	21.1 b	6.6 a
	High	118.0 a	5.4 b

**Table 2**Mean values of plant height, specific leaf area (SLA), and N concentration in green leaves of each plant morphotype (Mt) at each site (low and high grazing disturbance) and area (La Elvira and La Esperanza).

Morphotype	Grazing disturbance	Plant height (cm)	$SLA (mm^2 mg^{-1})$	N in green leaves (mg g <sup>-1</sup> )		
Evergreen tall shrubs						
La Elvira	Low	112.89	4.41	12.30		
	High	114.33	3.86	13.35		
La Esperanza	Low	92.31	4.44	16.23		
	High	107.00	5.35	16.85		
Deciduous shrubs						
La Elvira	Low	103.67	6.54	24.37		
	High	89.17	2.32	20.34		
La Esperanza	Low	109.92	15.35	28.02		
	High	102.67	14.62	26.90		
Dwarf shrubs						
La Elvira	Low	26.67	5.07	15.60		
	High	19.69	4.23	14.95		
La Esperanza	Low	_	_	_		
	High	11.09	7.85	12.84		
Perennial herbs						
La Elvira	Low	10.83	7.34	25.41		
	High	7.50	6.58	22.40		
La Esperanza	Low	_	_	_		
	High	_	_	_		
Perennial grasses						
La Elvira	Low	22.33	6.64	17.56		
	High	22.87	5.65	16.82		
La Esperanza	Low	27.19	5.37	16.38		
	High	20.64	4.54	17.86		

except for evergreen tall shrubs, at disturbed vegetation sites of both areas (Fig. 3c). In general, plant morphotypes that increased their covers at disturbed sites exhibited a wider range of variation in functional traits with grazing disturbance than the other of morphotypes (Fig. 3).

The range of variation in species attributes with grazing disturbance was wider in plant cover than in functional traits. In most of plant species, cover decreased at disturbed sites (negative values) and simultaneously plant height, SLA and N concentration in green leaves had either increased or decreased (Fig. 4a–c, respectively). Cover increased in few species at disturbed sites and SLA and the N concentration in green leaves decreased in most of these (Fig. 4b, c, respectively). The highest change in plant height and N concentration in green leaves was found in species whose cover was reduced by grazing disturbance. Additionally, the highest changes in SLA and N concentration in green leaves were found in species at La Elvira (Fig. 4b, c, respectively), while the highest change in plant height with grazing disturbance was observed in species at La Esperanza (Fig. 4a).

### 4. Discussion

Our results showed that cover was the plant trait most affected by grazing disturbance at community, morphotype, and species levels. Changes in plant cover were consistent with those reported for other arid and semiarid ecosystems (Bertiller and Bisigato, 1998; Bisigato and Bertiller, 1997; Schlesinger et al., 1990; Whitford, 2002). In contrast, canopy height, SLA, and N concentration in green leaves did not change with high grazing disturbance at the community level despite of these functional traits were affected in some morphotypes or species. Instead, the lack of differences in plant functional traits at the community level could be attributable to changes in the relative abundance of co-occurring morphotypes and species with different ecological strategies/functional traits in the vegetation assemblages (Westoby et al., 2002).

Consistently with other studies, our results indicated that changes in cover induced by high grazing disturbance differed among plant morphotypes (Díaz et al., 2007; Niu et al., 2010). In general, the cover of dwarf shrubs (with low N concentration in

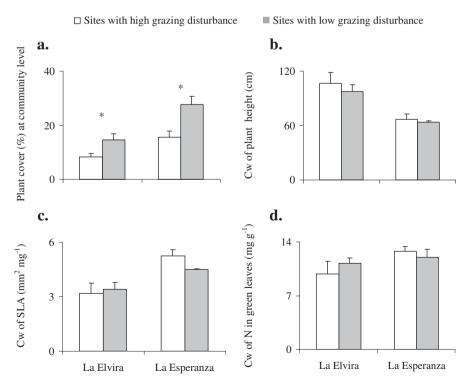


Fig. 1. (a). Total plant cover at community level, and community weighted mean (Cw) of (b). Plant height, (c). SLA, and (d). N concentration in green leaves at La Elvira and La Esperanza. Asterisks indicate significant differences between sites with low and high grazing disturbance at each area. Vertical lines indicate one standard error.

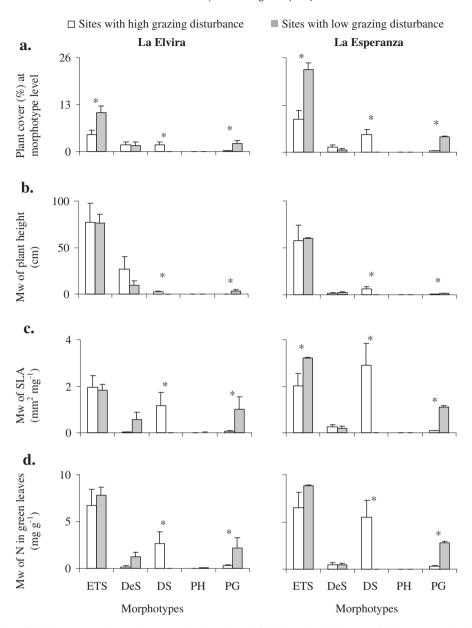


Fig. 2. Mean morphotype values of (a). Plant cover, and morphotype weighted mean (Mw) of (b). Plant height, (c). SLA and (d). N concentration in green leaves of plant morphotypes. Asterisks indicate significant differences between sites with low and high grazing disturbance at each morphotype. Vertical lines indicate one standard error. ETS: evergreen tall shrubs, DeS: deciduous shrubs, DS: dwarf shrubs, PH: perennial herbs, PG: perennial grasses.

green leaves and intermediate values of SLA) increased and that of perennial grasses and evergreen tall shrubs (with intermediate or low values of SLA and N concentration in green leaves) decreased under high grazing disturbance. Perennial grasses are generally highly preferred by herbivores (Baldi et al., 2004; Cingolani et al., 2005), and some evergreen tall shrubs (e.g. Atriplex lampa, Chuquiraga avellanedae, Chuquiraga erinacea var. hystrix, Schinus johnstonii) could also be alternatively grazed when grasses become scarce (Baldi et al., 2004; Bisigato and Bertiller, 1997). Accordingly, both plant morphotypes decreased in cover under high grazing disturbance (Cingolani et al., 2005; Landsberg et al., 2003). Decreasing cover of evergreen tall shrubs provides further evidence that grazing would favor short plants irrespective of grazing history (Díaz et al., 2007). However, cover reduction of decreaser morphotypes was not compensated by increaser ones. The cover of deciduous shrubs and perennial herbs was not affected by high grazing disturbance. In the case of deciduous shrubs, this probably

occurred because they exhibit structural defences such as thorny stems protecting short lived leaves with high N concentration from grazers (Hartley and Jones, 1998; Moreno et al., 2010; Pérez-Harguindeguy et al., 2003; Sternberg et al., 2000). Perennial herbs, with low chemical and physical defences, could escape from herbivore damage since they usually grow associated with well-defended shrub canopies (Callaway et al., 2005; Moreno and Bertiller, 2012; Rebollo et al., 2002).

Our findings also showed changes in functional traits within morphotypes. Perennial grass canopy had lower cover and lower SLA and N concentration in green leaves at sites with high than low grazing disturbance in both areas evidencing that grazing would promote plants with dense leaves and low N concentration in tissues (Díaz et al., 2007; Lambers et al., 2000). In contrast, dwarf shrub canopy was taller and exhibited higher values of SLA and N concentration in green leaves at sites with high than low grazing disturbance. This could be attributed to a large proportion of

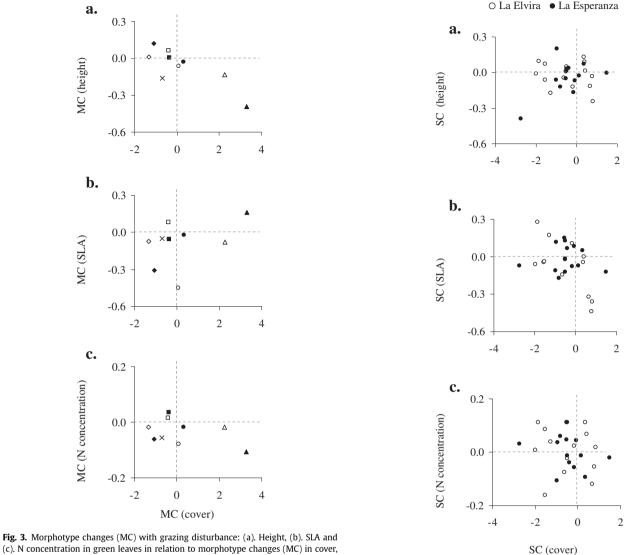


Fig. 3. Morphotype changes (MC) with grazing disturbance: (a). Height, (b). SIA and (c). N concentration in green leaves in relation to morphotype changes (MC) in cover, at La Elvira and La Esperanza. Evergreen tall shrubs at La Elvira ( $\square$ ) and La Esperanza ( $\blacksquare$ ), deciduous shrubs at La Elvira ( $\bigcirc$ ) and La Esperanza ( $\blacksquare$ ), dwarf shrubs at La Elvira ( $\triangle$ ) and La Esperanza ( $\blacksquare$ ), perennial herbs at La Elvira ( $\triangleright$ ), and perennial grasses at La Elvira ( $\triangleright$ ) and La Esperanza ( $\blacksquare$ ).

**Fig. 4.** Species changes (SC) with grazing disturbance: (a). Height, (b). SLA and (c). N concentration in green leaves in relation to species changes (SC) in cover at La Elvira  $(\bigcirc)$  and La Esperanza  $(\bigcirc)$ .

juvenile dwarf shrubs by colonization of denuded areas mostly by new dwarf shrub species. Juvenile plants could have higher SLA and N concentration in green leaves than adult plants (Coley and Barone, 1996; Hilli et al., 2008).

The range of response ratios of species plant cover (Niu et al., 2010) to high grazing disturbance varied from negative (SC = -2.73) to positive (SC = 1.48) values as was found in several studies (e.g. Carrera and Bertiller, 2013; Carrera et al., 2008; Golodets et al., 2009; Jaurena et al., 2012). However, the negative responses were higher and the positive responses were lower than those reported for plant species of other rangeland ecosystems (SC values ranging from – 1.95 to 2.37 from Jaurena et al., 2012; Niu et al., 2010). These might indicate that the ecosystems of the Patagonian Monte are more prone to wind and water soil erosion than other arid ecosystems of the world (Turnbull et al., 2012). We also found new evidence that species could respond to high grazing disturbance adjusting their functional traits such as height and SLA. Response ratios of the traits to high grazing disturbance ranged from -0.39 to 0.20 in plant height and from -0.44 to 0.28 in SLA. The negative responses found in our study were lower in height and higher in SLA while the positive responses were higher in height and lower in SLA than those reported for plant species of other rangeland ecosystems (-1.66 to 0.04 in height and -0.33 to 0.48 in SLA taken fromGolodets et al., 2009; Niu et al., 2010). There is less information about changes in N concentration in green leaves induced by high grazing disturbance than in other plant functional traits. Plant response ratios of N concentration in green leaves to high grazing disturbance (SC values ranging from -0.16 to 0.11) were within the range reported for plant species of other ecosystems submitted to grazing (SC values ranging from -0.18 to 0.18) (Sternberg et al., 2006; Zheng et al., 2011). In some plant species, decreasing cover was associated with decreasing plant height, SLA and N concentration in green leaves. Decreasing plant height and SLA have been proposed as effective ecological strategies for escaping from grazers and increasing resistance to grazing in rangelands with low competition for light and continuous disturbance (Díaz et al., 2001, 2007; Evju et al., 2009; Falster and Westoby, 2003; Golodets et al., 2009; McIntyre and Lavorel, 2007; Shipley, 1995; van der Wal et al., 2000). However, decreasing cover in other species was associated with increasing plant height, SLA and N concentration in green leaves. This could result from compensatory growth after removal of photosythetically active tissues by grazers (McNaughton, 1979). Also, high availability of soil resources and light in disturbed sites might favor shoot regrowth and consequently the increase in plant height, SLA and N concentration in green leaves (Zheng et al., 2011). Opposite grazing responses of plant species could be attributable to differences in phenotypic plasticity of plant traits (Jaurena et al., 2012). Plasticity of plant functional traits could prevent changes in plant abundance as a response to disturbances (Evju et al., 2009; Lennartsson et al., 1997).

Plant functional traits such as those evaluated in ours study are usually used to predict species responses to grazing disturbance and to link these changes in plant trait assessed at the species level to community or ecosystem function in subhumid grasslands of Argentina, Israel, and other parts of the world (Díaz et al., 2007; Jaurena et al., 2012; McIntyre, 2008; Westoby, 1998). However, our results showed that changes induced by high grazing disturbance at species and morphotype levels were counteracted at community level as was reported for Australian semi-arid and arid shrublands (Vesk et al., 2004). Accordingly, the prediction of grazing responses with single traits assessed at the species level is less feasible in semi-arid and arid rangelands, which are characterized by a patchy structure of vegetation and high diversity of morphotypes, compared with subhumid grasslands that have structurally simple and continuous plant covers (Vesk et al., 2004).

In conclusion, our findings showed that high grazing disturbance primarily affected plant cover at community, morphotype and species levels and that the changes in plant functional traits found at morphotype and species levels were counteracted at community level. These in turn would indicate that changes induced by high grazing disturbance would not affect canopy functioning and resistance against herbivory.

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### Appendix A. Supplementary Material

Supplementary data related to this article can be found online at http://dx.doi.org/10.1016/j.actao.2013.06.002.

# References

- Aerts, R., Chapin, F.S., 2000. The mineral nutrition of wild plants revisited: a reevaluation of processes and patterns. Adv. Ecol. Res. 30, 1–67.
- Ares, J.O., Bertiller, M.B., Bisigato, A.J., 2003. Modeling and measurement of structural changes at a landscape scale in dryland areas. Environ. Model. Assess. 8, 1–13
- Baldi, R., Pelliza-Sbriller, A., Elston, D., Albon, S.D., 2004. High potential for competition between guanacos and sheep in Patagonia. J. Wild Manage. 68, 924–938
- Barros, V., Rivero, M., 1982. Mapas de probabilidad de precipitación de la Provincia del Chubut. Monografía 54. Centro Nacional Patagónico, Puerto Madryn, Chubut. AR.
- Bernard-Verdier, M., Nava, M.L., Fayolle, A., Garnier, E., 2012. Community assembly along a soil depth gradient: contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. J. Ecol. 100, 1422–1433.
- Bertiller, M.B., Ares, J.O., 2008. Sheep spatial grazing strategies at the arid Patagonian Monte, Argentina. Range. Ecol. Manage 61, 38–47.

- Bertiller, M.B., Ares, J.O., Bisigato, A.J., 2002. Multi-scale indicators of land degradation in the Patagonian Monte, Argentina. J. Environ. Manage. 30, 704–715.
- Bertiller, M.B., Beeskow, A.M., Coronato, F.R., 1991. Seasonal environmental variation and plant phenology in arid Patagonia (Argentina). J. Arid Environ. 21, 1—11.
- Bertiller, M.B., Bisigato, A.J., 1998. Vegetation dynamics under grazing disturbance. The state-and-transition model for the Patagonian steppes. Ecol. Austral 8, 191–199.
- Bertiller, M.B., Mazzarino, M.J., Carrera, A.L., Dihel, P., Satti, P., Gobbi, M., Sain, C., 2006. Leaf strategies and soil N across a regional humidity gradient in Patagonia Oecologia 148, 612–624
- Bisigato, A.J., Bertiller, M.B., 1997. Grazing effects on patchy dryland vegetation in northern Patagonia. J. Arid Environ. 36, 639–653.
- Bisigato, A.J., Bertiller, M.B., Ares, J.O., Pazos, G.E., 2005. Effect of grazing on plant patterns in arid ecosystems of Patagonian Monte. Ecography 28, 561–572.
- Briske, D.D., 1996. Strategies of plant survival in grazed systems: a functional interpretation. In: Hodgson, J., Illius, A.W. (Eds.), The Ecology and Management of Grazing Systems. CAB International, Wallingford, pp. 33–67.
- Callaway, R.M., Kikodze, D., Chiboshvili, M., Khetsuriani, L., 2005. Unpalatable plants protect neighbors from grazing and increase plant community diversity. Ecology 86, 1856–1862.
- Campanella, M.V., Bertiller, M.B., 2008. Plant phenology, leaf traits, and leaf litterfall of contrasting life forms in arid Patagonian Monte, Argentina. J. Veg. Sci. 19, 75–85.
- Carrera, A., Bertiller, M., Larreguy, C., 2008. Leaf litterfall, fine-root production, and decomposition in shrublands with different canopy structure induced by grazing in the Patagonian Monte, Argentina. Plant Soil 311, 39–50.
- Carrera, A., Mazzarino, M., Bertiller, M., del Valle, H., Martinez-Carretero, E., 2009. Plant impacts on nitrogen and carbon cycling in the Monte Phytogeographical Province, Argentina. J. Arid Environ. 73, 192–201.
- Carrera, A., Bertiller, M., 2013. Combined effects of litter and microsite on decomposition process in arid rangelands. J. Environ. Manage. 114, 505-511.
- Cingolani, A.N., Posse, G., Collantes, M.B., 2005. Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands. I. Appl. Ecol. 42. 50–59.
- Coley, P.D., Barone, J.A., 1996. Herbivory and plant defenses in tropical forests. Annu. Rev. Ecol. Syst. 27, 305–335.
- Coombs, J., Hind, G., Leegood, R.C., Tienszen, L.L., Vonshsk, A., 1985. Analytical techniques. In: Coombs, J., Hall, D.O., Long, S.P., Scurlock, J.M.O. (Eds.), (edwarf Shrubs) Techniques in Bioproductivity and Photosyntesis. Pergamon Press, New York, pp. 219–228.
- Cruz, P., De Cuadros, F.L.F., Theau, J.P., Frizzo, A., Jouany, C., Duru, M., Carvalho, P.C.F., 2010. Leaf traits as functional descriptors of the intensity of continuous grazing in native grasslands in the South of Brazil. Range. Ecol. Manage. 63, 350–358.
- Day, T.A., Detling, J.K., 1990. Grassland patch dynamics and herbivore grazing preference following urine deposition. Ecology 71, 180–188.
- Defossé, G.E., Bertiller, M.B., Ares, J.O., 1990. Above-ground phytomass dynamics in grassland steppe of Patagonia, Argentina. J. Range Manage. 43, 157–160.
- del Valle, H.F., 1998. Patagonian soils: a regional synthesis. Ecol. Austral 8, 103—123. Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P., Zak, M.R., 2004. The plant traits that drive ecosystems: evidence from three continents. J. Veg. Sci. 15, 295—304.
- Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H., Campbell, B.D., 2007. Plant trait responses to grazing a global synthesis. Glob. Change Biol. 13, 313—341.
- Díaz, S., Noy-Meir, I., Cabido, M., 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? J. Appl. Ecol. 38, 497–508.
- Evju, M., Austrheim, G., Halvorsen, R., Mysterud, A., 2009. Grazing responses in herbs in relation to herbivore selectivity and plant traits in an alpine ecosystem. Oecologia 161, 77–85.
- Falster, D., Westoby, M., 2003. Plant height and evolutionary games. Trends Ecol. Evol. 18, 337–343.
- Golodets, C., Sternberg, M., Kigel, J., 2009. A community-level test of the leaf-heightseed ecology strategy écheme in relation to grazing conditions. J. Veg. Sci. 20, 392–402
- Hartley, S.E., Jones, C.G., 1998. Plant chemistry and herbivory, or why the world is green. In: Crawley, M.J. (Ed.), Plant Ecology. Blackwell Science, Oxford, pp. 284–324.
- Hilli, S., Stark, S., Derome, J., 2008. Water-extractable organic compounds in different components of the litter layer of boreal coniferous forest soils along a climatic gradient. Boreal Env. Res. 13, 92–106.
- Huntly, N., 1991. Herbivores and the dynamic of communities and ecosystems. Annu. Rev. Ecol. Syst. 22, 477–503.
- Instituto Nacional de Tecnologia Agropecuaria, 1990. Atlas de suelos de la República Argentina. Band 1. Project PNUD-Argentina 05-019, Bs As, Argentina.
- Jaurena, M., Lezama, F., Cruz, P., 2012. Perennial grasses traits as functional markers of grazing intensity in basaltic grasslands of Uruguay. Chil. J. Agr. Res. 72, 541–549.
- Lambers, H., Chapin, F.S., Pons, T., 2000. Mineral nutrition. In: Lambers, H., Chapin, F.S., Pons, T. (Eds.), Plant Physiological Ecology. Springer-Verlag, New York, pp. 239–298.

- Landsberg, J., James, C.D., Morton, S.R., Muller, W.J., Stol, J., 2003. Abundance and composition of plant species along grazing gradients in Australian rangelands. J. Appl. Ecol. 40, 1008-1024.
- Larreguy, C., Carrera, A.L., Bertiller, M.B., 2012. Production and turnover rates of shallow fine roots in rangelands of the Patagonian Monte, Argentina. Ecol. Res.
- Laughlin, D.C., Leppert, J.J., Moore, M.M., 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.
- Lennartsson, T., Tuomi, J., Nilsson, P., 1997. Evidence for an evolutionary history of overcompensation in the grassland biennial Gentianella campestris (Gentianaceae). Am. Nat. 149, 1147-1155.
- León, R.J.C., Bran, D., Collantes, M., Paruelo, J.M., Soriano, A., 1998. Grandes unidades de vegetación de la Patagonia extra andina. Ecol. Austral 8, 125–144.
- McIntyre, S., 2008. The role of plant leaf attributes in linking land use to ecosystem function in temperate grassy vegetation, Agr. Ecosyst, Environ, 128, 251–258.
- McIntyre, S., Lavorel, S., 2007. A conceptual model of land use effects on the structure and function of herbaceous vegetation. Agric, Ecosyst, Environ, 119, 11–21.
- McNaughton, S.J., 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. Am. Nat. 113, 691–703.
- Milchunas, D.G., Lauenroth, W.K., 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecol. Monogr. 63, 327-366.
- Milner, C., Hughes, R.E., 1970. Methods for the Measurement of the Primary Production, IBP Handbook N 6, Blackwell Sci. Pub. Co. Oxford.
- Moreno, L., Bertiller, M.B., 2012. Variation of morphological and chemical traits of perennial grasses in arid ecosystems. Are these patterns influenced by the relative abundance of shrubs? Acta Oecol. 41, 39-45.
- Moreno, L., Bertiller, M.B., Carrera, A.L., 2010. Changes in traits of shrub canopies across an aridity gradient in northern Patagonia, Argentina. Basic Appl. Ecol. 11, 693-701
- Mueller-Dombois, D., Ellenberg, H., 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, New York.
- Nelson, D.W., Sommers, L.E., 1982. Total carbon, organic carbon and organic matter. In: Page, A.L., Miller, D.H., Keeney, D.R. (Eds.), Methods of Soil Analysis, ASA. SSSA, Madison, Wis, pp. 539-579.
- Niu, K., Zhang, S., Zhao, B., Du, G., 2010. Linking grazing response of species abundance to functional traits in the Tibetan alpine meadow. Plant Soil 330, 215-223
- Noy Meir, I., 1973. Desert ecosystems: environment and producers. Annu. Rev. Ecol. Syst. 4, 25-52.
- Pazos, G.E., Bisigato, A.J., Bertiller, M.B., 2007. Abundance and spatial patterning of coexisting perennial grasses in grazed shrublands of the Patagonian Monte. J. Arid Environ. 70, 316-328.
- Pérez-Harguindeguy, N., Díaz, S., Cabido, M., 2003. Leaf traits and herbivore selection in the field and in cafeteria experiments. Aust. Ecol. 28, 642-650.
- Prieto, L.H., Bertiller, M.B., Carrera, A.L., Olivera, N.L., 2011. Soil enzyme and microbial activities in a grazing ecosystem of Patagonian Monte, Argentina. Geoderma 162, 281-287.

- Rebollo, S., Milchunas, D.G., Noy-Meyr, I., Chapman, P.L., 2002. The role of spiny plant refuge in structuring grazed shortgrass steppe plant communities. Oikos 98, 53-64.
- Reynolds, H.L., Hungate, B.A., Chapin, F.S., D'Antonio, C.M., 1997. Soil heterogeneity and plant competition in an annual grassland. Ecology 78, 2076-2090.
- Rossi, M.J., Ares, J.O., 2012. Depression storage and infiltration effects on overland flow depth-velocity-friction at desert conditions: field plot results and model. Hydrol. Earth Syst. Sci. 16, 3293-3307.
- Sala, O.E., Golluscio, R.A., Lauenroth, W.K., Soriano, A., 1989, Resource partitioning between shrubs and grasses in the Patagonian steppe. Oecologia 81, 501–505.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A., Whitford, W.G., 1990. Biological feedbacks in global desertification, Science 247, 1043-1048.
- Shipley, B., 1995. Structured interspecific determinants of specific leaf area in 34 species of herbaceous angiosperms, Funct, Ecol. 13, 312-319.
- Soil Survey Staff, 1998. Keys to Soil Taxonomy. USDA, Washington.
- Sokal, R.R., Rohlf, F.J., 1981. Biometry. Freeman, San Francisco. Sternberg, M., Gishri, N., Mabjeesh, S.J., 2006. Effects of grazing on *Bituminaria* bituminosa (L.) Stirton: a potential forage crop in Mediterranean grasslands. J. Agron. Crop Sci. 192, 399–407.
- Sternberg, M., Gutman, M., Perevolotsky, A., Ungar, E., Kigel, J., 2000. Vegetation response to grazing management in a Mediterranean herbaceous community: a functional group approach. J. Appl. Ecol. 37, 224-237.
- Turnbull, L., Wilcox, B.P., Belnap, J., Ravi, S., D'Odorico, P., Childers, D., Gwenzi, W., Okin, G., Wainwright, J., Caylor, K.K., Sankey, T., 2012. Understanding the role of ecohydrological feedbacks in ecosystem state change in drylands. Ecohydrology 5 174-183
- van der Wal, R., Egas, M., Van Der Veen, A., Bakker, J., 2000. Effects of resource competition and herbivory on plant performance along a natural productivity gradient. J. Ecol. 88, 317-330.
- Vesk, P.A., Westoby, M., 2001. Predicting plant species' responses to grazing. J. Appl. Ecol. 38, 897-909.
- 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.
- Westoby, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199, 213-227.
- Westoby, M., Eldridge, D., Freudenberger, D., 1999. The LHS strategy scheme in relation to grazing and fire. Proceedings of the International Rangeland Congress, Townsville. Australia 2, 893-896.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright, I.J., 2002. Plant ecological strategies: some leading dimensions of variation between species. Ann. Rev. Ecol. Syst. 33, 125-159.
- Whitford, W., 2002. Decomposition and nutrient cycling. In: Whitford, W. (Ed.), Ecology of Desert Systems. Academic Press, San Diego, pp. 235-274.
- Zheng, S.X., Lan, Z.C., Li, W.H., Shao, R.X., Shan, Y.M., Wan, H.W., Taube, F., Bai, Y.F., 2011. Differential responses of plant functional trait to grazing between two contrasting dominant C3 and C4 species in a typical steppe of Inner Mongolia, China. Plant Soil 340, 141-155.