

What causes changes in plant litter quality and quantity as consequence of grazing in the Patagonian Monte: Plant cover reduction or changes in species composition?

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Abstract In Patagonian Monte, as in other arid ecosystems, grazing has triggered changes in vegetation and soil such as plant cover reduction, changes in species composition and soil nutrient losses. Several mechanisms were proposed interconnecting these changes, but evidence supporting them is very scarce. On the basis of published data concerning plant cover by species along grazing gradients and leaf litter production of dominant species, we estimated the effects of grazing on a – quality (N, soluble phenolics and lignin concentrations) and b – quantity (leaf litterfall (LLF) and inputs of nitrogen, soluble phenolics and lignin to the soil) of leaf litter in the Patagonian Monte, discriminating the effect of plant cover reduction from that of species composition. We also evaluated the relationship between senesced leaves traits and the response of species to grazing (i.e. their relative change in plant cover). Grazing causes a reduction in LLF and in the inputs of nitrogen, soluble phenolics and lignin to the soil. In the case of LLF, this reduction was not only a result of the decrease in plant cover but also due to changes in species composition. In contrast, our results showed that the reduction in nitrogen, soluble phenolics and lignin inputs to the soil by LLF is only a consequence of plant cover reduction. Additionally, litter quality was affected through increasing concentration of N and secondary compounds (soluble phenolics and lignin). N and soluble phenolics concentration on senesced leaves were positively related to the response of species to grazing, suggesting that other factors instead of N are relevant to sheep foraging decisions.

Key words: leaf litter, N concentration, secondary compounds, soil resource, vegetation change.

INTRODUCTION

Grazing by domestic herbivores has both direct and indirect effects on ecosystems (Harrison & Bardgett 2008). Plant consumption, trampling, urination and defecation are the main direct effects, which can affect vegetation and soil. Indirect effects are mediated by feedbacks that mostly occur between plants and decomposers, affecting rates of nutrient cycling (Bardgett *et al.* 1998).

In arid environments, negative-feedback effects prevail and they were ascribed to plant cover reduction and species replacements, which can affect the quality and/or quantity of plant litter (Augustine & McNaughton 2006). Plant cover reduction can cause a decrease in litterfall, while species replacement can reduce the quantity and/or quality of litter. This is due to the fact that unpalatable species (i.e. species whose abundance increases as a consequence of grazing) produce less litter with larger amounts of secondary compounds compared with palatable species (i.e. species whose

abundance decreases as a consequence of grazing) (Cornelissen 1996; Wardle *et al.* 2004). Secondary compounds (e.g. phenolics, cellulose and lignin) slow down litter decomposition and nutrient mineralization in soil because of their inhibitory effects on micro organisms and/or retarding of microbial breakdown of organic matter (Aerts & Chapin 2000; Hättenschwiler & Vitousek 2000). In addition, it was proposed that these effects on soil nutrients favour unpalatable species because of their lower growth rates and reduced nutrient requirements (Wardle *et al.* 2004). Although the mechanisms involved in this feedback were proposed in the literature concerning grazing effects in arid ecosystems (Ritchie *et al.* 1998), several authors have highlighted that published evidence quantifying and understanding the causes of indirect effects of grazing on soil resources is surprisingly scarce (Bardgett *et al.* 1998; Semmartin *et al.* 2004).

Patagonian Monte ecosystems have been grazed by sheep since early 20th century (Ares *et al.* 1990). As in other arid ecosystems, this disturbance has triggered changes in vegetation (Bisigato & Bertiller 1997; Bertiller *et al.* 2002; Bisigato *et al.* 2005; Rodríguez *et al.* 2007) and soils (Carrera *et al.* 2007; Bisigato *et al.*

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2008). Plant cover decreases by 62% (Bisigato *et al.* 2005), grasses are partially replaced by shrubs (Bisigato & Bertiller 1997) and 17% of organic matter and nitrogen are lost from top soil under high-intensity grazing (Bisigato *et al.* 2008). Several authors have proposed that the effects of grazing on vegetation and soil are interconnected via plant litter (Bisigato & Bertiller 1997; Carrera *et al.* 2005; Vargas *et al.* 2006), but grazing effects on plant litter were only recently measured in this system (Carrera *et al.* 2008). That study found that grazing affects both quality and quantity of leaf litter. Leaf litterfall (LLF) is reduced by 39%, whereas the concentration of N, soluble phenolics and lignin in LLF increases by 28%, 35% and 28%, respectively. Because plant cover and species composition differed between the grazed and the ungrazed areas, these results were ascribed to changes in plant cover and species composition. However, the relative importance of these factors (i.e. plant cover and species composition) is unknown. In this study, we estimated the relative importance of plant cover reduction and changes in species composition on quality (N, soluble phenolics and lignin concentrations) and quantity (LLF and inputs of nitrogen, soluble phenolics and lignin to the soil) of leaf litter in the Patagonian Monte. We also evaluated the relationship between senesced leaves traits and the response of species to grazing (i.e. their relative change in plant cover (RCPC)).

METHOD AND MATERIALS

General approach

On the basis of published data regarding plant cover by species along grazing gradients and leaf litter production of dominant species, we estimated mean input of LLF, N, lignin and soluble phenolics to the soil, and mean N, lignin and soluble phenolics concentrations in LLF. These means were calculated as weighted averages, weighted by plant cover.

Study sites

All data included in this analysis were obtained from Estancia San Luis (42°38' 51" S, 65°23' 03" W), an area representative of Patagonian Monte ecosystems (Bisigato & Bertiller 1997). Vegetation has a random patchy structure covering between 15% and 60% of the soil. *Larrea divaricata* Cav., *Chuquiraga hystrix* D. Don., *Lycium chilense* Miers ex Bert. and *Atriplex lampa* Gill. ex Moq. dominate the upper layer (1–2 m), while the lower layer (<1 m) is mainly composed by perennial grasses (*Stipa tenuis* Phil., *S. speciosa* Trin. & Rupr. and *Poa ligularis* Nees ex Steud.). The general relief is very flat and soils are a complex of typic paleorthid and typic calciorthid (Bisigato & Bertiller 1997).

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Plant cover data

Plant cover data were obtained from Bisigato and Bertiller (1997), Bisigato (2000) and Bisigato *et al.* (2005). These studies reported plant cover measurements carried out along six grazing gradients located in paddocks with the usual stocking rate in the area (0.11–0.14 sheep ha⁻¹ throughout the year). In this study, we incorporated the ends of these grazing gradients, which were located at 300–1200 m (high grazing pressure = H) and 3000–4200 m (low grazing pressure = L) from the unique permanent watering point in each paddock. Thus, this study encompassed six low grazing pressure and six high grazing pressure sites.

Annual LLF by species data

Annual LLF data of 11 dominant species (*Atriplex lampa*, *Chuquiraga avellanadae* L., *Chuquiraga hystrix*, *Larrea divaricata*, *Larrea nitida* Cav. (evergreen shrubs), *Bougainvillea spinosa* (Cav) Heim., *Lycium chilense*, *Prosopis alpataco* Phil. (deciduous shrubs), *Poa ligularis*, *Stipa tenuis*, *Stipa speciosa* (perennial grasses)) were obtained from Campanella and Bertiller (2008). In that study, the annual LLF was determined using litter traps; LLF was monthly removed from the traps, oven-dried at 60°C for 48 h and weighed. Chemical attributes of senesced leaves (N, soluble phenolics and lignin concentrations) were obtained from Carrera *et al.* (2005), Vargas *et al.* (2006) and Campanella and Bertiller (2008). In these studies, N concentration was analysed by semi-micro Kjeldahl (Coombs *et al.* 1985), lignin concentration by the Van Soest (1963) procedure and soluble phenolics concentration by the Folin-Ciocalteu method (Waterman & Mole 1994). When more than one article reported chemical attributes of a particular species, we averaged all these values.

Calculations

For each paddock and grazing pressure (g), the mean nitrogen concentration in LLF was calculated as:

$$m[N]LLF_g = \left(\sum_{i=1}^s PC_{ig} LLF_i [N]_i \right) \left(\sum_{i=1}^s PC_{ig} LLF_i \right)^{-1}$$

where g = grazing pressure, s = species with LLF data, $[N]_i$ = nitrogen concentration in senesced leaves for species with LLF data (mg g⁻¹).

Homologous calculations were made to estimate mean soluble phenolics LLF and lignin LLF concentrations.

The mean LLF (mLLF) was estimated as the sum of each species' cover multiplied by each species' annual LLF weighted to total plant cover:

$$mLLF_g = \left(\sum_{i=1}^s PC_{ig} LLF_i \right) TPC_g \left(\sum_{i=1}^s PC_{ig} \right)^{-1}$$

where TPC = total plant cover (including species with and without LLF data). The term $TPC_g \left(\sum_{i=1}^s PC_{ig} \right)^{-1}$ is a fraction used to scale up from species with known LLF data only, to the whole community, including species with unknown LLF data.

Similarly, the mean nitrogen input to the soil by LLF (mNLF) was estimated as follows:

$$mNLF_g = \left(\sum_{i=1}^s PC_{ig} LLF_i [N]_i \right) TPC_g \left(\sum_{i=1}^s PC_{ig} \right)^{-1}$$

Analogous calculations were made to estimate mean soluble phenolics inputs to the soil by LLF (mSPLF) and lignin inputs to the soil by LLF (mLigLF).

To discriminate the effect of plant cover reduction from that of species composition, we also estimated mLLF, mNLF, mSPLF and mLigLF on two hypothetical conditions for each paddock ($n = 6$). The first condition (LH) corresponds to a site with the relative species composition of the low grazing pressure site in that paddock (L), but the total plant cover of the high grazing pressure site in that paddock (H). The second condition (HL) corresponds to the inverse situation.

We also calculated the RCPC of species with chemical data (s) as:

$$RCPC_i = (PC_{ih} TPC_i^{-1}) (PC_{il} TPC_i^{-1})^{-1}$$

where l and h indicate low and high grazing pressure sites, respectively. This index takes values lower than 1 when the relative species cover decreases with grazing (palatable species), whereas values greater than 1 indicate the increase of relative species cover with grazing (unpalatable species).

Data analysis

As our data encompass six grazing gradients containing a low grazing and a high grazing pressure site within each of six paddocks, we first included the paddocks as blocks in the analysis. However, block effects were not significant. In consequence, paddock was discarded as a factor in all analysis. The differences between sites (low/high grazing pressure) in the mean nitrogen, soluble phenolics and lignin concentrations in LLF were evaluated by one-way ANOVA. The effects of plant cover reduction and species composition on mLLF, mNLF, mSPLF and mLigLF were evaluated by two-way ANOVA. We organized the data into a single 11 species \times 3 senesced leaf traits matrix and submitted it to a Principal Component Analysis (PCA) based on the correlation matrix of variables. The eigenvector scores on PCA axis 1 were then correlated against RCPC and original data (senesced leaves traits).

RESULTS

Quality of plant litter

Nitrogen, soluble phenolics and lignin concentrations in LLF were higher in high grazing sites ($F_{1,10} = 6.856$, $P = 0.026$; $F_{1,10} = 11.878$, $P = 0.006$; $F_{1,10} = 8.825$, $P = 0.014$, respectively) (Fig. 1).

Quantity of LLF

Mean LLF was affected by changes in plant cover and species composition ($F_{1,20} = 9.782$, $P = 0.005$; $F_{1,20} =$

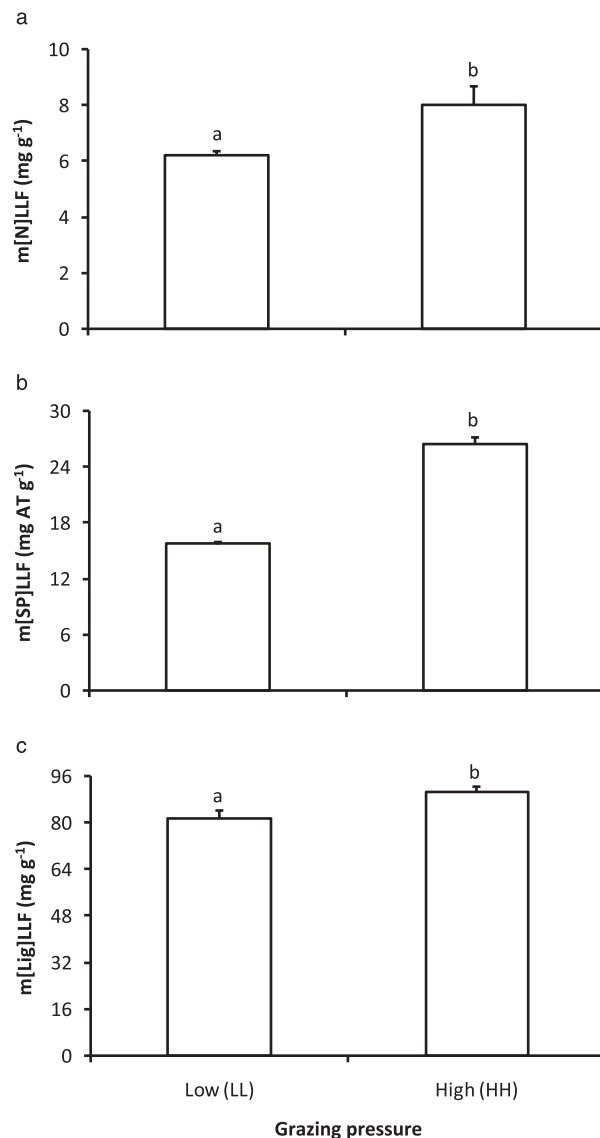


Fig. 1. Mean \pm 1 standard error of nitrogen (m[N]LLF) (a), soluble phenolics (m[SP]LLF) (b) and lignin (m[Lig]LLF) (c) concentrations in leaf litterfall on sites with low and high grazing pressure. Different lowercase letters indicate significant ($P < 0.05$) differences among sites.

6.286, $P = 0.021$, respectively) (Fig. 2a). However, mLLF was not significantly affected by plant cover–species composition interaction ($F_{1,20} = 0.570$; $P = 0.459$). Low grazing pressure sites showed the highest mLLF, while high grazing pressure sites exhibited the lowest mLLF. The hypothetical conditions (LH and HL) showed intermediate values of mLLF.

On the other hand, changes in mNLF, mSPLF and mLigLF inputs to the soil by LLF only resulted from plant cover changes ($F_{1,20} = 11.355$, $P = 0.003$; $F_{1,20} = 5.810$, $P = 0.026$; $F_{1,20} = 8.049$, $P = 0.010$, respectively) (Fig. 2b–d). These variables were lower in sites with low plant cover (i.e. high grazing pressure

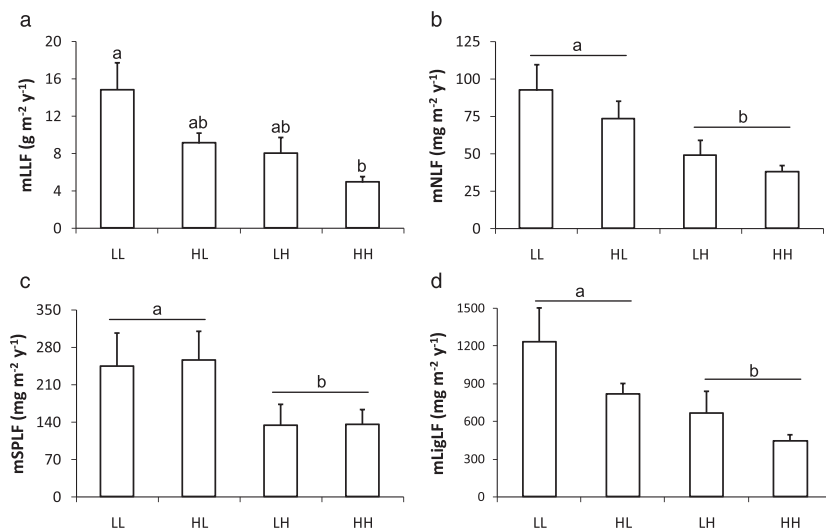


Fig. 2. Estimated mean leaf litterfall (mLLF) (a), and estimated mean inputs of nitrogen (mNLF) (b), soluble phenolics (mSPLF) (c), and lignin (mLigLF) (d) to the soil by leaf litterfall for situations with species composition and plant cover of low (L) or high (H) grazing pressure. Different letters above bars indicate significant differences among treatments (a) or plant cover levels (b–d) based on Tukey multiple-comparisons tests.

sites). The effects of species composition ($F_{1,20} = 1.653$, $P = 0.213$; $F_{1,20} = 0.021$, $P = 0.886$; $F_{1,20} = 3.708$, $P = 0.068$, respectively) and plant cover–species composition interaction ($F_{1,20} = 0.116$, $P = 0.737$; $F_{1,20} = 0.008$, $P = 0.930$; $F_{1,20} = 0.318$, $P = 0.579$, respectively) were not statistically significant.

Relationship between leaf chemistry and changes in plant cover

We found a positive relationship between the eigenvector scores on PCA first axis and RCPC of each species ($F_{1,9} = 12.964$, $P = 0.006$, Fig. 3a), showing a relationship between senesced leaf chemistry and the response of species to grazing (RCPC). Similarly, we found a positive relationship between the eigenvector scores on PCA first axis and N ($F_{1,9} = 14.549$, $P = 0.004$; Fig. 3b) and soluble phenolics concentrations in senesced leaves ($F_{1,9} = 10.733$, $P = 0.010$; Fig. 3c). In contrast, lignin concentration in senesced leaves was not related to the eigenvector scores on PCA first axis ($F_{1,9} = 1.795$, $P = 0.213$; Fig. 3d). Thus, the relative cover of those species whose senesced leaves show the highest concentrations of N and soluble phenolics increased with grazing, whereas the opposite occurred with those species showing low concentrations of those compounds in their senesced leaves.

DISCUSSION

Our results indicate that in more intensely grazed areas, there was a reduction in LLF and in the input of

nitrogen, soluble phenolics and lignin to the soil by LLF (Fig. 1). In the case of litterfall quantity, this reduction (from 14.83 to 4.88 $\text{g m}^{-2} \text{y}^{-1}$, Fig. 1a) was not only due to the decrease in plant cover (from 27.3 to 14.6%) but to changes in species composition as well. Species with the highest cover in lightly grazed sites, which also produce high litterfall, were among the species with the strongest reductions in plant cover as a consequence of grazing (data not shown). In contrast, our results suggest that the input of N, soluble phenolics and lignin to the soil by leaf litter was not affected by changes in species composition, but that they were significantly reduced by a decrease in plant cover; demonstrating that the increase in the concentration of N and secondary compounds related to changes in species composition in grazed areas did not compensate the reduction in LLF. In agreement with these results, decline in litterfall and/or nitrogen input as a consequence of grazing has been reported by other studies carried out in different ecosystems such as forests (McInnes *et al.* 1992; Smit & Kooijman 2001; Persson *et al.* 2005; Descheemaeker *et al.* 2006), grasslands (Potvin & Harrison 1984; Barger *et al.* 2004) and deserts (Jones 2000; Carrera *et al.* 2008).

In our study, litter quality was affected by grazing through increasing the concentration of nitrogen and secondary compounds (soluble phenolics and lignin). Several articles have reported changes in litter quality as a consequence of species replacements, which affects the concentration of nitrogen (Ritchie *et al.* 1998) and secondary compounds (Bardgett *et al.* 1998) in litterfall. However, N concentration in leaf litter is commonly reduced as a consequence of grazing (Ritchie *et al.* 1998; Smit & Kooijman 2001;

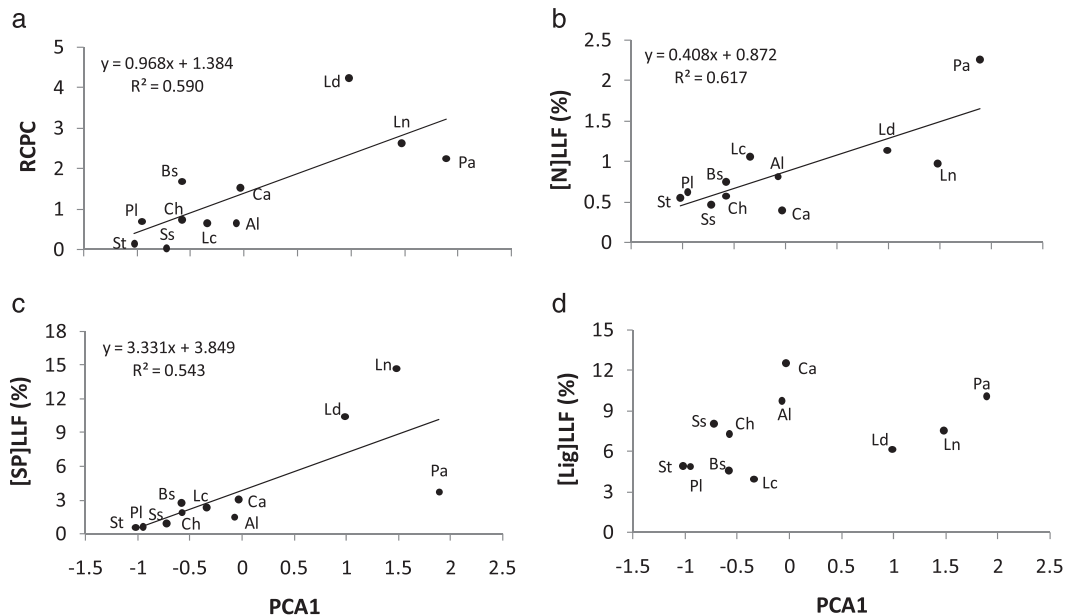


Fig. 3. Relationship between the eigenvector scores on Principal Component Analysis (PCA) axis 1 and relative change in plant cover (RCPC) (a), nitrogen ([N]LLF) (b), soluble phenolics ([SP]LLF) (c) and lignin ([Lig]LLF) (d) concentrations in leaf litterfall. Al, *Atriplex lampra*; Bs, *Bougainvillea spinosa*; Ca, *Chuquiraga avellaneda*; Ch, *Chuquiraga hystrix*; Lc, *Lycium chilense*; Ld, *Larrea divaricata*; Ln, *Larrea nitida*; Pa, *Prosopis alataco*; Pl, *Poa ligularis*; Ss, *Stipa speciosa*; St, *Stipa tenuis*.

Barger *et al.* 2004). On the contrary, and in agreement with our findings, a previous study carried out in the study area reported increased concentrations of N in leaf litter as a consequence of grazing (Carrera *et al.* 2008). A main explanation for this might be an increase in the relative contribution of unpalatable plants, with higher concentrations of these compounds in their senesced leaves (Fig. 3). These results, in accordance with Skarpe and Hester (2008), strongly suggest that herbivores avoid plant tissues rich in secondary compounds instead of having high N concentration, and indicate that other factors differing from [N] have a major influence on sheep grazing decisions (Bryant *et al.* 1991).

The higher concentrations of secondary compounds together with reduced inputs of litter in more intensely grazed areas probably retard decomposition and nutrient cycling. Studies carried out in other ecosystems worldwide (Melillo *et al.* 1982; Hättenschwiler & Vitousek 2000) and in the Patagonian Monte (Carrera *et al.* 2005; Vargas *et al.* 2006) have found that high phenolics and lignin contents strongly decelerate decomposition rates. Different mechanisms were proposed to explain this decelerating effect. For example, phenolics often have inhibitory effects on microbial activity and also bind nitrogen in tannin-protein complexes (Bernays *et al.* 1989). Similarly, lignin (a high molecular-weight carbohydrate) is highly resistant to decomposition (Meentemeyer 1978).

We found a strong relationship between senesced leaves chemistry and the response of species to grazing (Fig. 3). Other authors have also found relationships between chemical (Wardle *et al.* 2002; Pérez-Harguindeguy *et al.* 2003; Schädler *et al.* 2003; Fortunel *et al.* 2009) or physical (Díaz *et al.* 2001) leaf attributes and plant palatability or the response of species to herbivory in different ecosystems around the world. Although different traits were identified as relevant in each study, it seems that grazing induces changes in plant communities, which in turn lead to increased concentrations of phenolics, fibre and lignin in the leaves.

Our results suggest that low-intensity continuous sheep grazing effects on vegetation and soil in the arid Patagonian Monte may be interrelated by negative feedbacks mediated by plant litter, because the input of nutrients considerably diminished with grazing and could potentially reduce soil nutrient availability. Moreover, a previous study carried out in the Patagonian Monte found that soil-C and soil-N are reduced in highly grazing areas (Bisigato *et al.* 2008). In turn, changes in the nutrient status of soil can affect vegetation. In this study, we did not consider the effects of changes in soil nutrients on plant performance. However, Bisigato and Bertiller (1999) found that N fertilization strongly reduces the survival of seedlings of *Larrea divaricata*, an unpalatable species ('Ld' in Fig. 3), whereas this treatment did not affect the survival of seedlings of

Stipa tenuis, a palatable species ('St' in Fig. 3). Conversely, the reduction in soil N due to the decrease in mNLF could benefit unpalatable species such as *Larrea divaricata*, which in turn has low N requirements.

It is important to mention that the processes linking changes on vegetation and soil by grazing are complex, and can vary depending on the context (Bardgett & Wardle 2003). Thus, we do not intend to extrapolate our findings to all grazing systems. For example, stronger species replacements, such as those reported in grasslands conversion to shrublands (e.g. Schlesinger *et al.* 1990), could increase the importance of species composition on the variables related to LLF. On the other hand, more productive environments where grazing promotes the dominance of grazing-tolerant plants showing compensatory growth and enhanced concentrations of nutrients in remaining tissues could show different effects on plant litter quality and quantity (Wardle *et al.* 2004).

In conclusion, our results suggest that the reduction in LLF as a consequence of grazing in the arid Patagonian Monte is due to reduced plant cover and changes in species composition. In contrast, our results suggest that species composition would be unimportant explaining the reduction of N and secondary compounds inputs on soil. At the same time, the quality of litter would be affected by grazing through increasing the concentration of N and secondary compounds (phenolics and lignin). These changes may be the consequence of the relationship between senesced leaves chemistry and plant palatability. Future research should verify these results by direct measuring of litterfall by species under contrasting grazing pressures.

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