Bottom-Up and Top-Down Controls of Litter Decomposition Rates and N Dynamics in Arid Steppes.

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Abstract

Aims

Arid ecosystem soil processes are strongly bottom-up controlled by resource scarcity. However, grazing intensification can induce changes through multiple pathways and spatio-temporal scales. For example, by changing litter quality and site environmental conditions. Our purpuse was to understand the relative importance of top-down and bottom-up controls of litter decomposition and N dynamics in the Patagonian grass-shrub steppes.

Methods

We performed three litterbag decomposition experiments to evaluate: i) the interactive effects of litter traits and site environmental conditions (grazed *vs.* exclosure communities) (reciprocal transplants *in situ*), ii) the net effect of litter traits in a common garden (*ex situ*), and iii) the net effect of site environmental conditions using a foreign common litter substrate (*in situ*). The study was performed on three pairs of sites with areas under a long-term exclosure (> 25 years) or under year-round sheep grazing. Local litter included main community species composition and was sorted by grass and shrubs material.

Results

Grazing exclusion did not significantly alter litter decomposition, either through changes in grass litter traits that control decomposition or through changes in the site environmental conditions. Nevertheless, N released during litter decomposition was 286% higher in exclosures than in grazing commumnities. The difference was associated to changes in the grass litter chemical quality. The effects were maintained when we integrated results from the entire litter community.

Conclusion

Our study suggests that decomposition rates in arid steppes are mainly bottom-up determined, but top-down controls shaping grass litter traits importantly alter the flux of N during decomposition.

Introduction

Herbivores' impacts on litter decomposition process and nutrient dynamics are key aspects of ecosystem functioning. However, and despite this subject has been actively studied in the last decade, generalizations are complex. Such complexity is partially due to the multiple pathways and spatio-temporal scales along which herbivores can affect different vegetation and soil components, and also through variations among ecosystems, livestock management practices and experimental approaches (Bardgett and Wardle 2003, Pastor et al. 2006, du Toit and Olff 2014, Wang and Wesche 2016, Zhou et al. 2016). Arid steppes are ecosystems where productivity is low, litter remains a long time as standing-dead material, the soil cover is irregular, and soil nutrient content is low (Kéfi et al. 2007). Wind and radiation generate changes in the availability and quality of the aboveground litter that enters the soil (Austin et al.

2016, Throop and Belnap 2019). Such context from vegetation and environmental traits may entail a dominant *bottom-up control* on litter decomposition and other ecosystem processes. On the other hand, the main land-use in these ecosystems is grazing by domestic herbivores, which can exert a *top-down control* (Fig. 1). Grazing intensification is widely observed to change the composition of plant species and soil properties, both closely related to the litter decomposition process and nutrient fluxes (Bakker et al. 2009, Giese et al. 2009, 2013, Reichmann et al. 2013, Peco et al. 2017, Sun et al. 2018). Hence, the joint evaluation of *bottom-up* and *top-down controls* on the litter decomposition process and nutrient recycling should result in a better understanding of how grazing management can alter ecosystem functioning (Frank et al. 2017, Penner et al. 2019).

Top-down effects of herbivores may control ecosystem function through two main pathways (Hunter and Price 1991, Wardle et al. 2004). First, through intraspecific changes in vegetation traits, by altering growth rate and biomass allocation, and after a longer-term, by directionally shifting species composition (Fig. 1: *vegetation pathway*, Augustine and McNaughton 1998, Paruelo et al. 2008, Porensky et al. 2016, Niu et al. 2016, Sun et al. 2018). Large herbivores selectively graze species and plant parts with high tissue quality. In low productive ecosystems as arid steppes, grazers drive the dominance of aboveground litter with high C:N, high lignin or chemical defences content, which are traits generally slowing litter decomposition rates and nutrient flux (Bardgett and Wardle 2003, Semmartin et al. 2004, Díaz et al. 2007, Parton et al. 2007, Bakker et al. 2009). However, in arid steppes, the entire species pool entails a strong selection for traits adapted to low resource availability (Coley 1982, Milchunas and Lauenroth 1993, Adler et al. 2004, Fig. 1: *bottom up controls on vegetation*), which may mask the effect of grazing-induced changes in species composition on litter decomposition rates (Semmartin et al. 2004, Giese et al. 2009).

The second pathway of herbivore impacts is by changing the environmental conditions of decomposition (Fig. 1: *environmental pathway*, Bardgett and Wardle 2003, Schrama et al. 2013). Through biomass consumption and trampling, big herbivores may increase soil compaction and soil water evaporation, decreasing soil biotic activity and litter decomposition rates, and affecting C and N stocks (Giese et al. 2009, Golluscio et al. 2009, Eldridge et al. 2016, Wang et al. 2018). Hypothetically, *top-down* effects of herbivores may change the arid ecosystem function through both pathways, cascading down to the decomposition process and reducing C and nutrients return to the soil (Fig. 1, Bardgett and Wardle 2003, Wang et al. 2015, 2018, Sun et al. 2018). Instead, if low quality and low activity of decomposers is a general pattern, despite the long-term influence or absence of herbivores, *bottom-up controls* defined by the ecosystem traits will regulate the decomposition process in these ecosystems (Semmartin et al. 2004, Giese et al. 2009, Penner et al. 2019, Fig. 1).

Community changes due to grazing impact mainly depend on herbivores guilds, the ecosystem herbivory history (coevolution) and soil and vegetation traits (Milchunas and Lauenroth 1993, Porensky et al. 2016 a, b, Wigley et al. 2020). Within a plant community, some of the species may show significant changes in their traits because of herbivory, while others may be more resistant to change (Vesk and Westbody 2001, Cingolani et al. 2005, Díaz et al. 2007). Most studies regarding grazing impacts on decomposition include either some individual species, the population of which increases or decreases with grazing (e.g.

Semmartin et al. 2004), or local litter mixtures with pooled composition (e.g. Giese et al. 2009, Wang et al. 2015). Classifying the plant community into compartments, for example according to their sensitivity to disturbances such as grazing, can be very useful for the interpretation and extrapolation of results.

Arid steppe vegetation is commonly represented by two functional groups: tussock grasses and shrubs. Differently to other communities, where both woody and herbaceous vegetation change importantly with herbivore impact (e.g. Wigley et al. 2020), the Occidental District Patagonian steppe has shown a preserved grass-shrub proportion after the long-term exclusion from sheep grazing (Cipriotti and Aguiar 2005, 2010, Cipriotti et al. 2019). However, the long-term influence of sheep grazing intensification changed the identity of grass dominant species in the community, substantially decreasing palatable species (highly preferred by herbivores) and increasing non-preferred species (Cipriotti and Aguiar 2005, 2010, Oñatibia et al. 2015, 2020, Oñatibia and Aguiar 2019). Shrub species have shown few or idiosyncratic variations in their composition and abundance after long-term herbivore exclusions (Cipriotti and Aguiar 2005, 2010, Golluscio et al. 2009, Cesa and Paruelo 2011, Cipriotti et al. 2019). Thus, when grazing-induced changes in species composition occur mostly within one of the two dominant life forms, considering the community as a whole could mask the changes (Carrera et al. 2008), while considering only sensitive species could overestimate grazing effects (Semmartin et al. 2004). Notwithstanding the foregoing, the effects of grazing through the *environmental pathway* could have consequences on the litter decomposition of both vegetation components either affected or not by the *vegetation pathway*. Therefore, to analyze the *top-down* impacts of grazing on the litter decomposition process, it is necessary to combine the effects trough the *vegetation pathway* and the *environment pathway*, and to consider the relative abundance of main vegetation components (Fig. 1).

Our objective was to analyse the effects of long-term grazing exclusion compared to year-round sheep grazing on the decomposition process. *Top-down* effects were assessed by analysing two type of *ecosystem pathways*, which influence the decomposition of community components represented by grasses and shrub species (Fig. 1). Based on local published data (see above), we assumed that shrub species composition and abundance did not differ between areas under long-term grazing or its exclusion. Specifically, we performed three litterbag decomposition experiments to analyse: (i) the single effect of the *environmental pathway* (site conditions) affecting shrubs, and the interactive effects of the vegetation (litter traits) and *environmental pathways* affecting grasses (reciprocal transplants *in situ*), (ii) the net effect of the *vegetation pathway*, by changing the quality of aboveground grass litter (common *ex situ* garden), and (iii) the net effect of the *environmental pathway* by changing litter decomposition of a foreign common substrate in grazing and exclosure areas. Finally, we calculated the decomposition and N release flux, by integrating results from grasses and shrubs and considering its proportional biomass contribution in the ecosystem (scaling-up). Our three complementary experiments approach allowed the joint assessment of *bottom-up* and *top-down litter decomposition controls*.

Methods

Study system

The study was conducted in the experimental field station of INTA (Instituto Nacional de Tecnología Agropecuaria) located in Río Mayo, Chubut Province, Argentina (45° 41´ S, 70° 16´ W). Mean annual precipitation is 132 mm, 60 % of which falls between April and September; mean annual temperature is 9.3 °C (average data between 1982–2019, INTA 2020). Soils are coarse-textured Aridisols, with gravels and low organic matter (0.4%), and low net N mineralization (0.28 mg m^{-2}, Yahdjian et al. 2006). Vegetation corresponds to the Occidental district of Patagonian arid steppes (Cipriotti et al. 2012, see dominant species in Table 1). Total vegetation cover varies between 30 to 65%, and aboveground net primary productivity ranges between 27 to 86 g m^{-2} year^{-1} (depending on precipitation) divided between tussock grasses and shrubs in equal contribution (Cipriotti et al. 2012). Sheep were introduced in the region towards the end of the 19th century and became an important economic activity. Stocking rates in the study field have been ~ 0.2 sheep ha^{-1} during the last 50 years, which represents an intermediate grazing intensity for the region (Oñatibia and Aguiar 2016). After > 25 years of sheep grazing exclosure, vegetation structure and physiognomy remained without important modifications, but tussock grasses dominance changed by increasing the relative biomass of palatable grasses (Cipriotti and Aguiar 2005).

Table 1
Species composition and each species abundance of vegetation components (grasses and shrubs) representing exclosure and grazing communities. Numbers represent the relative aboveground litter mass (proportion within each) in grazing and exclosure plots (n = 3), based on previous studies of the western Patagonian arid steppe.

	Exclosure	Grazing
Grasses		
Pappostipa speciosa Trin. et Rupr	0.25	0.70
Pappostipa humilis Cav.	0.20	0.20
Poa ligularis Nees ap. Steud	0.50	0.10
Bromus pictus Hook	0.05	0.00
Shrubs		
Mulinum spinosum Cav. Pers	0.40	0.40
Adesmia volckmanii Philippi	0.30	0.30
Senecio filaginoides De Candolle	0.30	0.30

Experimental Design

Three litterbag decomposition experiments were performed to test our model (Fig. 1). We selected three paddocks under a long-term sheep year-round grazing (350–700 has), each one including an adjacent long-term grazing exclosure (blocks, n = 3). Exclosures impeded big herbivores (mainly sheep) but allowed small wild herbivore access, and were established 28 (8 ha), 39 (5 ha) and 57 years (1 ha) before

the start of the experiment. Inside each paired plot (grazing and exclosure), four areas were randomly selected, at a minimum distance of 50 m from each other, where all experimental determinations were performed (24 experimental areas). The experimental sampling and determinations were performed in the field in the period between 2010 and 2013. In this period, mean annual temperature ranged between 8.8 and 10.1 °C, whereas annual precipitations between 140 and 152.1 mm year^{-1} (INTA 2020).

Litter and soil determinations

We sorted the steppe vegetation community into two groups: grasses and shrubs. Grass composition was different between grazing and exclosure conditions (Table 1, based on Golluscio et al. 2009, Oñatibia et al. 2015). Grasses comprised the four dominant species of the community. Other *Poaceae* species and forbs were excluded due to their low relative abundance. Shrubs comprised the three dominant species, and composition was the same between grazing and exclosure conditions (Cipriotti and Aguiar 2005, Golluscio et al. 2009, Oñatibia and Aguiar 2016). Litter was collected from individual plants dispersed within a broad area of the experimental sites during summer 2010. We selected fresh (yellow tissue) aboveground litter parts contributing important biomass amounts, avoiding coarse woody tissues with very low decomposability or very small leaves (in shrubs). Grass litter included blades, sheaths and culms, and shrubs litter included fine branches and thorns. Origin of grass species from grazing or exclosure plots was preserved, shrub litter from grazing and exclosures was pooled under a 50:50 mixture to build litterbags. Litter was placed in 15 x 20 cm fiberglass bags with 2 mm mesh (Robertson et al. 1999), containing 3 g air-dry weight with different litter species proportions (Table 1). The litter mesh size allowed access to soil microorganisms and mesofauna (Robertson et al. 1999, Araujo et al. 2012).

Litter quality at the beginning of the experiments was evaluated through five fresh litter random samples from each litter type (shrubs, grasses from grazing and exclosure conditions, and *Lolium arundinaceum*, see below). In these samples we estimated initial handling losses (weight pre-post experiment establishment), water content (60 °C oven-dried for 48 hours), ash content (ground samples 4 hour burning in 500 °C muffle) and total C and N concentration (LECO-CR12 dry combustion analyser and semi-micro Kjeldahl method, respectively) (Robertson et al. 1999).

Site environment under exclosure and grazing conditions was characterized by soil samples collected in the same sampling areas as the experiments (4 x 6 plots). Variables measured were soil water gravimetric content (wet-dry weight, 100 °C oven), soil bulk density (g cm^{-3}), and soil total C and N concentration (LECO-CR12 dry combustion analyser and semi-micro Kjeldahl method, respectively). In each sampling area, 2−3 sub-samples were collected using a 4 cm diameter and 10 cm height cylinder (4 groups per site and grazing condition). Nutrient (C-N) stock (ton/ha) was estimated from concentration and bulk density data. Soil temperature was measured with a digital thermometer buried 2−4 cm from soil surface (3 sub-samples). Litterbags collected from the field were carefully cleaned, oven-dried during 48 hours at 60−70 °C, and then weighed with a high precision scale. Total N content (semi-micro Kjeldahl method) was estimated in all samples from the latest harvest date (25 months for experiments 1 and 3, and 12 months for experiment 2, see below).

Experiment 1: Top-down (vs. bottom-up) effects through vegetation and environmental pathways.

The *environmental pathway* was represented by the soil properties under long-term grazing or exclosure sites (paired plots), and the *vegetation pathway* was represented by the species traits related to grazing or exclosure. This second pathway was only considered for the grass vegetation component (Table 1). Hence, under our experimental approach, the decomposition of shrubs was affected by the *environmental pathway* and the decomposition of grasses was affected by both the *environmental and vegetation pathways* (Fig. 1). To evaluate the interaction between pathways, litter from the grass component was tested under a reciprocal transplant experiment, where litter collected from grazing and exclosure plots (vegetation, Table 1) was decomposed in both paired grazing and exclosure plots (environments). Experiment 1 started in January 2011, bags were placed in four experimental areas per plot, each containing 3 litter types with 3 samples, which were collected after 6, 12, and 25 months. Litterbags were located randomly within the grass matrix (avoiding sites below shrubs), fixed to the soil surface, and protected from animal trampling with wire nets. We predicted that grazing exclosure accelerates litter decomposition through both the *vegetation pathway* and the *environmental pathway*. This experiment also allows comparing the effects of *bottom-up controls* (litter and environmental local traits) with the effects of *top-down controls* (grazing changes in litter and environmental traits) affecting litter decomposition.

Experiment 2: Net top-down effects through the vegetation pathway (litter traits).

The purpose was to isolate the effects of litter traits from those bottom-up controls due to the environmental conditions of the arid steppe. To do this, we conducted an experiment in an *ex-situ* common garden in a temperate location (litterbags exposed to site climate and soil conditions). Litterbags included grasses, with the composition from grazing and exclosure conditions, and shrubs (Table 1). Experiment 2 started in December 2011 and was established in an experimental field in the Faculty of Agronomy University of Buenos Aires (34° 35´ S, 58° 35´ W), under a randomised complete block design (*n* = 5 blocks) with 3 collection dates (2, 6, and 12 months). We predicted that grazing exclosure accelerates decomposition and N release rates by increasing the chemical quality of grasses. The combination with results from Experiment 1 allows evaluating differences between litter types under local (arid) *vs.* foreign (mesic) environmental conditions.

Experiment 3: Net top-down effects through the environmental pathway (site condition).

In this case, we aimed to evaluate the *environmental pathway*, regardless of *the bottom-up* effects that determined the litter traits in arid conditions. Hence, we used the litter from a temperate-origin grass (*fescue, Lolium arundinaceum* (Schreb) Darbysh) as a common substrate, which was decomposed in grazed and exclosure plots (*in situ*). This grass species is a foreign litter for local decomposers, collected from temperate grasslands (35° 55´ S, 61° 10´ W), and not present in the Occidental District. *L. arundinaceum* was also included in experiment 2, as a reference. This experiment was carried out simultaneously with experiment 1. We predicted that grazing exclosure accelerates decomposition rates

and N release by increasing soil organic matter and soil water retention (Giese et al. 2009, Schrama et al. 2013, Eldridge et al. 2016).

Estimating top-down effects on ecosystem fluxes

We estimated mass and N fluxes during litter decomposition by scaling results through the biomass production (Table 1). The green biomass in peak production in these ecosystems with a very short growing season can be used as a proxy for the annual net primary productivity (Sala and Austin 2000). Biomass cover per species was estimated in early summer season (2012) through a point intercept method, in two random 50 m transects per plot with 101 points per transect (paired plots in 3 grazing-exclosure blocks). Covers from each of the three dominant grass species and the three dominant shrub species were converted to green and total biomass, using the model proposed by Flombaum and Sala (2007, 2008). Results from each vegetation component cover (%) and their biomass values matched those reported in preliminary studies (summarized in Cipriotti *et al.* 2012). Green biomass production was assumed to be equivalent to litter's annual biomass input. Nitrogen biomass was calculated from N concentration of grasses and shrubs measuared in litter mixtures as detailed above (see Table 2). Under an additive model assumption (non interactive effects), decomposition rates ($g\ g^{-1}\ y^{-1}$) of grasses and shrubs (or N released from litter) from each plot were weighted by their biomass ($g\ m^{-2}$), and then summed. We predicted that the (additive) mixture of grass and shrub litter would still show differences in the decomposition process between grazing and exclosure conditions, displaying a top-down control.

Table 2

Grazing vegetation pathway: Common garden decomposition and litter chemical traits of litter mixtures of grasses from exclosure-origin (E-grasses), from grazing-origin (G-grasses) and shrubs species. Values show mean ± S.E. (n = 5, ANOVA df = 2, 8). Letters indicate differences across treatments (P < 0.05, Tukey tests).

	E-grasses	G-grasses	Shrubs	F	P
Litter decay rate (k, year^{-1})	1.16 ± 0.167 a	1.04 ± 0.16 a	0.83 ± 0.02 a	*2.97*	*0.1085*
Litter N released (%)	23.65 ± 7.22 a	-85.46 ± 19.05 b	12.36 ± 5.14 a	*17.19*	0.0013
Litter Total C (%)	43.86 ± 0.42 b	42.42 ± 0.05 c	47.93 ± 0.13 a	125.1	**< 0.0001**
Litter Total N (%)	0.32 ± 0.01 b	0.17 ± 0.02 c	0.48 ± 0.02 a	67.41	**< 0.0001**
Litter C:N (ratio)	136.8 ± 6.83 b	249.8 ± 19.81 a	100.79 ± 5.0 b	39.04	**< 0.0001**

Data analyses

Decay rates were calculated for each sample through the slope (k) of the negative exponential function of dry weight of litter remaining organic mass (m_1/m_0) through time [t, years, [$m_1/m_0 = e^{(-kt)}$]. Nitrogen released from the decomposing litter was estimated from the quantity of N at the end of the experiment

relative to the initial N quantity $\{Nrel = 100 - [(N_1 * m_1) / (N_0 * m_0)]\}$, being N and m, N concentration and dry mass at final ($_1$) and initial ($_0$) time of decomposition experiment. Data were analysed with linear mixed-effect models using R software (version 2.13.0, package nlme, function lme) (Pinheiro et al. 2011, R Core Team 2011). In a random intercept model, grazing condition was used as a fixed effect, and a nested structure for data in experimental areas, plots and blocks represented the random effects. A constant variance function structure (varIdent) was included when variance heterogeneity was detected (Pinheiro et al. 2011). For variables with more than one determination date (soil water content and soil temperature), data were both analysed for each date and in a complete model including the date in the nested structure.

Results

Top-down effects through vegetation and environmental pathways: Experiment 1

The decomposition rates from grasses litter, both originated under grazing or exclosures, were similar between grazing and exclosure environments (*Vegetation x Environment*: $F_{1,42}$ = 3.14, *P* = 0.08, Fig. 2A). Shrub litter decomposed 5% faster in exclosure than in grazing areas ($F_{1,20}$ = 10.27, *P* < 0.004, Fig. 2B). Grass litter decay rates were on average 1.5-fold faster than shrub litter ($F_{1,42}$ = 85.57, *P* < 0.0001).

N released during decomposition was strongly dependent on the origin of grasses (Fig. 2C). Grasses from exclosures released, on average 286% more N than grasses from grazing conditions, and this difference was observed under both grazing and exclosure environments (*Vegetation*: $F_{1,42}$ = 44.8, *P* < 0.0001, *Vegetation x Environment*: $F_{1,42}$ = 0.19, *P* = 0.66). Shrub litter released, on average, 14 % more N in exclosures than in grazing sites, but the difference was marginally significant ($F_{1,20}$ = 3.99, *P* = 0.06, Fig. 2D). Grasses originated in exclosures released 1.06-fold more N than shrubs (Fig. 2D), whereas grasses from grazing conditions released 0.25-fold more N than shrubs ($F_{1,40}$ = 53.41, *P* < 0.0001). Nitrogen was, on average, released from all litter substrates. Only a few samples (7 of 24) from grazing-origin grasses showed N retention (between 1.5 and 36 % N). The variation of N release among samples (*in situ*) was higher in grasses from grazing-origin (CV = 189%), compared to grasses from exclosure-origin (CV = 22%), and shrubs (CV = 18%).

Top-down effects through the vegetation pathway: Experiment 2

Grass litter from exclosure-origin had 45% higher C:N ratio compared to grazing-origin grasses (Table 2). Despite differences in tissue quality, litter decay rates in a common garden (*ex-situ*) did not depend on the origing of grasses (Table 2). However, after one year of decomposition, the exclosure-origin grasses released 128% more N than those of grazing-origin, which qualitatively retained N during decomposition (Table 2). Shrub litter had the highest C (%) and N (%) contents, but its C:N ratio was similar to the

exclosure-origin grasses (Table 2). Unlike *in situ* observations, shrub litter had similar decomposition rates than grass litter in the common garden (Table 2).

Top-down effects through the environmental pathway: Experiment 3

Environmental conditions of exclosure plots were slightly different from those of grazing plots (Table 3). Soil total C (%) and N (%) concentrations were 13% and 17% higher (p < 0.05) in exclosure than in grazing environments, respectively. Soil C:N ratio and total C or N stocks (ton ha^{-1}) were equivalent between grazing conditions (Table 3). Soil bulk density in exclosures was 7% lower than in grazing environments (p < 0.05, Table 3). Concerning soil gravimetric moisture and temperature, only one out of four estimation dates were different between grazing conditions, being 5% and 11 % higher in exclosures than in grazing plots, respectively (P < 0.05 in January 2011, Table 3).

Table 3
Grazing environmental pathway: soil properties in exclosures and grazing conditions. Values represent mean ± S.E. at 0–10 cm soil depth, and ANOVA parameters for grazing fixed effect. Soil moisture and temperature variables include model parameters of date and grazing fixed effects.

	Exclosure	Grazing	Df	F	P
Soil Total C (%)	0.53 ± 0.04	0.47 ± 0.01	1, 35	4.67	**0.038**
Soil Total N (%)	0.07 ± 0.01	0.06 ± 0.00	1, 35	5.05	**0.031**
Soil C:N (ratio)	7.85 ± 0.11	7.74 ± 0.31	1, 35	0.06	0.80
Soil Bulk Density (g cm^{-3})	1.36 ± 0.06	1.45 ± 0.12	1, 59	5.55	**0.022**
Soil Total C stock (tn ha^{-1})	6.93 ± 0.22	7.19 ± 0.55	1, 20	0.32	0.58
Soil Total N stock (tn ha^{-1})	0.92 ± 0.05	0.92 ± 0.08	1, 20	< 0.01	0.99
Soil gravimetric moisture (%, 0–10 cm depth)					
January 2011	3.78 ± 0.57	3.67 ± 0.92	1, 33	6.38	**0.017**
June 2011	4.41 ± 0.58	4.16 ± 0.32	1, 35	2.88	0.099
January 2012	1.67 ± 0.24	1.39 ± 0.27	1, 35	0.60	0.44
February 2013	6.82 ± 0.17	6.86 ± 0.22	1, 59	0.02	0.89
Grazing			1, 162	37.66	**< 0.0001**
Date			3, 33	357.01	**< 0.0001**
Grazing × Date			3, 162	4.10	**0.008**
Soil temperature (ºC, ~ 2 cm depth)					
January 2011	34.51 ± 2.90	30.70 ± 2.53	1, 59	40.21	**< 0.0001**
June 2011	3.87 ± 1.47	3.45 ± 2.94	1, 59	1.72	0.19
January 2012	32.61 ± 3.68	30.68 ± 2.01	1, 59	3.35	0.07
February 2013	25.31 ± 2.31	24.19 ± 1.96	1, 59	1.07	0.31
Grazing			1, 20	2.65	0.12
Date			3, 66	311.8	**< 0.0001**
Grazing × Date			3, 66	1.11	0.35

The *environmental pathway* did not affect the decomposition process of the foreign grass substrate (*L. arundinaceum*, Decomposition rate, k: Exclosured plots = 0.43 ± 0.03; Grazing plots = 0.37 ± 0.01; $F_{1,20}$=3.04, P = 0.096). Litter N release was not different between exclosured and grazing plots either (~ 55% N, $F_{1,20}$=3.19, P = 0.09). The values of *L. arundinaceum* litter decay rate observed under the arid steppe local environmental conditions (*in situ*) were, on average, 24 % and 52 % faster than local litter from grasses and shrubs, respectively and independently from grazing conditions (Litter type: $F_{3,84}$ = 58.17, P < 0.0001, *Environment*: $F_{1,4}$ = 1.61, P = 0.27; Litter x Env.: $F_{3,84}$ = 2.18, P = 0.10). However, N release was similar to that from shrubs and grasses from exclosures, and 273% higher than that from grazing origin grasses (Litter type: $F_{3,84}$ = 21.09, P < 0.0001, *Environment*: $F_{1,4}$ = 0.97, P = 0.38; Litter x Env.: $F_{3,84}$ = 1.04, P = 0.37).

Under the common garden environment (*ex situ*), *L. arundinaceum* decay rate differed from the decay rate values of local litter, being on average 2.6-fold faster than all steppe litter components (Decomposition rate, k: 2.62 ± 0.24, $F_{3,12}$ = 20.53, P = 0.0001). N release was 193% and 461% higher than shrubs and grasses from exclosures (N release = 0.69 ± 0.03, $F_{3,9}$ = 76.15, P = 0.0001). *L. arundinaceum* litter had a lower C concentration (average ± S. E.: 40.24 % ± 0.04 %) and a higher N concentration (0.56 % ± 0.02 %) compared to local litters (F_3 = 60−213, p < 0.0001).

Top-down effects on litter decomposition fluxes

Top-down effects were consistent after scaling-up the mass and N fluxes during decomposition. The average green biomass was 573 kg ha^{-1} (38% grasses and 62% shrubs biomasses). These results were not altered by grazing conditions (Table 4). Litter decomposition flux was 13% lower in exclosured than in grazing conditions ($F_{1,20}$ = 6.81, P = 0.02, Fig. 3A). The grass component had 25% lower decomposition flux under exclosured than grazing conditions ($F_{1,20}$ = 9.78, P = 0.005). There were no differences in shrub litter decomposition flux ($F_{1,20}$ = 1.70, P = 0.21). Total flux of N released from litter was 40 % higher in exclosured than grazing conditions ($F_{1,20}$ = 19.35, P = 0.0003, Fig. 3B). The effect on N flux from the grass component was 451% higher in exclosures ($F_{1,20}$ = 50.68, P < 0.0001), while the shrub component N flux did not differ between grazing conditions ($F_{1,20}$ = 1.79, P = 0.20). Results pattern was similar when the total biomass data were used instead of green biomass in the apportionment (Online Resource 1).

Table 4

Green aboveground biomass and N content. Data was estimated from vegetation cover data and Flombaum and Sala (2007) models for green biomass in peak production. N concentration was based on litter data from Table 2. Values show mean ± S.E. (n = 3).

	Exclosure	Grazing	Anova: Grazing
Green biomass (kg ha^{-1})			
Grasses	208.2 ± 8.6	253.9 ± 29.8	$F_{1,8}$ = 2.83, P = 0.14
Shrubs	364.9 ± 43.8	382 ± 17.9	$F_{1,8}$ = 0.06, P = 0.81
Shrubs + Grasses	573.1 ± 40	635.9 ± 25.6	$F_{1,8}$ = 1.38, P = 0.27
N in green biomass (kg ha^{-1})			
Grasses	0.67 ± 0.02	0.47 ± 0.04	**$F_{1,8}$ = 9.64, P = 0.015**
Shrubs	1.75 ± 0.19	1.82 ± 0.07	$F_{1,8}$ = 0.065, P = 0.81
Shrubs + Grasses	2.42 ± 0.19	2.28 ± 0.06	$F_{1,8}$ = 0.21, P = 0.66

Discussion

The long-term grazing or its exclusion had different consequences for decomposition rates and the release of N during decomposition in Patagonian steppes. Both the grass component litter traits (*vegetation pathway*) and the soil environment (*environmental pathway*) differed according to grazing history (long-term exclosures or grazing conditions). However, broadly, decomposition rates did not differ between grazing conditions, which indicates that this critical ecosystem process is strongly *bottom-up controlled*. Nonetheless, the *top-down* effect was evident on the release of N during litter decomposition since exclosures markedly increased the N release, especially through the *vegetation pathway*. These effects were also observed when considering the flux of N during decomposition, by integrating the biomass production and decomposition rates from the two main components of the community: grasses and shrubs. Our experimental approach, based on three complementary experiments evaluating the conceptual model from Fig. 1, allowed a joint evaluation of the *bottom-up* and *top-down controls* in the litter decomposition process and nutrient recycling. It allowed connecting community components and ecosystems pathways to analyse the complex impacts of grazing management on ecosystem functioning. It also guided the scaling-up modelling (Fig. 3).

Bottom-up controls on litter decomposition rates

We observed no evident *top-down* effects from the long-term grazing history in grass decomposition rates from either *vegetation* or *environmental pathways*. These results were consistent among the experiments.

Given the differences found in both litter and environmental traits, our expectations were of a greater decomposer carbon use efficiency and higher decomposition rates under exclosure than under grazing conditions. Litter chemical quality was higher in grasses from exclosures (lower C:N), possibly because of the higher abundance of palatable species (Table 2, Semmartin et al. 2004). Also, soil compaction was lower and the surface-layer stock of C and N was higher in exclosures than in grazing plots (Table 3, Golluscio et al. 2009). The effect of grazin through the *environmental pathway* was slightly evident in the case of shrubs, in which the decomposition rate was faster in exclosure than in grazing plots (Fig. 2). But apparently, this effect was not determinant to alter the decomposition process when litter had a lower C content, as in the case of grasses (see Table 2 and *L. arundinaceum* results). The high and long influence of abiotic photodegradation in arid lands might erase grazing effects on the biotic controls of litter decomposition (Pastor et al. 2007, Golluscio et al. 2009, Wang et al. 2015). However, radiation can also stimulate litter biotic decomposition by selective degradation of lignin (Austin et al. 2016). This, in combination with an enhancement of soil environmental conditions, may explain the faster decomposition rates of shrub litter (with higher lignin than grasses) in exclosure plots. The lack of differences in the grass component decomposition rates between grazing and exclosures suggests the manifestation of a strong *bottom-up control* in the decomposition process.

Bottom-up controls regulate the rates of decomposition by shaping both the abiotic environment, as soil cover, water and nutrient availability, and the overall traits in the plant community (Frank et al. 2017, Penner et al. 2019). Studies in semiarid grasslands reached similar results, also suggesting a strong *bottom-up* control of decomposition process. In Inner Mongolian semi-arid grasslands, grazing generates important impacts on vegetation traits and environmental conditions. But neither decomposition rates nor N recycling were sensitive to grazing exclosures, moderate winter grazing or long-term heavily grazed conditions (Giese et al. 2009). In Yellowstone grasslands, the effect of migratory grazing ungulates (elk) did not alter litter decomposition rates (Penner and Frank 2019). In these two studies, decomposition rates were found to be highly dependent on precipitations variations, hence a *bottom-up* control. Under our experimental approach, some other results reinforce this hypothesis. All litter types decomposing under the arid environmental conditions released N during decomposition, whereas at the common garden under a temperate and mesic environment, grazing-origin grasses retained N and exclosure-origin grasses and shrubs released it. Furthermore, the quality differences between *L. arundinaceum* and the arid-originated litter were highly evident in the common garden, but less noticeable in the arid steppe environmental conditions. Hence, these results suggest that the decomposition process under *in situ* arid environmental conditions appeared to express a low sensitivity to litter quality differences. As mentioned before, the exception was observed in shrub litter, which manifested higher differences to grasses *in situ* than in the common garden. Possibly, *top-down* controls would emerge as important under a stronger disturbance scenario, where differences in shrub species abundance and composition become evident, and divergence in grass composition stronger (Oñatibia and Aguiar 2019, Cipriotti et al. 2019).

Top-down controls on N released during litter decomposition

Unlike the high stability observed in decomposition rates from grasses, we detected a high sensitivity of N released from grass litter to long-term sheep grazing or exclosure, especially mediated by the *vegetation pathway* (Table 2, Fig. 2). N released from litter was considerably higher in long-term exclosures than in grazing conditions. These results remark the relevance of grazing impact on local N cycle during litter decomposition, resembling observations in other arid and semiarid systems, although the directions and magnitudes of the effects are variable (e.g. Shariff et al. 1994, Carrera et al. 2008, Bakker et al. 2009, Giese et al. 2013, Bosco et al. 2016, Sun et al. 2018). Nitrogen release or retention during litter decomposition is highly controlled by litter N concentration and the stoichiometric requirements of the decomposers (Manzoni et al. 2008, Bakker et al. 2009). It is posible that grasses originated under grazing conditions have a C:N ratio near the critical value for net immobilization during decomposition (Manzoni et al. 2008). We submit that this critical value was reached in the common garden (mesic) environment (net N retention), but under the arid steppe environment, the threshold was not reached and in most cases we estimated a N release. This, again, may be the result of a complex interaction between the photodegradation and the activity of decomposers, the balance of which might differ between arid and mesic environments. Also, local arid decomposers might exert a higher adaptation to access N from low-quality litter and from soil transfering than mesic decomposers (Zechmeister-Bolstenstern et al. 2015, Bonanomi et al. 2017).

The differences in the release of N during litter decomposition due to herbivory history (grazing or exclosure) remained when the decomposition process was additively integrated by considering the relative contribution of grasses and shrubs in the community (Fig. 1, Fig. 3). Litter decomposition flux was higher under grazing conditions after integrating results from shrubs and grasses and their local annual biomass production. This highlights that the effects of grazing on these processes must consider variations in *vegetation* and *environmental pathways*, the dynamics of vegetation components and their biomass productivity, in order to analyse impacts under a proper scenario. Despite the higher contribution of shrubs in the flux of N, it was not enough to mask differences in the flux of N in the grass component (Fig. 3). The lower N release from grasses originated under grazing conditions may be related to the higher proportion of the low palatable species *Pappostipa speciosa* in the litter mixture (Table 1). This species has the lowest leaf N content compared to other local grasses (Semmartin et al. 2004, Yahdjian et al. 2006). It has been observed to be dominant under moderate grazing intensity, but its abundance is weakened both under exclosure or higher grazing intensity conditions (Oñatibia et al. 2015). Hence, this result might be highly dependent on local species composition and grazing intensity.

Conclusions

Excluding sheep grazing for a > 25 years term produced changes in vegetation and site environmental traits. Such changes resulted in acceleration of the N cycling but did not promote important changes in the rate of litter decomposition, either for grasses or shrubs components. In other words, our study suggests that arid traits are controlling the Patagonian steppe decomposition rates from *bottom-up* drivers, and this control is large enough to erase the effects of grazing history. However, top-down controls that shape part of litter community traits are important enough to alter the flux of N during

decomposition. Our study showed that the multiple-experiment approach allowed disentangling a complex network of effects and responses. We achieved this by including different community litter components and species traits and environmental changes promoted by contrasting grazing histories. These complementary studies enhanced our capacity to predict grazing disturbance consequences on ecosystem functioning.

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