Long-term impact of domestic ungulates versus the local controls of the litter decomposition process in arid steppes

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Abstract

Aims Soil processes in arid ecosystems are strongly controlled by resource scarcity. Grazing intensification can induce changes in ecosystem processes through multiple pathways, adding new constraints to those of local conditions. We focus on grazing-induced changes in litter traits and soil environment that may affect litter decomposition and N dynamics in temperate grass-shrub steppes.

Methods We performed three litterbag decomposition experiments to evaluate: i) the effect of litter traits in a common garden (ex situ), ii) the effect of soil environment using a foreign common litter substrate (in situ), and iii) the interactive effects of litter traits and soil environment (grazed vs. exclosure communities, reciprocal transplants in situ). Field experiments were replicated in three blocks with paired plots under a long-term exclosure (> 25 years) and under year-round sheep grazing. Local litter included mixtures of species of grasses and shrubs, separately.

Results Grazing exclusion did not alter litter decomposition rates, either through changes in litter traits or in soil environment. Nevertheless, N released during grass litter decomposition was 286% higher in exclosures than in grazing communities. The difference was associated to changes in litter C:N ratio. The effects were maintained when results were integrated to the entire litter community.

Conclusion Our study suggests that litter decomposition rates in arid steppes are strongly controlled by local drivers. Ungulate grazing does not have an important influence on litter mass loss, but it can exert a strong control on N flux during decomposition, by changing grass litter traits.

Keywords Ecosystem functioning · Grazing intensification · Litter traits · Patagonian arid steppe

Introduction

Herbivores’ impacts on the litter decomposition process and nutrient dynamics are key aspects of ecosystem functioning. Despite this subject has been actively studied in the last decade, generalizations are complex.
Herbivores can affect vegetation and soil components in different ways, according to variations among ecosystems and livestock management practices (Bardgett and Wardle 2003, Pastor et al. 2006, du Toit and Olff 2014, Wang and Wesche 2016, Zhou et al. 2017). 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 and patchy (Kéfi et al. 2007). Wind and incident radiation regulates the availability of the aboveground litter that enters the soil by horizontal movement and mass loss through photodegradation, respectively (Austin et al. 2016, Throop and Belnap 2019). Such context from local vegetation, soil community, and soil environmental conditions may entail a dominant legacy shaping the litter decomposition process. However, the main land-use in these ecosystems is grazing by domestic herbivores, whose impacts can also affect the controls of litter decomposition (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, evaluating how grazing management regulates the controls of the litter decomposition process and nutrient recycling can substantially contribute to a better understanding of arid ecosystem functioning (Bardgett and Wardle 2003, Wang et al. 2018, Penner and Frank 2019).

Ungulate herbivores may control the decomposition process through making changes in vegetation and soil environment, hereafter called the vegetation and environmental pathways, respectively (Fig. 1, Wardle et al. 2004, Frank et al. 2018). Changes in the vegetation pathway can occur through directional changes in species composition, and also by intraspecific changes in plant traits (Fig. 1 arrow 5, Augustine and McNaughton 1998, Paruelo et al. 2008, Semmartin and Ghersa 2006, 2008, Porensky et al. 2016, Niu and Letchowicz 2016, Sun et al. 2018). Plant community species composition directionally changes due to long-term selective grazing on highly palatable species. In low productive steppes, grazers drive the dominance of aboveground litter with high C:N, high lignin or chemical defences content. These traits generally decrease litter decomposition rates and nutrient recycling (Bardgett and Wardle 2003, Semmartin et al. 2004, Diaz 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 (Fig. 1 arrow 3, Coley et al. 1985, Milchunas and Lauenroth 1993, Adler et al. 2004). Such dominance of arid traits exerts a strong local control, and may mask the effect of grazing-induced changes on the litter decomposition process (Semmartin et al. 2004, Giese et al. 2009, Penner and Frank 2019).

Ungulate herbivores can also generate changes in the environmental pathway affecting litter decomposition (Fig. 1 arrow 6, 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, Kooch et al. 2020). Also, soil nutrient content and distribution, especially N, can change widely due to animal excreta (Bardgett and Wardle 2003, Giese et al. 2013, Bahamonde et al. 2017). These changes in the environmental pathway could directly modify the abiotic decomposition process, but possibly the main way would act indirectly through modifying the activity of decomposers. The decomposer community composition and abundance, meanwhile, can also change depending on the history of the site (Frank et al. 2003, Dudinszky et al. 2019, Toledo et al. 2021). Grazing site history can also affect the interaction between the vegetation and environmental pathways affecting litter decomposition, if it causes changes the ability from soil organisms to decompose litter traits from local (grazed vs. excluded) community (home-field advantage, Veen et al. 2015).

Hypothetically, ungulate herbivores affect the controls of litter decomposition process, and the return of C and nutrients to the soil, through the changes on the pathways from the vegetation and the environment (Fig. 1, Bardgett and Wardle 2003, Wang et al. 2015, 2018, Sun et al. 2018). Instead, if low litter quality and low activity of decomposers is a general pattern, the legacy of the local ecosystem regulates the controls of the decomposition process in these ecosystems, regardless the long-term influence or absence of herbivores (Semmartin et al. 2004, Giese et al. 2009, Penner and Frank 2019, Fig. 1).

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 with herbivore impact (e.g. Wigley et al. 2020), the Occidental District
Patagonian steppe preserved the 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 analyse the impacts of grazing on the controls of the litter decomposition process, it is necessary to combine the effects through the vegetation pathway and the environmental 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. Effects were assessed by analysing the vegetation and environmental pathways, which influence the litter decomposition of community components represented by grasses and shrub species (Fig. 1). In the grass component, litter represented the species composition under exclusion or grazing conditions, hereafter referred as E-grasses or G-grasses, respectively. 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 the effect of ungulates through: (i) the vegetation pathway, by changing aboveground grass litter traits (ex situ common garden), and (ii) the environmental pathway by using as litter a foreign common substrate in sites under long-term grazing or exclosure, and (iii) the interactive effects of the vegetation and environmental pathways affecting grasses (in situ reciprocal transplants), and the single effect of the environmental
pathway (site conditions) affecting shrubs. 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 robust assessment of the influence of long-term ungulate grazing in reference of the local legacy of the arid steppe litter decomposition controls.

Methods

Study system

We studied our conceptual framework (Fig. 1) in steppes located 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 and 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 and Aguiar 2012, see dominant species in Fig. 2). 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) attributed to tussock grasses and shrubs in equal contribution (Cipriotti and Aguiar 2012, see dominant species in Fig. 2). 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) attributed to tussock grasses and shrubs in equal contribution (Cipriotti and Aguiar 2012). Sheep were introduced in the region towards the end of the nineteenth 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 exclusion, vegetation structure and physiognomy remained without important modifications, but tussock grasses dominance changed under grazing long-term exclusion, by increasing the relative biomass of palatable grasses (Cipriotti and Aguiar 2005).

Experimental design

Three litterbag decomposition experiments were performed to test our model (Fig. 1). Field design consisted in three blocks (replicates) with paired plots of areas under a long-term sheep year-round grazing (320–880 ha), and adjacent areas under long-term grazing exclusion (1–8 ha). Grazing plots were in three different paddocks (Fig. 2 a). Sheep exclosures were established 28 (8 ha), 39 (5 ha) and 57 years (1 ha) before the start of the experiment, age was part of the block design. Inside each plot (grazing or exclusion), four experimental units were randomly selected, at a minimum distance of 50 m from each other, where all experimental determinations were performed. 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 (G-grasses) and exclosure conditions (E-grasses, Fig. 2 b, c, based on Golluscio et al. 2009, Oñatibia et al. 2015). Grasses comprised the four dominant species of the community (see Fig. 2 b, c). 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 (Fig. 2 b, c, Cipriotti and Aguiar 2005). 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. Grass litter included blades, sheaths and culms, and shrubs litter included fine branches and thorns (Fig. 2). For shrubs we did not use coarse woody tissues with very low decomposability or very small leaves. Origin of grass species from grazing or exclosure plots was preserved, to include possible variations in intraspecific traits due to grazing (e.g. Semmartin and Ghersa 2006). Shrub litter from grazing and exclosures was pooled under a 50:50 mixture to use in litterbags. Species litter was weighed individually to construct proportions reported in Fig. 2 (b, c).

Litterbags were 15 × 20 cm fiberglass bags with 2 mm mesh (Robertson et al. 1999), containing 3 g air-dry weight litter. All litter types and treatments included 3 samples to be collected in different dates
The litter mesh size allowed access to soil microorganisms and mesofauna (Robertson et al. 1999, Araujo et al. 2012). This study did not consider the effect of macrofauna on litter decomposition. A previous study in the same system reported that the exclusion of macro- and mesofauna had no effect on litter mass loss (Araujo et al. 2012). Experiments 1 and 3 were carried out with the same litter (same collection), which was carefully stored in freezers until processing.

Litter quality at the beginning of the experiments was evaluated through five fresh litter samples from each litter type (shrubs, E-grasses, G-grasses, 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 h), ash content (ground samples 4 h 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). Litterbags collected from the field were carefully cleaned, oven-dried during 48 h 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).

Site environment under exclosure and grazing conditions was described by soil samples collected in all the sampling units in areas closed to litter bags (Fig. 2a, 3 replicates with 4 sampling units within each condition). 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 unit, 2–3 samples were collected using a 4 cm diameter and 10 cm height cylinder. 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 samples).

Experiment 1: Ungulate effects through the vegetation pathway

The objective was to isolate the effects of litter traits (Fig. 1 arrow 5) from those local 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 E-grasses, G-grasses, and shrubs (Fig. 2b, c). As a reference, this experiment also included samples from the foreign litter (mesic origin) from experiment 2 (see below). Experiment 1 was established in an experimental field in the Faculty of Agronomy University of Buenos Aires (34° 35´ S, 58° 35´ W). Climate is temperate humid (1100 mm mean annual precipitation, 18 °C mean annual temperature). Experiment consisted in five blocks (replicates) to control for a slight slope variation, where litterbags were set on soil surface. In each block, litterbags included 3 samples per litter type to be collected 2, 6, and 12 months after the start of the experiment, in December 2011. Experiment duration was shorter than field experiments (see below), because of the faster decomposition rates under mesic conditions.

Experiment 2: Ungulate effects through the environmental pathway

In this case, we evaluated the environmental pathway (Fig. 1 arrow 6), regardless of the local legacy effects from arid litter traits. Hence, we used the litter from Lolium arundinaceum (Schreb) Darbysh, hereafter called Lolium as a common substrate, which was decomposed in grazing vs. exclosure environments (Fig. 2a). 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. This experiment was carried out simultaneously with experiment 3 (see below).

Experiment 3: Ungulate effect on local vegetation and environmental pathways

The environmental pathway was represented by the soil properties under long-term grazing or exclosure (paired plots), and the vegetation pathway was represented by plant trait differences related to ungulates (Fig. 1 arrows 5 and 6). This second pathway was only considered for the grass vegetation component (E-grasses vs. G-grasses, Fig. 2b, c). The decomposition of shrubs was affected by ungulates through the environmental pathway and the decomposition of grasses was affected by ungulates through both the environmental and vegetation pathways (Fig. 2b, c). To evaluate the interaction between pathways, litter from the grass component was tested under a reciprocal transplant experiment, where E-grasses and G-grasses (vegetation, Fig. 2b, c) was decomposed in both paired grazing and exclosure plots (environments, Fig. 2a). Litterbags were placed in four experimental units within paired plots, replicated in three blocks (Fig. 2a). Each experimental unit contained 3 samples per litter type to be collected after 6, 12, and 25 months after the start of the experiment, in January 2011. Litterbags were located randomly interspersed among grasses plants (avoiding sites below shrubs), fixed to the soil
surface with stakes, and protected from animal trampling with wire nets.

Ungulate effects on litter decomposition and N release fluxes at ecosystem level

We estimated mass and N fluxes during litter decomposition by scaling up results through the biomass production. 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 (summarised in Cipriotti and Aguiar 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 measured in litter mixtures as detailed above. 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 sample unit were weighted by their biomass (g m$^{-2}$), and then summed.

Data analyses

Decay rates were calculated for each sample unit through the slope (k) of the negative exponential function of dry weight of litter remaining organic mass (m$_{t}$/m$_{0}$) through time \{t, years, m$_{t}$/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 \{N$_{rel}$ = 100- [(N$_{f}$ x m$_{f}$) / (N$_{0}$ x m$_{0}$)]\}, being N and m, N concentration and dry mass at final (f) and initial (0) time of decomposition experiment. Positive values denote N release and negative values mean N retention in litter. Data were analysed with linear (lm) and linear mixed-effect (lme, package nlme) models, and Tukey tests with function/package emmeans, using R software (version 2.13.0) (Pinheiro et al. 2018, R Core Team 2018). A constant variance function structure (varIdent) was included when variance heterogeneity was detected (Pinheiro et al. 2018). The datasets generated during the current study are published in the MENDLEY repository (https://doi.org/10.17632/f88w6mv55r.1).

In experiment 1, in the common garden, litter chemistry was analysed by a single linear model and a Tukey test. Litter decomposition rates and N release was analysed with linear mixed-effects models, where the fixed factor was Litter type (shrubs, E-grasses, G-grasses), and the random factor was the nested structure of data within blocks (N = 5). Results from Lolium litter in the common garden was also compared in a second model. In experiment 2, and for shrubs litter in experiment 3, the fixed factor was the environmental pathway (exlosure vs. grazing sites). In the experiment 3, grasses litter was analysed by the vegetation pathway (E-grasses vs. G-grasses), the environmental pathway, and their interaction (reciprocal transplant). In experiments 2 and 3, the random factor was the nested structure of data in experimental units within blocks (4 × 3). When more than one sample was taken within each experimental unit it was also included in the nested structure (i.e. for soil determinations). For variables with more than one determination date (soil water content and soil temperature), the date of measurement was included in the nested structure as the lowest level. These data were also analysed individually for each date. In experiment 3, other models with the same random factor, but “litter type” as a fixed factor were applied to compare results among shrubs, E-grasses, G-grasses and Lolium, all incubated together. Blocks (and exclosure age) did not have a directional effect in litter decomposition rates or N release results (see Suppl. Information Online Resource 1 and 2).

Results

Ungulate effects through the vegetation pathway:

Experiment 1

Grass litter from exlosures (E-grasses) had 45% higher C:N ratio compared to litter from grazed paddocks (G-grasses, Table 1). Despite these differences in tissue quality, litter decomposition rates in a common garden (ex-situ) did not depend on the origin of grasses (Table 1). However, after one year of decomposition, E-grasses litter released 128% more N than G-grasses litter, which retained N during decomposition (positive vs. negative rates, Table 1). Shrub litter had the highest C (%) and N (%) contents, but its C:N ratio was similar.
to E-grasses (Table 1). Shrub litter had similar decomposition rates than grass litter in the common garden (Table 1).

Ungulate effects through the environmental pathway: Experiment 2

Soil total C (%) and N (%) concentrations were 13% and 17% higher \((p < 0.05)\) in exclosure than in grazing environments, respectively (Table 2). Soil bulk density in exclosures was 7% lower than in grazing environments \((p < 0.05, \text{ Table 2})\). Concerning soil gravimetric moisture and temperature, only one out of four estimation dates show differences, being 5% and 11% higher in exclosures than in grazing plots, respectively \((p < 0.05)\) in January 2011, Table 2).

The environmental pathway did not affect the decomposition process of the foreign grass substrate \((L. \text{ arundinaceum})\), Decomposition rate, \(k\): Exclosure 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 exclosed and grazing plots either \((~55% \text{ N, F} \(1,20 = 3.19, p = 0.09)\). Compared to the litter of arid origin, under the arid steppe environmental conditions, the decomposition rate of \(Lolium\) litter was, on average, 24% and 52% faster than local litter from grasses and shrubs, respectively \((p < 0.05)\) in January 2011, Table 2).

The decomposition rates from G-grasses and E-grasses were similar between grazing and exclosure environments \((\text{Vegetation: } F_{1,42} = 0.36, p = 0.55, \text{ Environment: } F_{1,42} = 0.33, \text{ Vegetation x Environment: } F_{1,42} = 3.14, p = 0.08, \text{ Fig. 2a})\). Shrub litter decomposed 5% faster in exclosure than in grazing areas \((\text{Environ-} \text{ment: } F_{1,20} = 10.27, p < 0.004, \text{ Fig. 2b})\). Grass litter decay rates were on average 1.5-fold faster than shrub litter \((\text{Litter type: } F_{1,42} = 85.57, p < 0.0001)\).

N released during decomposition was strongly dependent on the origin of grasses \((\text{Fig. 2c})\). E-grasses released, on average 286% more N than G-grasses, and this difference was observed under both grazing and exclosure environments \((\text{Vegetation: } F_{1,42} = 0.36, p = 0.55, \text{ Environment: } F_{1,42} = 0.33, \text{ Vegetation x Environment: } F_{1,42} = 3.14, p = 0.08, \text{ Fig. 2a})\). Shrub litter decomposed 5% faster in exclosure than in grazing areas \((\text{Environ-} \text{ment: } F_{1,20} = 10.27, p < 0.004, \text{ Fig. 2b})\). Grass litter decay rates were on average 1.5-fold faster than shrub litter \((\text{Litter type: } F_{1,42} = 85.57, p < 0.0001)\).

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Table 1 Grazing vegetation pathway: Common garden decomposition experiment 1 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. \((n = 5, \text{ ANOVA df} = 2, 8)\). Letters indicate differences across treatments \((P < 0.05, \text{ Tukey tests})\). Positive values denote N release and negative values mean N retention in litter

| Litter trait                           | 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 or retained (%)     | 23.65±7.22 a | −85.46±19.05 b | 12.36±5.14 a | 17.19 | \textbf{0.0013} |
| Litter Total C (%)                    | 43.86±0.42 b | 42.42±0.05 c | 47.93±0.13 a | 125.1 | \textbf{<0.0001} |
| Litter Total N (%)                    | 0.32±0.01 b  | 0.17±0.02 c  | 0.48±0.02 a  | 67.41 | \textbf{<0.0001} |
| Litter C:N (ratio)                    | 136.8±6.83 b | 249.8±19.81 a | 100.79±5.0  | 39.04 | \textbf{<0.0001} |
N release among samples (in situ) was higher in G-grasses (CV = 189%), compared to E-grasses (CV = 22%), and shrubs (CV = 18%, see Online Resource 2).

**Ungulate effects on litter decomposition and N release fluxes at ecosystem level**

Ungulate 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 biomass). These results were not altered by grazing conditions (Table 3). Litter decomposition flux was 13% lower in exclosures than in grazing conditions (F\(_{1,20} = 4.67, p = 0.038\)). 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\(_{1,20} = 0.02\)). Results pattern was similar when the total biomass data were used instead of green biomass in the apportionment (Online Resource 3).

**Discussion**

The long-term grazing or its exclusion had different consequences for litter decomposition rates and the release of N in Patagonian steppes. Broadly, decomposition rates did not differ between grazing conditions. This indicates that this critical ecosystem process is strongly controlled by local conditions shaping vegetation and environmental pathways (Fig. 1 arrows 3 and 4). Nonetheless, the effects from ungulates were evident on the recycling of N during
litter decomposition. Sheep grazing exclosures markedly increased the N release from litter, especially through changes on the vegetation pathway (Fig. 1 arrow 5). 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 connecting the complex impacts of grazing management on ecosystem functioning.

Local arid legacy controls litter decomposition rates

We observed no evident long-term ungulate effects on grass decomposition controls, nor mediated by the vegetation or environmental pathways (Fig. 1 arrows 5, 6). These results were consistent among the experiments (Fig. 3a, Table 1, and Lolium results). Our expectations were of a greater decomposer carbon use efficiency and higher decomposition rates under exclosure than under grazing. Litter quality was higher in E-grasses (lower C:N) than in G-grasses, possibly because exclusion of sheep for several years increase the abundance of palatable species (Table 1, Semmartin et al. 2004). Also, soil compaction was lower and the surface-layer concentration of C and N was higher in exclosures than in grazing plots (Table 2, Golluscio et al. 2009). The effect of grazing through the environmental pathway was slightly evident in the case of shrubs, in which the decomposition rate was faster in exclosed than in grazing plots (Fig. 3b). But, this effect did not change the decomposition process when litter had a lower C content, as in the case of grasses (see Fig. 3a, Table 1 and Lolium results). Concerning grass litter decomposition rates, we did not detect changes in the ability of decomposers associated with litter origin or its quality (Keiser et al. 2014, Veen et al. 2015, Fig. 3a, Online Resource 1, 2). A possible caveat is that our study design did not considered the variations within the community structure. Soil biota inhabiting in microsites created by the grasses matrix or under shrubs islands, and its activity, could differ (Gonzalez Polo and Austin 2009, Bezmer et al. 2010, Steinauer et al. 2020). Hence, soil organisms’ interactions with litter traits could also be different among microsites.

Studies in semiarid grasslands suggest a strong local control of decomposition process. In Inner Mongolian semi-arid grasslands, 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 highly dependent on precipitations variations. This hypothesis is also supported by the fact that quality differences between the exotic Lolium litter and the arid-originated litter were highly evident in the common garden experiment, but less noticeable in the arid steppe experiment. This result suggest that under the arid steppe environmental conditions, grass decomposition rates are less sensitive to changes in litter traits compared to more humid environments (Keiser et al. 2014).

### Table 3

|                | Exclosure | Grazing | Anova: Grazing |
|----------------|-----------|---------|----------------|
| **Green biomass (kg ha⁻¹)** |           |         |                |
| Grasses        | 208.2 ± 8.6 | 253.9 ± 29.8 | F₁,₈ = 2.83, p = 0.14 |
| Shrubs         | 364.9 ± 43.8 | 382 ± 17.9 | F₁,₈ = 0.06, p = 0.81 |
| Shrubs+Grasses | 573.1 ± 40  | 635.9 ± 25.6 | F₁,₈ = 1.38, p = 0.27 |
| **N in green biomass (kg ha⁻¹)** |           |         |                |
| Grasses        | 0.67 ± 0.02 | 0.47 ± 0.04 | F₁,₈ = 9.64, p = 0.015 |
| Shrubs         | 1.75 ± 0.19 | 1.82 ± 0.07 | F₁,₈ = 0.065, p = 0.81 |
| Shrubs+Grasses | 2.42 ± 0.19 | 2.28 ± 0.06 | F₁,₈ = 0.21, p = 0.66 |

Flombaum and Sala (2007) models for green biomass in peak production. N concentration was based on litter data from Table 1. Values show mean ± S.E. (n = 3).
Ungulates affect N recycling during litter decomposition

Unlike the high stability observed in decomposition rates, we detected a high sensitivity of N released from grass litter to ungulate effects, especially mediated by the vegetation pathway (Table 1, Fig. 3c). N release was considerably higher in E-grasses than G-grasses litter. 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).

During decomposition, soil organisms retain N and accumulate it in litter, until reaching a critical value where the N is released. This critical value depends on the initial litter N concentration (or C:N ratio), the stoichiometric requirements of the decomposers, and their resource use efficiency (Manzoni et al. 2008, 2017, Ågren et al. 2013, Mooshammer et al. 2014). All litter types under the arid environmental conditions exceeded the critical value and showed a net N release during decomposition. In the case of G-grasses, despite its high C:N value, the critical value was also reached in the arid environment in most cases. However, it was not reached in the mesic environment, where a net N retention was shown (Fig. 3a, Table 1). Possibly, C was the limiting factor for decomposers in the arid steppe, hence N was released, and N was the limiting factor in the mesic common garden (Gonzalez Polo and Austin 2009, Mooshammer et al. 2014). Both the stoichiometric requirements form decomposers and their C an N use efficiency could differ among ecosystems, life histories and microsites within the ecosystem (Keiser et al. 2014, Zechmeister-Bolstenstern et al. 2015, Bonanomi et al. 2017, Manzoni et al. 2017). These are subjects that need further exploration in relation to nutrient recycling during decomposition.

The effect of ungulates in the release of N during litter decomposition remained when the decomposition process was integrated to the entire litter community, by considering the relative contribution of grasses and shrubs (scaling-up to ecosystem level, Fig. 4). Litter decomposition flux was higher under grazing than exclosure conditions after scaling-up results (Fig. 4a). Despite the higher contribution of shrubs in the flux of N (Fig. 3d), it was not enough to mask differences in the
flux of N in the grass component (Fig. 4b). These results highlight that the effects of ungulates on soil processes must consider variations in vegetation and environmental pathways (including soil decomposers), the community vegetation components, and their biomass productivity, in order to analyse impacts under a proper scenario. The lower N release from G-grasses may be related to the higher proportion of the low palatable species *Pappostipa speciosa* in the litter mixture (Fig. 2c). 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. Also, further research on how ungulate impacts can affect decomposer communities (Dudinszky et al. 2019, Toledo et al. 2021) and their function should help elucidating the impacts for the N recycling.

Conclusions

Excluding sheep grazing for a > 25 years term accelerated the recycling of N, but did not promote important changes in the rate of litter decomposition. Our study suggests that the arid Patagonian steppe decomposition rates are strongly controlled by local characteristics driving litter traits and soil properties, and this control is large enough to mask the effects of grazing history. However, the long-term grazing history that shape part of litter community traits (the vegetation pathway) are important enough to alter the recycling of N during decomposition. Our multiple-experimental design allowed disentangling a complex network of effects and responses. We achieved this by including different community litter components and species traits, and soil environmental changes promoted by contrasting grazing histories. These approach enhanced our capacity to predict ungulate disturbance consequences on ecosystem functioning.

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Code availability

Codes from the main results are published in the Mendeley repository (https://doi.org/10.17632/f88w6mv55r.1). Codes from soil data analysis and litter biomass are available from the corresponding author on reasonable request.

Authors’ contributions

Maria-Victoria Piazza and Enrique Chaneton conceptualized the study. Maria-Victoria Piazza led material preparation, data collection and analysis. Gastón R. Oñatibia and Martín R. Aguiar contributed to study design and field activities. Martín R. Aguiar and Enrique Chaneton were responsible for funding acquisition. The first draft of the manuscript was written by Maria-Victoria Piazza and Enrique Chaneton.
Chanetón, and all authors commented on previous versions of the manuscript. Gastón R. Oñatibia and Martín R. Aguiar contributed, read and approved the final manuscript.

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Declarations

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