Controls of forage selective defoliation by sheep in arid rangelands

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Abstract.   Selective grazing by domestic livestock is a major control of plant community structure and dynamics in drylands. However, grazing impact predictions supporting management decisions are frequently based on average biomass consumption, neglecting selectivity. We evaluated the relative importance of grazing pressure, total and each species density, and plant dead biomass proportion as drivers of selective defoliation by sheep in three dominant native grass species in Patagonian steppes. Species were *Poa ligularis*, *Festuca pallescens,* and *Pappostipa speciosa*, which *a priori* present different preference degree by sheep. The relevance of these drivers for differently preferred species has not been simultaneously studied. We recorded the defoliation frequency and degree of the three species (dependent variables) throughout 112 field surveys. Besides, we recorded grazing management and vegetation structure descriptors (independent variables). *Poa ligularis* was highly defoliated (90% of plants), and grazing pressure was the leading driver (asymptotic exponential relationship). For *F. pallescens*, almost 70% of plants were defoliated, and defoliation non-linearly increased as grazing pressure rose and linearly decreased as both its dead biomass proportion and *P. ligularis* density increased. For *P. speciosa*, defoliation was low (20% of plants) and linearly decreased as both its dead biomass proportion and the density of the other two species increased. Grazing pressure played a negligible role in this species. These patterns confirmed that *P. ligularis*, *F. pallescens*, and *P. speciosa,* respectively, present high, intermediate, and low preference degree by sheep. In conclusion, our findings suggest that (1) selective defoliation can be satisfactorily predicted as function of grazing pressure, species densities, and plant dead biomass proportion; (2) grazing pressure becomes a more relevant driver as species preference rises and its effect on defoliation is markedly non-linear; (3) the dead biomass proportion and the abundance of highly preferred species are the leading factors determining less preferred species defoliation; and (4) grazing pressure management by itself is not enough to reduce the high defoliation of preferred species and increase the defoliation of non-preferred species. This knowledge is critical for developing effective management practices to control forage species defoliation in rangelands worldwide where species with different preference by herbivores coexist.

Key words: domestic livestock; drylands; forage species; grazing pressure; Patagonian steppes; rangeland management; selectivity; species preference.

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INTRODUCTION

Selective grazing by domestic livestock is one of the major drivers of plant community structure and dynamics in rangeland ecosystems (Milchunas and Lauenroth 1993, Golluscio et al. 1998*a*, Oesterheld et al. 1999). Herbivore consumption modifies the competitive balance among plants, leading to changes in the relative abundance of species or functional types (Noy-Meir et al. 1989, Briske and Heitschmidt 1991, Anderson and Briske 1995, Moretto and Distel 1999, Lezama et al. 2014, Eldridge et al. 2018). These effects of livestock depend on the grazing pressure. In arid and semi-arid rangelands, while light grazing could raise productivity and enhance forage quality, intensive and chronic grazing generally reduces the forage value due to a biomass reduction of highly preferred species and their replacement by less or non-preferred species (e.g., James et al. 1999, Tobler et al. 2003, Oñatibia et al. 2015, 2020). This impact usually occurs along with vegetation cover decline and soil erosion increase (Ravi et al. 2010, Augustine et al. 2012, Oñatibia et al. 2018). For this reason, domestic livestock activities have been identified as one of the major degradation and desertification drivers (Brown et al. 1997). As domestic grazing is the most common and widespread land use in arid rangelands (Milchunas and Lauenroth 1993, Asner et al. 2004), understanding herbivore forage preference and the main controls of selective consumption patterns becomes particularly relevant to generate effective rangeland management strategies (Malechek and Leinweber 1972).

Domestic herbivores present a selective behavior while foraging at different levels, from individual plants to landscapes (Senft et al. 1987, Bailey et al. 1996, Laca et al. 2010, Bailey and Brown 2011). At fine scales, animals select individual plants or plant parts depending on their biomass quality (i.e., nutrient concentration and secondary chemistry), which is mainly determined by plant species identity, the proportion of standing-dead biomass, morphology, and the phenological stage (Stuth 1991, Paruelo et al. 2008). Thus, preferred species plants are more heavily grazed than those of less preferred species (Provenza 1995). At intermediate scales, livestock select patches according to the relative abundance of preferred species and their nutritive quality (Senft et al. 1987). Finally, at broader scales, livestock select landscapes depending on the dominant vegetation types, the topography, and water availability (Bailey et al. 1996), but also other factors such as weather (thermal comfort) or predator avoidance. In short, at all scales, domestic herbivores select forage resources that allow them to optimize energy and nutrient intake per unit of plant biomass, avoiding toxic compounds (McNaughton 1984, Senft 1989, Provenza 1995, Bailey and Brown 2011). This selective behavior generally promotes over- and under-grazing symptoms at different scales (Senft et al. 1985, Bailey and Brown 2011). Nevertheless, the relative importance of the different drivers determining domestic herbivore selectivity patterns is still not understood.

It has been stressed that grazing pressure is the most important driver of both herbivore selectivity and grazing impacts on vegetation. As grazing pressure increases, animal selectivity decreases (Wilson and MacLeod 1991, Vallentine 2001, Animut et al. 2005, Bailey and Brown 2011, Oesterheld and Semmartin 2011). Grazing pressure management has the potential to alter defoliation frequency and intensity. At high stocking levels, available forage biomass per animal is low, forcing livestock to consume species which are less preferred to maintain high rates of intake (Hart et al. 1993). However, livestock performance may decline and vegetation may deteriorate, representing a potential ecological and economic risk with short- and long-term consequences (Senft 1989, Hart and Ashby 1998, Oñatibia et al. 2020). In addition to grazing pressure and species preference, selective defoliation of a particular plant species can be determined by factors as forage availability of this species or alternative co-existing species (community composition), forage accessibility, season of grazing, herbivore characteristics (see the review of Papachristou et al. 2005 for small ruminants and Seither et al. 2012, Cuchillo-Hilario et al. 2018, Jerrentrup et al. 2020 for cattle-sheep comparisons), and the presence of other herbivore species (e.g., Cuchillo-Hilario et al. 2017). Despite the relevance of these determinants of selectivity, in many cases, predictions regarding livestock impacts on arid and semi-arid rangelands are based on average biomass consumption,

ignoring the uneven effect on species and individual plants with different preference degree (Paruelo et al. 2008, Soder et al. 2009, Oñatibia and Aguiar 2019).

In the case of Patagonian steppes (Argentina), domestic livestock were introduced more than 100 yr ago, and sheep stocks increased during more than 60 yr. However, during the last decades, sheep population has sharply declined due to demographic causes associated to forage resources deterioration (Soriano and Movia 1986, Golluscio et al. 1998a, Texeira and Paruelo 2006). In general, flock management has been extensive, in large paddocks, where flocks stay all year round, behaving as semi-natural populations (Paruelo et al. 1998, Golluscio et al. 1998a). This kind of management exacerbates selective grazing and, along with unsuitable stocking rates, it is associated with forage supply reduction and desertification (Golluscio et al. 2005, Oñatibia et al. 2015). Although sheep grazing habits have been proposed as one of the main causes of Patagonian steppes degradation (Golluscio et al. 1998a), field experimental evidence about selective sheep defoliation is scarce.

Sheep diet in Patagonian steppes is mainly composed of grass species (Golluscio et al. 1998a, Pelliza et al. 2001). Within this life form, sheep prefer grass species commonly considered palatable, highly productive, and more mesophytic (e.g., *Poa ligularis*, *Bromus pictus,* and *Festuca pallescens*; Golluscio et al. 1998a). The selection of these preferred species is associated with their relatively high protein content and digestibility (Somlo et al. 1985). On the contrary, species of the genus *Pappostipa* present low contribution to sheep diet, mainly due to the fact that they contain low protein values (Golluscio et al. 1998b).

Our objective was to identify the drivers of sheep defoliation of three dominant native grass species in Northwestern Patagonian steppes, and to evaluate the relative importance of each driver for each species. The drivers studied were as follows: grazing pressure during the previous year, the abundance of both focus species and alternative species, the season of grazing (winter or summer), and the dead biomass proportion of the individual plants. Defoliation was estimated through the frequency of defoliated tussocks and their defoliation degree (plant defoliation level). We focused on *Poa ligularis*, *Festuca pallescens*,

and *Pappostipa speciosa*, which *a priori* would present different preference degree by sheep (Golluscio et al. 1998a, Oñatibia and Aguiar 2016). We aimed to objectively identify the level of preference for the three main grass species based on the defoliation response patterns to grazing pressure. Our working hypothesis was that, aside grazing pressure, the density of the focus species, the structure of their tussocks (standing-dead biomass proportion), and the community composition (availability of other forage species) interact with the identity of a particular forage species, modifying its level of defoliation. The relative importance of these drivers changes with the species preference degree by sheep.

Methods

Study site description

The study area covers about 10 000 km^2 and is located in western Patagonia, Argentina (from 71°10′–70°20′ W, 41°00′–41°15′ S in Rio Negro Province to 71°00′–71°35′ W, 45°40′–45°20′ S in Chubut Province; Fig. 1). This area corresponds to a coenocline dominated by shrub-grass and grass steppes of the Occidental and Subandean Districts of Patagonian Phytogeographic Province (León and Facelli 1981, Paruelo et al. 2004, Cesa and Paruelo 2011). The climate is cold-temperate and precipitation ranges from 160 to 500 mm east to west. Most precipitation falls during the cold season, between May and September (Paruelo et al. 1998). Soils in the northern area correspond to a complex of Ustic Paleargids, Udic Argiustolls, and Typic Haplargides. In the southern area, soils are Typic Cryoborols in the west and Typic Calciorthids in the east (Cesa and Paruelo 2011). Vegetation in the eastern portion corresponds to shrub-grass steppes. Dominant grass species are *Pappostipa speciosa* (Trin. et Rupr.), *Pappostipa humilis* (Cav.), *Poa ligularis* (Nees ap. Steud) and *Bromus pictus* (Hook). Dominant shrub species are *Azorella prolifera* (Cav.) G.M. Plunkett & A.N. Nicolas (ex-*Mulinum spinosum*), *Adesmia volckmannii* (Philippi) and *Senecio filaginoides* (De Candolle). In the western portion, vegetation is characterized by grass steppes dominated by *Festuca pallescens* (St. Yves), accompanied, but in lower proportion, by *Poa ligularis* and *Rytidosperma virescens* (E. Desv; Golluscio et al.1982). The main
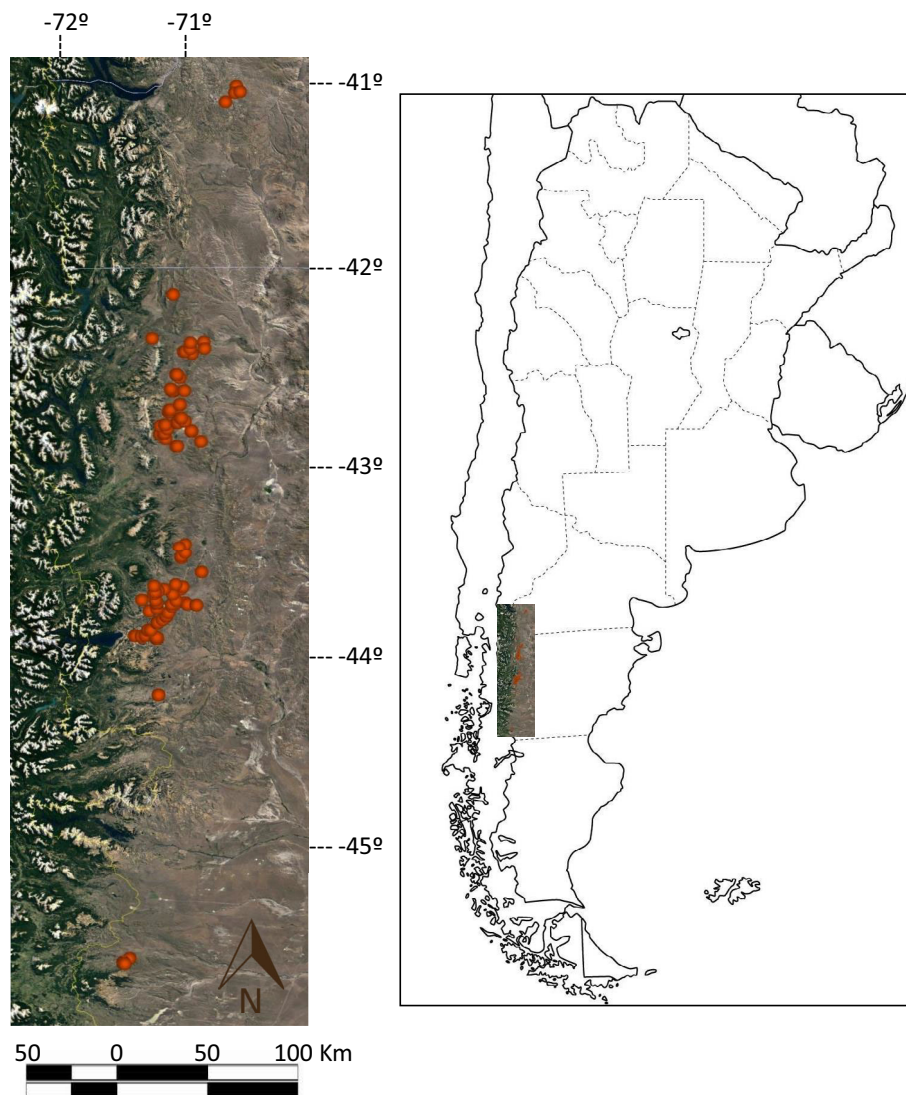
Fig. 1. Study area in western Patagonia. Red points represent each vegetation survey.

transition between these communities is evidenced as a change in species abundance and life forms dominance, which is mainly attributed to the precipitation gradient (León and Facelli 1981, Bertiller et al. 1995).

Data collection

We performed a field observational study where we recorded descriptors of sheep defoliation (dependent variables) as well as vegetation structure and grazing management (independent variables). The study was conducted in a group of 70 paddocks, distributed across the study area (Fig. 1). Paddock sizes ranged between 574 and 8317 ha (3735 ha, on average) and they exhibited a wide range of grazing management (from grazing exclosure during several years to grazing at a wide range of stocking rates, in different seasons and during different time periods). We compiled a database including (1) 112 field vegetation surveys (some paddocks were surveyed more than once) performed between 1990 and 2005; (2) data on grazing management of each individual paddock during the previous year to each vegetation

survey performed (from 1989 to 2005); and (3) average aboveground net primary productivity (ANPP) of each paddock estimated from remotely sensed data.

Vegetation surveys were performed in order to estimate defoliation frequency, plant defoliation degree, density, and plant structure of each focus species. These field observations were made throughout all seasons of the year, including surveys during January, February, April, May, June, July, August, September, and November. Inside each paddock, we selected a representative area of the dominant plant community (topographic, physiognomic, and floristically homogeneous) with an average grazing use condition (representative of the use of the paddock), avoiding areas near watering points, fencing or resting places. In all cases, the homogeneous area within which each vegetation survey was carried out was bigger than 10 ha. Inside these areas, we randomly outlined a 100-m transect. Every 10 m along that transect, we recorded the nearest individual plant of each studied species (*Poa ligularis*, *Festuca pallescens,* and *Pappostipa speciosa*) within 5 m radium. In most cases, individual plants of the three species were found, obtaining data from 10 plants per species per transect. We measured the distance between each plant and the transect point in order to estimate specific density by the closest individual method (see Greig Smith 1983 for methodological details). For this estimation, the distance of the 10 plants was averaged per transect. When individuals of a species were absent within 5-m radium from a sampling point, the value of density in this point was zero, and it was considered in the average density calculation at transect level through weighted average, considering the average distance in the number of points where individuals were present: (average distance among points with plants × number of points presenting plants/total number of points [10]). In few cases, where there were no individuals of one species present within the 5-m radium along the ten points, the specific density at transect level was zero. In each individual plant, we measured the defoliation degree and we visually quantified the standing-dead biomass proportion (including grey leaves; see Appendix S1: Fig. S1), at a scale of 5% intervals (Oñatibia and Aguiar 2019). Plant defoliation degree (level of defoliation) was

estimated taking into account the number of tillers consumed in each plant, according to a visual scale (0 = no defoliation, 1 = one tiller defoliated, 2 = more than one but not all tillers defoliated, and 3 = all tillers defoliated; Golluscio et al. 1998*b*). We considered defoliation degree 1 and defoliation degree 2 as separate categories, because they may indicate the biological difference between a single bite (an herbivore defoliates the plant and immediately leaves it) vs. more than one bite (an herbivore stays defoliating the plant for a longer time). This differential behavior might represent different preference degree among plants. Finally, we calculated the specific defoliation frequency, as the proportion of plants with defoliation signs.

Database on the grazing management of each paddock included the following information: (1) number of sheep; (2) animal categories included in the flock (mainly adult ewes and rams, but also lambs and first mating ewes in few situations); and (3) dates for the start and end of each grazing event. All sheep were Merino breed. We estimated grazing pressure in each paddock as the ratio between forage consumption (kg·dry matter ha^{-1}·yr^{-1}) and average ANPP (kg dry matter·ha^{-1}·yr^{-1}) of the area where vegetation survey was performed as a proxy of forage production. To estimate consumption, we used livestock stocking density, days of occupation, and daily consumption per animal considering animal categories. As reference, we considered that forage intake of a 40-kg sheep is 1 kg dry matter·d^{-1} (Agricultural Research Council 1980).

To estimate ANPP for each site, we selected a range of 1–4 representative MODIS pixels, which included the area where each vegetation survey was performed. For those pixels, the Normalized Difference Vegetation Index (NDVI) was extracted from the period 2001–2015. The NDVI is closely correlated with the fraction of photosynthetically active radiation absorbed by green vegetation (Sellers et al. 1992, Huete et al. 2002), which multiplied by the incoming photosynthetically active radiation (information available from weather stations), represents the photosynthetically active radiation absorbed by vegetation (APAR). This latter variable was used to estimate ANPP according to Monteith's model (Monteith 1972) of Eq. 1 (see Grigera et al. 2007, Irisarri et al. 2012 for methodological details)

$$ANPP_{ti} = APAR_{ti} \times RUE \qquad (1)$$

where $APAR_{ti}$ is the photosynthetically active radiation absorbed by green tissues ($MJ \cdot m^{-2} \cdot d^{-1}$) in the place where transect i was outlined; and RUE is the radiation use efficiency for aboveground production (g dry matter/MJ). For this study, we used RUE values from Patagonian steppes by Baldassini et al. (2012). ANPP values of Equation 1 expressed in g dry matter $\cdot m^{-2} \cdot d^{-1}$ were converted into kg dry matter $\cdot ha^{-1} \cdot yr^{-1}$ to estimate grazing pressure from forage consumption and ANPP in the same units, integrated over a year. We used average annual ANPP values data for all sites instead of data for individual years because remotely sensed data availability does not cover the whole period studied.

Data analysis

In order to study the main drivers of the proportion of defoliated plants and the defoliation degree in each species, we conducted a series of analyses. First, we used univariate models only considering the grazing pressure as an independent variable, given the relevance of understanding its isolated effect. Grazing pressure is the main control of defoliation, being critical for grazing management. Second, we considered all predictive variables using multiple regression models. Values of each response variable within each survey were averaged to obtain a single value per species per transect. We applied generalized linear models with a logit link for the proportion of defoliated plants, as prescribed for proportional response variables (Zuur et al. 2007). The same procedure was applied for the defoliation degree after transforming this variable into proportions, dividing each value by 3. We adjusted different functional forms for the relationship between the logit of the response variables (proportion of defoliated plants and defoliation degree) and grazing pressure (Table 1). The parameters of these models presented contrasting interpretations (Table 1). Best univariate model for each species was selected by means of Akaike information criterion (Burnham and Anderson 2002), which considers the trade-off between fit (residual error) and parsimony (i.e., model complexity in terms of number of parameters). For the multiple logistic regression models of each species, we considered a

Table 1. Models adjusted to the relationship between each response variable (rv; proportion of defoliated plants and defoliation degree) as a function of each predictive variable (pv; the grazing pressure, the density, the standing-dead biomass proportion).

Model name	Equation
Linear	$\text{logit}(rv) = a + b \times pv$
Type II functional response†	$\text{logit}(rv) = \frac{(\max(rv) - \min(rv)) \times rv}{k + pv} + \min(rv)$
Type III functional response†	$\text{logit}(rv) = \frac{(\max(rv) - \min(rv)) \times rv^2}{k^2 + pv^2} + \min(rv)$
Monomolecular‡	$\text{logit}(rv) = a \times (1 - e^{-b \times pv})$

† Soetaert and Herman (2009).
‡ Bolker (2007).

priori, in addition to grazing pressure, a set of independent variables: the density of the focus species, the density of each alternative forage species, the total grass density (sum of the three studied species), and the dead biomass proportion of the focus species. Most field surveys were performed when herbivores were grazing into the paddocks or immediately after herbivores' removal, but some surveys were performed in paddocks without animals at the sampling time. Thus, during an exploratory phase, we also considered cumulative resting time (days without herbivores) and cumulative grazing time (days with herbivores) as predictive variables. As these variables were not correlated with the response variables (and were correlated with grazing pressure), they were not considered in the main analyses. We adjusted models for the whole data set and for winter and summer periods separately (depending on when the last grazing event occurred or when data were collected in the case of exclosures). Multiple logistic regression models were simplified by removing the parameters that did not substantially improve the fit, following the parsimony criterion. Finally, we evaluated if response variables were correlated between each pair of species through Pearson's correlation analysis. All statistical analyses were performed with R software (version 3.4.3, 2017), packages bestglm, MASS, car, and AICcmodavg.

RESULTS

The relationship between the proportion of defoliated plants and grazing pressure varied
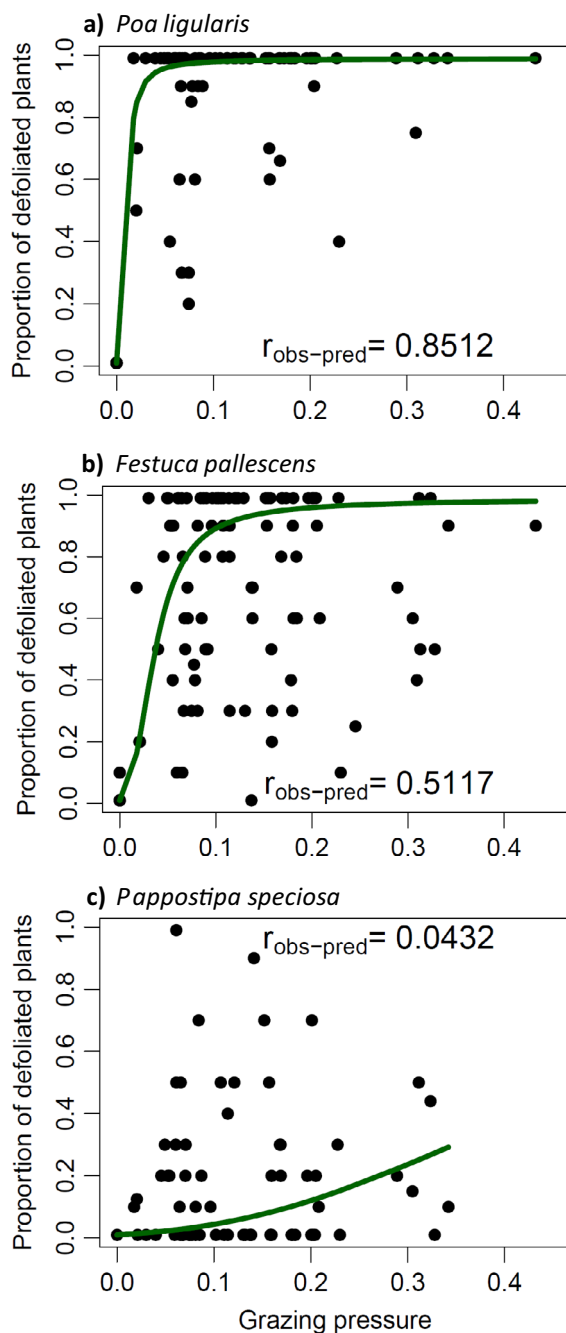
Fig. 2. Proportion of defoliated plants as function of

grazing pressure (univariate models) for each species: (a) *Poa ligularis* ($n = 88$), (b) *Festuca pallescens* ($n = 106$), and (c) *Pappostipa speciosa* ($n = 78$). The best-fitting model for each species corresponds to the type II functional response (Table 1; see the estimate of each model's parameter in Appendix S1: Table S1). Grazing pressure was estimated as the quotient between forage consumption and average ANPP of the area where each vegetation survey was performed.

exponential, although its strength was lower (observed-predicted $R = 0.5117$; $P < 0.001$). The 100% of defoliated plants was reached at a greater grazing pressure than for *P. ligularis* (Fig. 2b). For *P. speciosa*, sheep defoliated a low proportion of plants regardless of grazing pressure. The relationship between the proportion of defoliated plants and grazing pressure was weak (Fig. 2c; observed-predicted $R = 0.0432$; $P < 0.001$). Similar patterns were found for the degree of defoliation of individual plants, where grazing pressure explained the highest variability for *P. ligularis*, intermediate for *F. pallescens*, and the lowest for *P. speciosa*. In these latter two species, the relationship was very weak (Appendix S1: Fig. S2).

Best multiple models to predict the proportion of defoliated plants and the defoliation degree of plants differed, among species, in the number and sort of variables contained. These models were selected from more complex ones, which *a priori* included all evaluated variables. For *P. ligularis*, the most parsimonious model to estimate the proportion of defoliated plants included only grazing pressure as predictive variable (Table 2; Figs. 2a, 3a). Including the other variables (plant density, dead biomass proportion, and other species abundance) did not significantly improve the model predictive power. The average proportion of defoliated plants (both observed and predicted by the model) was higher than 90% (Fig. 3a). The most parsimonious model to estimate the defoliation degree of *P. ligularis*' plants included, aside the grazing pressure as a nonlinear response (asymptotic exponential), the density of *P. ligularis* (observed-predicted $R = 0.7419$). The defoliation degree linearly increased as the density decreased (Appendix S1: Table S2). In the case of *F. pallescens*, the proportion of defoliated plants increased until reaching a plateau as

among the studied grass species (Fig. 2). For *P. ligularis*, the relationship was asymptotic exponential, and 100% of defoliated plants was reached at very low grazing pressure (Fig. 2a; observed-predicted $R = 0.8512$; $P < 0.001$). For *F. pallescens*, the relationship was also asymptotic

grazing pressure rose, and it linearly decreased as both the dead biomass proportion and the density of *P. ligularis* increased (observed-predicted $R = 0.6366$; Table 2). The model did not improve when the abundance of this focus species (*F. pallescens*) was incorporated. The average proportion of defoliated plants (observed and predicted by the model) was almost 70% (Fig. 3 b). The defoliation degree of *F. pallescens*' plants increased non-linearly with grazing pressure and linearly decreased as the dead biomass proportion rose (observed-predicted $R = 0.4887$; Appendix S1: Table S2). For *P. speciosa*, the most parsimonious model to predict the proportion of defoliated plants included the dead biomass proportion and the joint abundance of both *P. ligularis* and *F. pallescens* (observed-predicted $R = 0.5122$; Table 2; Fig. 3c). As these predictive variables increased, the proportion of defoliated plants linearly decreased. The inclusion of grazing pressure did not significantly improve the model. The average proportion of defoliated plants (observed and predicted by the model) was lower than 20% (Fig. 3c). The defoliation degree of *P. speciosa* plants showed the same pattern as the proportion of defoliated plants (observed-predicted $R = 0.5437$; Appendix S1: Table S2).

The season when grazing occurred, summer or winter, interacted with the other predictive variables to determine the proportion of defoliated plants and the defoliation degree in the three species. Thus, multivariate models to predict these variables in summer were different from those for winter (Appendix S1: Tables S3 and S4). For *P. ligularis*, in summer, the proportion of defoliated plants increased non-linearly with grazing pressure, and linearly with *P. ligularis* density (observed-predicted $R = 0.9432$; Appendix S1: Table S3). Otherwise, in winter-grazed sites, the proportion of defoliated plants linearly increased with the grazing pressure and linearly declined as the density and the dead biomass proportion rose (observed-predicted $R = 0.3972$; Appendix S1: Table S3). For *F. pallescens*, the proportion of defoliated plants in summer non-linearly increased with grazing pressure and linearly decreased as *P. ligularis* density, the dead biomass proportion and *F. pallescens* density increased (observed-predicted $R = 0.6514$; Appendix S1: Table S3). In winter, the proportion of defoliated plants of this species rose non-linearly with grazing pressure and linearly decreased with *P. ligularis* density and the dead biomass proportion (observed-predicted $R = 0.5011$; Appendix S1: Table S3). Thus, the grazing pressure, the *P. ligularis* density, and the dead biomass proportion affected the proportion of defoliated plants of *F. pallescens* in the same way, both in summer and winter. For *P. speciosa*, the proportion of defoliated plants in summer increased with grazing pressure and the density of *P. speciosa*, and decreased as the dead biomass proportion and *P. ligularis* plus *F. pallescens* densities rose (observed-predicted $R = 0.6425$; Appendix S1: Table S3). All these responses were best modeled

Table 2. Selected best-fitting models to predict the proportion of defoliated plants for each species: *Poa ligularis* ($n = 88$), *Festuca pallescens* ($n = 106$), and *Pappostipa speciosa* ($n = 78$).

Characteristic	Estimate	SE	t/z	p	AIC
Poa ligularis†					
Grazing pressure	0.009546	0.002156	4.428	2.85e-05***	331.2
Festuca pallescens‡					
Grazing pressure	8.701.191	0.358029	24.30	<2e-16***	
Dead proportion	−0.036392	0.001827	−19.92	<2e-16***	4419.4
Density of *P. ligularis*	−0.114862	0.006824	−16.83	<2e-16***	
Pappostipa speciosa§					
Dead proportion	−0.043721	0.002162	−20.223	<2e-16***	
Density of *F. pallescens* + *P. ligularis*	−0.138076	0.009640	−14.323	<2e-16***	2308.7

Notes: The table shows the estimate of each parameter and its standard error, the t value for univariate model and z value for multivariate models, the p value, and the Akaike for the selected model of each species.

† For *Poa ligularis,* the relationship with the grazing pressure was best modeled as a type II functional response (Table 1).

‡ For *Festuca pallescens,* the relationship with the grazing pressure was best modeled as a monomolecular function and the rest of variables were best modeled as linear functions (Table 1).

§ For *Pappostipa speciosa,* the relationships with both predictive variables were best modeled as linear functions (Table 1).

a) *Poa ligularis*

$r_{obs-pred}$ = 0.8512

Observed prop. of defoliated plants

b) *Festuca pallescens*

$r_{obs-pred}$ = 0.6366

Observed prop. of defoliated plants

c) *P appostipa speciosa*

$r_{obs-pred}$ = 0.5122

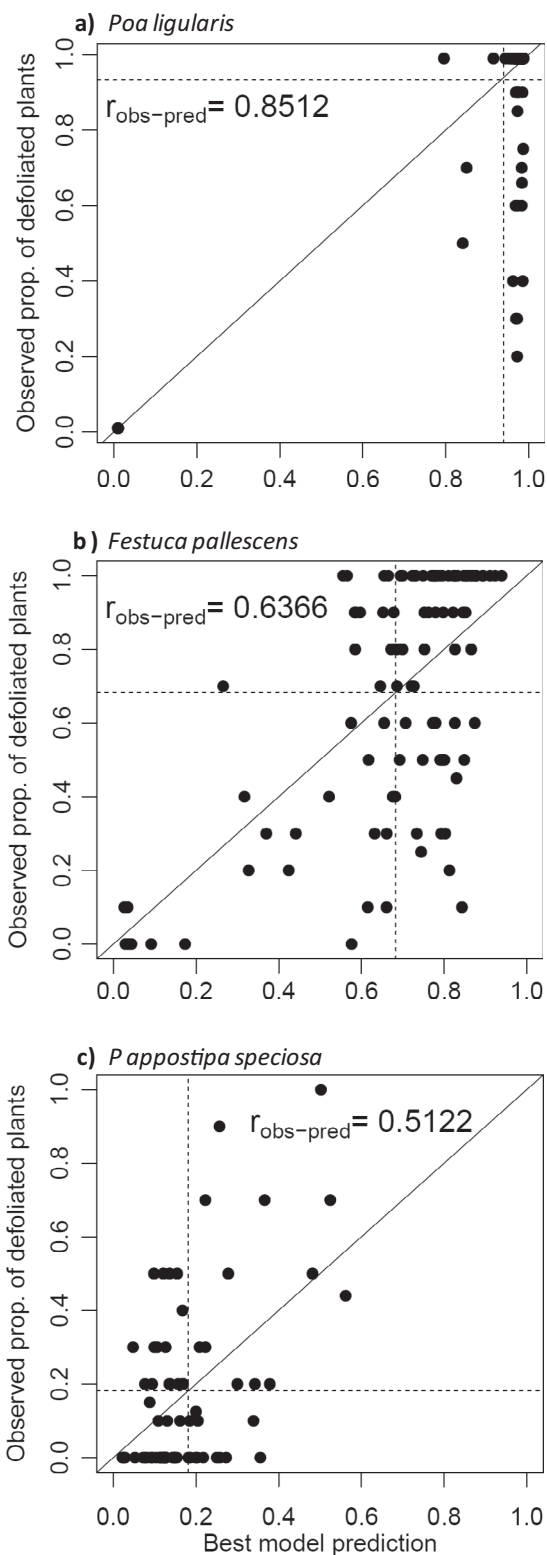Observed prop. of defoliated plants

Best model prediction

Fig. 3. Relationship between observed and

(Fig. 3. *Continued*)
predicted proportion of defoliated plants, generated by the best-fitting multiple logistic regression model for each species: (a) *Poa ligularis* ($n = 88$), (b) *Festuca pallescens* ($n = 106$), and (c) *Pappostipa speciosa* ($n = 78$). Dashed lines indicate observed and predicted means, and the solid line corresponds to the 1:1 relation.

as linear functions. In winter, the proportion of defoliated plants of this species linearly decreased with the rise of *P. ligularis* plus *F. pallescens* densities, the dead biomass proportion and the *P. speciosa* density (observed-predicted $R = 0.5336$; Appendix S1: Table S3). The defoliation degree of plants of the three species also exhibited different patterns in summer from those found in winter (see further details in Appendix S1: Table S4).

Finally, the proportion of defoliated plants in each transect was positively correlated among species. Thus, as one species presented high defoliation in a given transect, the others showed the same trend. *Poa ligularis* and *F. pallescens* exhibited the highest correlation coefficient (Pearson $R = 0.7115$; $P < 0.001$; $n = 83$), *F. pallescens* and *P. speciosa* showed intermediate correlation coefficient (Pearson $R = 0.5795$; $P < 0.001$; $n = 75$), and *P. ligularis* and *P. speciosa* showed the lowest correlation coefficient (Pearson $R = 0.3634$; $P < 0.001$; $n = 69$).

DISCUSSION

Our study showed empirical evidence of the preference by sheep among the main grasses of the western Patagonian steppes and on the main controls of sheep selectivity. Drivers considered in this study had not previously been evaluated simultaneously. Our approach allowed evaluating the relative importance of each driver on the defoliation pattern of each species. Field results indicated that defoliation patterns markedly depended on the grass species identity and confirmed that the studied species exhibit substantial differences in their preference degree by sheep: *P. ligularis*, *F. pallescens,* and *P. speciosa,* respectively, present high, intermediate, and low preference. These distinct preferences may be attributed to differences in species nutritive value and defenses, associated to differences in their chemical and morphological traits, such as

content of N, C, P, lignin, cellulose, and silica, leaf thickness, leaf tensile strength, and specific leaf area (Adler et al. 2004). For *P. ligularis*, the main driver of plant defoliation was grazing pressure. The relevance of the other evaluated variables was substantially lower. In addition to grazing pressure, plants of *F. pallescens* were more defoliated when the dead biomass proportion of plants and the abundance of *P. ligularis* decreased. For *P. speciosa*, the defoliation of plants was negatively related to their dead biomass proportion and the abundance of the two more defoliated species. In this species, defoliation was not strongly related to grazing pressure. Otherwise, the season when grazing occurred interacted with the other variables to determine defoliation patterns in the three species. Our findings support our hypothesis and suggest that (1) grazing pressure becomes a more relevant driver of defoliation as species preference increases; (2) grazing pressure effects on defoliation are markedly nonlinear; (3) preferred species abundance and the dead biomass proportion are the leading factors determining less preferred species defoliation, while grazing pressure played a minor role; and (4) grazing pressure management by itself is not enough to reduce the high defoliation of preferred species and increase the defoliation of non-preferred species.

The most preferred species, *Poa ligularis*, was highly consumed in all grazed situations, including those presenting low grazing pressure. This selection pattern indicates that herbivory by sheep could place preferred species at a competitive disadvantage due to severe defoliation, even under grazing conditions considered light or moderate (e.g., Teague et al. 2013). In turn, as a consequence of this shift in the competitive abilities, grazing can indirectly promote the dominance of species with low preference degree within the community (e.g., Moretto and Distel 1999). Reductions in grazing pressure do not lead to the recovery of dominance by preferred species over the short-term (Distel et al. 2005). These results support the notion that many continuously grazed rangelands may suffer a gradual degradation of their condition due to the reduction of high-quality forage species and the increase of less preferred ones, even under low animal stocking rate (Teague and Dowhower 2003, Teague et al. 2013). To avoid this process, it

has been proposed that grazing-rest (reducing herbivory frequency) might improve the status of preferred species populations, by preventing the repeated defoliation caused by continuous grazing (Moretto and Distel 1999, Paruelo et al. 2008, Oñatibia and Aguiar 2019, Oñatibia et al. 2020). Even though the scientific evidence supporting this statement is controversial (Briske et al. 2008), recent studies indicate that increasing the length of rest relative to graze time increase the plant biomass and ground cover compared to continuous grazing (McDonald et al. 2019). In Patagonian steppes, it has been recently demonstrated that grazing-rest enhance the growth of dominant forage grasses, especially during wet years (Oñatibia and Aguiar 2019). Nonetheless, it must be considered that resting a paddock implies a reduction in the number of animals (if the economic condition allows it) or to raise the stocking rates in other paddocks (if ranchers want to keep the animal number constant). This aspect highlights that ecological solutions to environmental problems are, in many cases, limited by economic or social constraints.

Defoliation patterns of the least preferred species (*P. speciosa*) indicate that increasing grazing pressure, even at high levels, may not significantly change the proportion of defoliated plants of species presenting low preference degree. This result contradicts, at least under the conditions of this study, the idea that increasing grazing pressure enhances the consumption of low-preferred species by decreasing the availability of forage per animal and, therefore, their selectivity (Hart et al. 1993). Manipulating grazing pressure within the wide range studied would not be enough to achieve greater use of less preferred species. To lead animals to consume a greater variety of plants, including this kind of species, other management tools may be necessary. For example, it has been shown that the consumption of *P. speciosa* (species with low N content) increases when the diet is strategically supplemented with urea (Golluscio et al. 1998*b*).

Dead biomass proportion of plants determined defoliation, mainly in the less selected species (*F. pallescens* and *P. speciosa*). It has been shown that the accumulated dead biomass can be an antiherbivore defense, reducing defoliation of forage species at individual plant level (Paruelo et al. 2008, Mingo and Oesterheld 2009). Besides,

grazing can modify plant structure and the dead biomass proportion, promoting a positive plant–animal feedback (Paruelo et al. 2008, Oñatibia and Aguiar 2019). Since defoliation is expected to reduce the standing-dead biomass proportion of plants in the medium and long term, past defoliation can determine current defoliation (Oñatibia and Aguiar 2019). This aspect may be managed together with the length of grazing-rests (periods when plants can accumulate dead biomass) to modify defoliation patterns. In short, results found here suggest that defoliation can also be controlled modifying the dead biomass proportion of plants through the management of the interaction between plant structures and grazing pressure.

The specific models predicted the proportion of defoliated plants at a satisfactory accuracy level, given the great environmental variability of the region studied. However, there was a relatively important proportion of the variability unexplained by the models, highlighting the ecological complexity of plant–animal interactions in these rangelands, which was not captured by the present study. Estimating grazing pressure through average animal consumption at paddock level is, no doubt, a source of uncertainty as herbivory pressure in a given patch may differ from the paddock average (Senft et al. 1985, Bailey 2005, Teague et al. 2013, Oñatibia and Aguiar 2018). Our results, showing that defoliation of less preferred species correlates with the defoliation of more preferred ones rather than with grazing pressure, would indicate that grazing intensity in the patch measured could only be partially represented by the paddock average consumption. Anyway, grazing pressure at paddock level becomes relevant as predictor because grazing management decisions are generally made at this level. Finally, other aspects associated with herbivore characteristics, which might be relevant as controls of selective defoliation and were not considered in this study, are animal age or category (e.g., ewes, lambs, rams), weight, body size, sex, and breed, as they may determine different animal nutritive requirements and behavior when foraging (e.g., Demment and Van Soest 1985, Stuth 1991).

Understanding diet selection and having the ability to predict diet shifts in response to changes in prey availability and prey quality are major issues in ecology (Sih and Christensen 2001). Though many studies contributed to understand selectivity patterns and prey replacement (e.g., Murdoch and Oaten 1975), empirical evidence on the main drivers of domestic herbivores selective defoliation and their relative importance in managed rangelands is scarce. Here, we developed novel conceptual models based on empirical field data that predict selective defoliation as function of grazing pressure, species abundance (community composition), and dead biomass proportion. This predictive value allows developing effective management practices to control key forage species defoliation, promoting a sustainable production in rangelands worldwide where species differently preferred by domestic herbivores coexist.

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