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## GRAZING ABANDONMENT NEGATIVELY AFFECTS FORAGE QUALITY IN IBERIAN ATLANTIC GRASSLANDS

### *El abandono del pastoreo afecta negativamente a la calidad del pasto en pastizales atlánticos ibéricos*

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**ABSTRACT:** Forage quality in mountain grasslands is an important factor for maintaining or improving animal performance. Previous studies identified plant traits beneficial for animal nutrition; however, little is known regarding their maintenance in plant communities. Our main hypothesis was that grazing favors plants with high regrowth capacity and low resource utilization efficiency, promoting the production of high-quality forage. To test the hypothesis, we conducted a grazer exclusion experiment in an Iberian Atlantic grassland combined with a *response-effect* framework based on various plant traits and an appropriate statistical methodology to measure the relative contribution of species turnover and intraspecific trait variability (ITV) after grazing abandonment. Our results showed that forage quality declined after short-term grazing abandonment, via strong ITV effects and weak species turnover effects. Strong species turnover effects might appear after longer period of abandonment if, as expected, tall grasses with low tissue quality outcompete species with high tissue quality.

**KEY WORDS:** Community response; effect traits; forage quality; grazer exclusion; intraspecific variability; species turnover.

**Abbreviations:** ITV, intraspecific trait variability; SLA, specific leaf area; H, plant height; CN, plant carbon to nitrogen ratio; CWM, community weighted mean; dBRDA, distance-based redundancy analysis.

**RESUMEN:** La calidad del pasto en los pastizales de montaña es un factor importante para mantener o mejorar el rendimiento animal. Estudios previos han identificado atributos vegetales beneficiosos para la nutrición animal; sin embargo, poco se sabe sobre su mantenimiento en comunidades vegetales. Nuestra principal hipótesis sostiene que el pastoreo favorece a las especies con una alta capacidad de rebrote y una baja eficiencia de utilización de recursos, promoviendo así la producción de pasto de alta calidad. Para testar la hipótesis, realizamos un experimento de exclusión del pastoreo en un pastizal de la montaña atlántica, combinado con un marco teórico de *respuesta-efecto* basado en varios atributos vegetales y una metodología estadística apropiada para medir la contribución relativa del recambio de especies y la variabilidad intraespecífica de los atributos (ITV) tras el abandono del pastoreo. Nuestros resultados mostraron que la calidad del pasto disminuyó tras el abandono del pastoreo a corto plazo, principalmente debido al efecto de la ITV. Los efectos por recambio de especies podrían aparecer tras un período más largo de abandono si, tal y como es esperable, las gramíneas altas con tejidos de baja calidad nutritiva sustituyen a las especies de mayor calidad.

**PALABRAS CLAVE:** Respuesta de la comunidad; atributos de efecto, calidad del forraje, exclusión de herbívoros, variabilidad intraespecífica, recambio de especies.

## 1. Introduction

Cattle and small ruminants, such as sheep and goats, consume 80% of the total animal feed produced worldwide (Herrero *et al.*, 2013). Grasslands occupy approximately 40% of the global terrestrial surface and provide many ecosystem services, including most of the biomass used by livestock (Lee *et al.*, 2017; Moreno García *et al.*, 2014). Therefore, forage quality (i.e., digestibility and nutritional value) in grassland systems influences the amount of consumed feed, efficiency of rumination, rate of animal weight gain, quality and volume of produced milk, and animal reproductive success (Herrero *et al.*, 2015). The quality of forage grasses is improved by reducing the proportion of fiber and increasing the proportion of protein (Lee *et al.*, 2017; Waghorn & Clark, 2004). Although much research has been carried out focusing on the introduction of traits beneficial for animal nutrition into plants, little is known regarding the maintenance of such traits in plant communities (Parsons *et al.*, 2011).

Grazing by domestic and wild ungulates affects ecosystem functions related to forage quality by promoting some plant traits over others (Deléglise *et al.*, 2015; Peco *et al.*, 2017). Thus, a response-effect framework based on plant traits (Lavorel & Garnier, 2002) may be a useful tool to understand the response of specific plant traits to grazing as well as their effect on the nutritional quality of produced forage. Plants use two main strategies against herbivores: avoidance (or defense) and tolerance (Díaz *et al.*, 2007; Van Der Meijden *et al.*, 1988). The latter, which is common in grasslands with high resource availability and long evolutionary history of grazing (Cingolani *et al.*, 2005), favors plant species with fast regrowth rate after defoliation (Peco *et al.*, 2017) and produces high-quality forage (Díaz *et al.*, 2007). Additionally, herbivores enhance nitrogen (N) inputs to the soil through their urine and feces, increasing the abundance of grass species with low fiber content and high N content (Pontes *et al.*, 2010, 2007). In this type of grassland, grazing abandonment promotes plant species that more efficiently compete for

light and utilize resources (Díaz *et al.*, 2001; McNaughton, 1984; Milchunas *et al.*, 1988), producing forage of low nutritional value.

Previous studies on Iberian Atlantic grasslands have shown that a reduction in forage quality occurred after cessation of grazing; specifically, lower protein concentration and digestibility, and higher fiber content were present (Odrizola *et al.*, 2014). In this study, we propose a hypothesis for the mechanism behind these changes in forage quality that is based on the tolerance strategy of the plants: grazing favors plants with high regrowth capacity and low resource utilization efficiency, promoting the production of forage with high nutritional value; conversely, grazing abandonment favors plants with the ability to compete for light and that have high resource utilization efficiency, promoting the production of low-quality forage. To test this hypothesis, grazing abandonment by mixed livestock (sheep, cattle, and horses) was experimentally simulated (five years of exclusion) using grazer-exclusion fences in productive grasslands of the Atlantic Iberian Peninsula. Then, in line with the mass-ratio hypothesis, plant traits of the most abundant (structural) species (covering at least 80% of the area) were measured to assess the effect of grazing abandonment on forage nutritional quality. The mass-ratio hypothesis states that the traits of dominant species largely determine the effect of plant communities on ecosystem functions (Grime, 1998). On the basis of this hypothesis, previous studies have successfully used the community weighted mean (CWM) of structural species to assess the effects of land-use changes on ecosystem processes (e.g., Garnier *et al.*, 2004, 2007; Quétier *et al.*, 2007). Usually, functional trait studies consider plant species as functionally homogeneous entities with no phenotypic plasticity; thus, the effect of intraspecific trait variability (ITV) on response capacity (plasticity) is disregarded. Nevertheless, most quantitative plant traits are highly variable within species (Albert *et al.*, 2010; Cornelissen *et al.*, 2003; Lepš *et al.*, 2011; Westoby *et al.*, 2002). Moreover, Lee *et al.* (2017) reported that intraspecific physiological responses were an im-

portant driver of forage quality worldwide. In order to include plasticity effects on community response to grazing abandonment and overcome the limitations of previous studies, plant traits were measured in two grassland sites in this study (Alotza & Uzkuiti) under grazing and non-grazing conditions. Additionally, the relative contribution of species turnover and ITV after grazing abandonment was measured using the statistical methodology developed by Lepš *et al.* (2011).

The objectives of this study were to test 1) whether grazing abandonment promotes the production of forage with low nutritional value; and 2) whether species turnover and ITV after grazing reinforce each other through selection of similar plant traits. Although previous studies have attempted to associate the response of plant traits to grazing (or cutting and nutrient addition) with their effects on herbivore nutrition (Cingolani *et al.*, 2005; Cruz *et al.*, 2010; Deléglise *et al.*, 2015; Moreno García *et al.*, 2014; Pontes *et al.*, 2010, 2007), to our knowledge, this is the first study to measure the relative contribution of species turnover and ITV after grazing abandonment using a specific statistical methodology.

**2. Materials and Methods**

*2.1. Study area*

Experiments were conducted in two semi-natural grasslands, Alotza (43°0'10.6" N, 2°5'22" W; 1,223 m elevation) and Uzkuiti (43°0'50" N, 2°4'3" W; 1,300 m elevation), located in the Aralar Natural Park, which is an 11,000 ha protected area located in the Atlantic Basque Country, Spain. The climate is oceanic with a mean annual temperature of 7°C and a mean annual precipitation of 1,330 mm. Aralar grasslands are used by mixed livestock in a moderate/high stocking rate (3.2 livestock units ha<sup>-1</sup> d<sup>-1</sup>; 13% beef cattle, 52% dairy sheep, and 35% horses; Odriozola *et al.*, 2014). Livestock herds are managed based on a short-distance transhumance system using lowland farms in winter/spring (December to April) and, more extensively, the upland grasslands in summer/fall (May to November). The park comprises productive native grasslands (mean aboveground net primary production of 1.97 ± 0.39 t dry mass ha<sup>-1</sup> yr<sup>-1</sup>; unpublished data)

with a calcareous substrate (Gibbons & Moreno, 2002). The grasslands (*Jasiono laevis-Danthonietum decumbentis* Loidi; Loidi, 1982) have a high conservation value (code 6230, 92/43/EEC; European Commission, 2013) and are associated with the production of a local cheese, Idiazabal, from the milk of the Latxa sheep breed (Batalla, 2015).

*2.2. Experimental design*

In May 2005, we installed a permanent 50 m × 50 m fence plot at each site (Alotza, Uzkuiti) to establish grazer exclusion plots (E plots). Attached to each E plot, we delineated a 50 m × 50 m plot (G plots), in which sheep, cattle, and horses were allowed to graze continuously during the vegetative period (May-November). Both sites are located in a flat terrain and have similar environmental characteristics and grazing pressures (Table 1). Species composition was not significantly different between E and G plots prior to fence establishment in May 2005 (Odriozola *et al.*, 2017). Soil from each plot was analyzed in July 2010 to measure pH, Kjeldahl total N (mg L<sup>-1</sup>), available phosphorus (P; mg L<sup>-1</sup>), available potassium (K; mg L<sup>-1</sup>), calcium (Ca; mg L<sup>-1</sup>), and magnesium (Mg; mg L<sup>-1</sup>). Soil water content was measured at 15 cm soil depth and at 2 h intervals from June 2010 to October 2011, using Em50 data loggers connected to an ECH2O sensor system (Decagon Devices Inc., Pullman, WA, USA).

*2.3. Plant sampling and traits*

In June 2010, the floristic composition in each plot was determined in 15 randomly placed 1 × 1 m<sup>2</sup> quadrats. Species abundance was measured as canopy cover using the following index: presence (<1%) and a scale from 1 (1-10%) to 10 (91-100%). Plant species nomenclature followed that of the standard floras (Table A1).

In this study, we evaluated the traits of the five most abundant (structural) species, common bent (*Agrostis capillaris* L.), chewing fescue (*Festuca nigrescens* subsp. *microphylla* [St.-Yves] Markgr.-Dannenb.), heath bedstraw (*Galium saxatile* L.), field wood-rush (*Luzula*

Table 1: Elevation, mean soil water content (MSWC, cm<sup>3</sup> cm<sup>-3</sup>) pH, soil nitrogen (mg L<sup>-1</sup>), soil phosphorous (mg L<sup>-1</sup>), soil potassium (mg L<sup>-1</sup>), soil calcium (mg L<sup>-1</sup>), soil magnesium (mg L<sup>-1</sup>), soil texture, and grazing intensity measured in two Iberian Atlantic grasslands (Alotza and Uzkuiti). LU, grazing livestock unit; cattle of over two years, 1.0 LU; sheep, 0.122 LU; horses, 1.2 LU.

Tabla 1: Altitud, media del contenido de agua en suelo (MSWC, cm<sup>3</sup> cm<sup>-3</sup>) pH, nitrógeno en suelo (mg L<sup>-1</sup>), fósforo en suelo (mg L<sup>-1</sup>), potasio en suelo (mg L<sup>-1</sup>), calcio en suelo (mg L<sup>-1</sup>), magnesio en suelo (mg L<sup>-1</sup>), textura del suelo, e intensidad de pastoreo medidas en dos pastos ibéricos atlánticos (Alotza y Uzkuiti). LU, unidad de ganado mayor; vacas mayores de 2 años, 1,0 LU; ovejas, 0,122 LU; caballos, 1,2 LU.

	Elevation (m)	MSWC	pH	N	P	K	Ca	Mg	Soil texture			Grazing intensity			
									Clay (%)	Silt (%)	Sand (%)	L.U.	Sheep (%)	Horse (%)	Cattle (%)
Alotza	1,225	0.29	5.1	6.27	7	97	389	70	44	39	17	4.5	54	12	34
Uzkuiti	1,300	0.40	5.1	5.33	6	83	413	85	42	38	20	4	40	26	34

*campestris* [L.] DC.), and white clover (*Trifolium repens* L.), which covered 88% of the total area in Alotza G, 89% of the total area in Alotza E, 82% of the total area in Uzkuiti G, and 84% of the total area in Uzkuiti E. For the characterization of species in G plots, four exclusion cages of 1 m<sup>2</sup> were placed at least 20 m away from each other in May 2012 prior to the grazing period to collect plants with no signs of defoliation by grazers or of trampling. In July 2012, the cages were removed, and individual plants were collected from each plot for evaluation.

The following traits were used to assess the ecological response to grazing (i.e., response traits): plant height (H, cm) and specific leaf area (SLA, m<sup>2</sup> kg<sup>-1</sup>), since they each represent two key dimensions of plant function (Díaz *et al.*, 2007, 2016). H is related to successional status and response to grazing (Díaz *et al.*, 2007), and SLA is related to relative growth rate and resource utilization efficiency (Westoby *et al.*, 2002). The traits used to estimate forage nutritional value (i.e., effect traits) were leaf N content (LNC, mg g<sup>-1</sup>) and carbon (C) to N ratio (CN). LNC is positively correlated to forage nutritional value and livestock productivity, and CN is related to fiber content and is negatively correlated with livestock productivity (Lee *et al.*, 2017). SLA, LNC, and CN were measured in seven randomly selected, fully grown, undamaged individuals from each species, whereas H was measured in 25 individuals from each species using a metallic ruler (Cornelissen *et al.*, 2003). SLA was defined as the one-sided area of a fresh leaf divided by its oven-dry mass. Hydrated and expanded leaves were scanned using an Epson Expression 10000 XL scanner (Epson, Suwa, Japan), and the area of each image (containing all the leaves of an individual) was measured using Win Folia 2008 (Regent Instruments, Ontario, Canada). The mass of the same leaves was measured using a precision balance after oven drying at 60°C for at least 72 h (Cornelissen *et al.*, 2003). After removing the petiole or rachis, powdered leaf samples were prepared and used to determine the C and N contents using combustion elemental analysis (AOAC, 1990). CN was obtained by dividing the C content by the N content per leaf dry mass.

#### 2.4. Data analysis

Distance-based redundancy analysis (dbRDA) was applied to test the null hypothesis of no effect of grazing abandonment on the abundances of the five structural species (Legendre & Legendre, 2012). The response matrix was created by Hellinger-transformation of the five-species composition matrix and computing Euclidean distances (Legendre & Gallagher, 2001). Analysis of variance (ANOVA) was fitted to each of the five structural species and four traits (H, SLA, LNC, and CN) to test the null hypothesis of no effect of grazer exclusion in the ITV of measured traits. Tukey's post-hoc test was used to separate the means. In all analyses, site (Alotza & Uzkuiti), treatment (G and E), and their interactions were used as explanatory variables.

The relative contribution of species composition and ITV to community response under grazer exclusion conditions was determined as described by Lepš *et al.* (2011). CWMs calculated using fixed trait averages (i.e., fixed mean trait value of each species for all individuals measured in the four plots) were only affected by changes in community floristic composition (species turnover), whereas CWMs calculated using specific trait averages for each field plot (i.e., specific mean trait value of each species in each plot) were affected by both changes in composition and ITV (i.e., ITV effect = specific average - fixed average). Linear models were used to test the null hypothesis of no effect of grazer exclusion on each community variable. Spearman correlation was performed to test the relationship between fixed and specific CWMs of response (H and SLA) and effect (LNC and CN) traits.

Variations in each trait were partitioned into fixed effects (species turnover), ITV effects, and their covariation by using the sum of squares (SS) decomposition of ANOVAs or linear models. Total variation in specific averages is the total variation in community trait averages (i.e., variation in fixed averages and ITV effects). Thus, if  $SS_{\text{specific}} = SS_{\text{fixed}} + SS_{\text{ITV}}$ , then changes in composition and ITV operate independently; if  $SS_{\text{specific}} > SS_{\text{fixed}} + SS_{\text{ITV}}$ , both effects are positively correlated; and if  $SS_{\text{specific}} < SS_{\text{fixed}} + SS_{\text{ITV}}$ , both effects are negatively correlated (Lepš *et al.*, 2011). The R code and data are provided in Supplementary Data B and C, respectively.

### 3. Results

#### 3.1. Effect of grazing abandonment on structural species composition

The permutation test of dbRDA revealed significant effects of grazing abandonment on the abundance of the five structural species (Table A2). *T. repens* was clearly associated with G plots, whereas *G. saxatile* was associated with E plots (Figure 1). *A. capillaris* tended to be associated with E plots, whereas *L. campestris* and *F. microphylla* were not affected by the plot type (Figure 1).

#### 3.2. Effect of grazing abandonment on ITV

The five structural species had high ITV in all plots regarding the studied traits (Tables 2, A3). In E plots, H and SLA showed high ITV since the individuals of the same species were considerably taller and had lower SLA (Table 2). In G plots, species also tended to have higher LNC and lower CN; however, the results were not consistent. For instance, *G. saxatile* had low LNC in the G plot of Uzkuiti, but high LNC in the G plot of Alotza (Table 2). Moreover, the LNC and CN of *F. microphylla* and *T. repens* were not affected by the plot type (Table A3c, 3d); in all plots, *F. microphylla* had low LNC and high CN, whereas *T. repens* had the highest LNC and the lowest CN (Table 2).



Table 2: Fixed and specific descriptive statistics of measured traits in five structural species under grazing and grazer-exclusion conditions in two Iberian Atlantic grasslands (Alotza and Uzkuiti). Agr cap, *Agrostis capillaris*; Fes mic, *Festuca microphylla*; Gal sax, *Galium saxatile*; Luz cam, *Luzula campestris*; Tri rep, *Trifolium repens*. Results of two-way ANOVAs performed for each species and trait are shown in Table A3. Different letters indicate significant differences at  $P < 0.05$ .

Tabla 2: Estadísticos descriptivos fijos y específicos de los atributos medidos en las cinco especies estructurales bajo condiciones de pastoreo y exclusión en dos pastos ibéricos atlánticos (Alotza y Uzkuiti). Agr cap, *Agrostis capillaris*; Fes mic, *Festuca microphylla*; Gal sax, *Galium saxatile*; Luz cam, *Luzula campestris*; Tri rep, *Trifolium repens*. Los resultados del ANOVA 2-factorial llevado a cabo para cada especie y atributo han sido presentados en la Table A3. Las diferentes letras indican diferencias significativas al  $P < 0,05$ .

	Fixed		Specific							
			Alotza Grazing		Alotza Exclusion		Uzkuiti Grazing		Uzkuiti Exclusion	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
<b>Height (cm)</b>										
Agr cap	15.1	0.8	7.5 A	0.5	14.9 B	0.7	11.7 C	0.4	26.4 D	1
Fes mic	15.7	0.7	8.9 A	0.8	14.7 B	0.5	12.3 C	0.3	27 D	0.6
Gal sax	8.7	0.4	5.1 A	0.5	8 B	0.4	6.9 B	0.3	14.6 C	0.5
Luz cam	10.4	0.5	6.2 A	0.5	10 B	0.6	8.1 B	0.3	17.2 C	0.7
Tri rep	7.1	0.3	5.1 A	0.4	7.5 B	0.3	7 B	0.5	8.9 B	0.6
<b>SLA (m<sup>2</sup> kg<sup>-1</sup>)</b>										
Agr cap	21.3	1.2	24.1 A	1.6	17.3 B	2	27 A	1.9	16.7 B	1.8
Fes mic	11.1	0.3	11.7 A	0.3	10.4 B	0.7	12.1 A	0.6	10.2 B	0.4
Gal sax	36.9	1.5	41.5 A	1.4	35.9 A	1.9	42.5 A	2.8	27.7 B	1.5
Luz cam	20.7	1.1	23.1 A	0.5	21.4 A	1	26.7 B	0.9	11.7 C	0.6
Tri rep	29.1	0.9	28.9 A	1.9	26.6 B	1.6	33 A	1.6	27.9 B	1.7
<b>Leaf N content (mg g<sup>-1</sup>)</b>										
Agr cap	18.3	0.7	18.7 A	0.8	14.4 B	0.2	22.7 C	1.1	17.3 A	1.1
Fes mic	14.9	0.5	15.3 A	0.7	12.9 A	1.1	14.9 A	0.7	16.4 A	1.2
Gal sax	24.9	0.8	24.1 AB	1.3	28.9 C	0.9	26.2 AC	0.9	20.4 B	0.9
Luz cam	15	0.7	19 A	0.5	16.5 AB	1	14.4 B	0.8	10.1 C	0.3
Tri rep	35.3	1.3	31.9 A	2.5	29.7 A	1.4	40 B	2.3	39.7 B	1.1
<b>Leaf C to N ratio</b>										
Agr cap	25.4	0.9	24.3 A	0.9	31.1 B	0.5	19.9 C	0.8	26.3 A	1.6
Fes mic	31	1.1	29.8 AB	1.6	36 A	2.6	30.2 AB	1.3	28.1 B	1.9
Gal sax	20.7	0.7	21.1 A	1.2	17.2 B	0.5	19.3 AB	0.7	25.4 C	1.3
Luz cam	32.4	1.6	23.9 A	0.7	28.2 AB	1.8	32.5 B	1.6	44.9 C	1.3
Tri rep	13.6	0.6	15.1 A	1.6	15.4 A	0.6	12.3 B	0.7	11.6 B	0.3

### 3.3. Relative contribution of species turnover and ITV to the response to grazing abandonment

Weak and inconsistent effects of grazing abandonment were observed when CWMs based on fixed trait averages were considered (Figure 2). H and CN tended to be higher, whereas LNC tended to be lower in E plots (Figure 2A, C, and D). However, SLA was reduced in the E plot of Alotza but increased in the E plot of Uzkuiti

(Figure 2B). However, strong and consistent effects of grazing abandonment were observed when specific CWMs were considered (Figure 2). H and CN were markedly higher, whereas SLA and LNC were markedly lower in E plots (Figure 2). Additionally, strong correlations were observed between response (H and SLA) and effect (LNC and CN) traits using both fixed and specific CWMs (Table 3). Plots with high H had low SLA and LNC but high CN; accordingly, plots with low H had

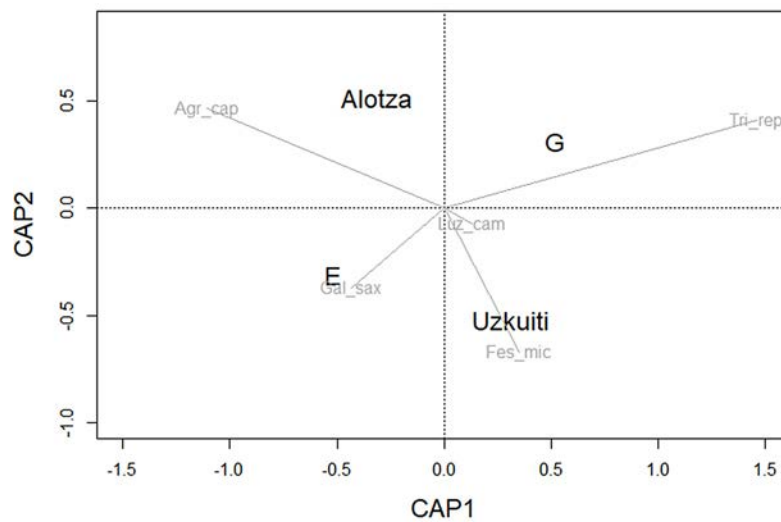


Figure 1. Distance-based redundancy analysis (dbRDA) triplot for associating structural species composition to fixed factors. Structural species composition as constrained by fixed factors, site (Alotza, Uzkuiti) and treatment (G, E). Permutation analysis of the dbRDA is provided in Table A2. G, grazing; E, grazer exclusion; Agr cap, *Agrostis capillaris*; Fes mic, *Festuca microphylla*; Gal sax, *Galium saxatile*; Luz cam, *Luzula campestris*; Tri rep, *Trifolium repens*. CAP1 and CAP2 represent the main and the second ordination axes respectively, in terms of represented variability.

Figura 1. Diagrama del análisis de redundancia basado en distancias (dbRDA) donde se asocia la composición de especies estructurales con los factores fijos. Composición de especies estructurales, constreñida por los factores fijos, Sitio (Alotza, Uzkuiti) y Tratamiento (G, E). El análisis de permutación del dbRDA ha sido presentado en la Tabla A2. G, pastoreo; E, exclusión; Agr cap, *Agrostis capillaris*; Fes mic, *Festuca microphylla*; Gal sax, *Galium saxatile*; Luz cam, *Luzula campestris*; Tri rep, *Trifolium repens*. CAP1 y CAP2 representan el primer y segundo eje de ordenación respectivamente, en términos de variabilidad representada.

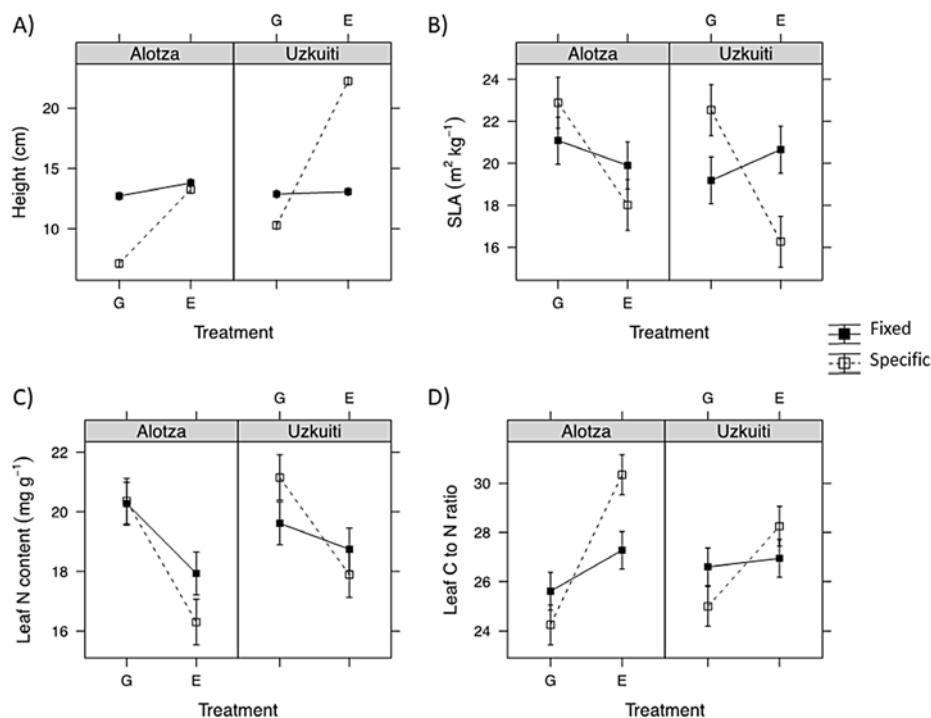


Figure 2. Fixed and specific community weighted means (CWMs) of measured traits in five structural species under grazing (G) and grazer-exclusion (E) conditions in two Iberian Atlantic grasslands (Alotza and Uzkuiti). Error bars represent 95% confidence intervals.

Figura 2. Medias ponderadas a nivel de comunidad (CWMs) fijas y específicas de los atributos medidos en las cinco especies estructurales bajo condiciones de pastoreo (G) y exclusión (E) en dos pastos ibéricos atlánticos (Alotza y Uzkuiti). Las barras de error representan el intervalo de confianza del 95%.

Table 3: Spearman correlation between fixed and specific community weighted means (CWMs) of measured traits in five structural species under grazing and grazer-exclusion conditions in two Iberian Atlantic grasslands (Alotza and Uzkuiti). A) Spearman correlation coefficients for fixed CWMs; B) Spearman correlation coefficients for specific CWMs.

Tabla 3: Correlación Spearman entre las medias ponderadas a nivel de comunidad (CWMs) fijas y específicas de los atributos medidos en las cinco especies estructurales bajo condiciones de pastoreo y exclusión en dos pastos ibéricos atlánticos (Alotza y Uzkuiti). A) Coeficiente de correlación Spearman para CWMs fijas; B) Coeficiente de correlación Spearman para CWMs específicas.

A)

	Height	SLA	Leaf N content
SLA	-0.64 ***		
Leaf N content	-0.77 ***	0.54 ***	
Leaf C to N ratio	0.62 ***	-0.65 ***	-0.94 ***

NS  $P > 0.05$ , \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

B)

	Height	SLA	Leaf N content
SLA	-0.87 ***		
Leaf N content	-0.65 ***	0.76 ***	
Leaf C to N ratio	0.72 ***	-0.80 ***	-0.96 ***

NS  $P > 0.05$ , \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

high SLA and LNC but low CN (Table 3). Species turnover and ITV selected similar H values after grazing abandonment, i.e., turnover and ITV effects were positively correlated; however, the contribution of turnover was almost negligible (Figure 3A). The difference in SLA between grazing regimes was mainly due to intraspecific variability; however, the interaction fraction (Site × Treatment bar in Figure 3B) showed negative covariance between turnover and ITV. This reflects the fact that while individuals of the same species presented lower SLA in the E plot of Uzkuiti, species with higher fixed SLA were more abundant in the same plot (Figure 2B). This inconsistency between turnover and ITV was not observed in Alotza (Figure 2B). For LNC and CN, turnover and ITV effects were important and consistent, i.e., both effects were positively correlated, and selected similar trait values (i.e., low LNC and high CN) after grazing abandonment (Figures 3C-3D).

#### 4. Discussion

Grasslands provide multiple ecosystem services, including forage supply for livestock (Herrero *et al.*, 2015). However, information on the maintenance of plant traits that support forage nutritional value in grasslands is limited (Parsons *et al.*, 2011). Consequently, decision making is conducted based on empirical observations of the performance of the grass crop, but the mechanisms behind this performance are rarely

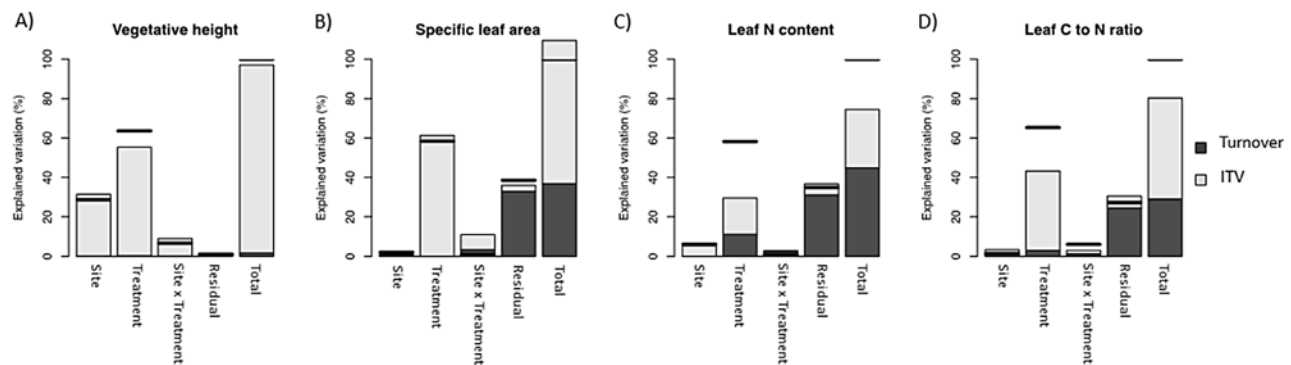


Figure 3. Decomposition of specific community weighted mean (CWM) variability into species turnover and intraspecific variability effects. Dark grey, changes in species composition; pale grey, changes in intraspecific variability. Black horizontal bars denote total variation (variation in specific averages). Fractions correspond to mean squares taken from ANOVA tables in Table A4. Space between the top of the column and the bar corresponds to covariation. Bar above the column indicates positive covariation/positive correlation between species turnover and intraspecific variability; bar across a column indicates negative covariation/negative correlation between species turnover and intraspecific variability; bar at the top of a column indicates independent effects. Values were standardized by total variation in specific averages.

Figura 3. Descomposición de la variabilidad de la media ponderada a nivel de comunidad (CWM) específica en los efectos debidos al recambio de especies y a la variabilidad intraespecífica. Gris oscuro, cambios en la composición de especies; gris claro, cambios en la variabilidad intraespecífica. Las barras negras horizontales indican la variación total (variación en medias específicas). Las fracciones corresponden a las medias cuadradas tomadas de las tablas de ANOVA de la Tabla A4. El espacio entre la parte superior de la columna y la barra corresponde a la covariación. La barra por encima de la columna indica una covariación positiva/correlación positiva entre el recambio de especies y la variabilidad intraespecífica; la barra que atraviesa la columna indica una covariación negativa/correlación negativa entre el recambio de especies y la variabilidad intraespecífica; La barra a la par de la parte superior de la columna indica efectos independientes. Los valores han sido estandarizados en base a la variación total de las medias específicas.

considered (Pontes *et al.*, 2015). In the present study, we aimed to investigate the underlying mechanisms of grassland community response to grazing using a framework based on plant traits (Cingolani *et al.*, 2005; Cruz *et al.*, 2010; Deléglise *et al.*, 2015; Moreno García *et al.*, 2014; Pontes *et al.*, 2010, 2007). To our knowledge, this is the first study of forage quality that has measured the relative contribution of species turnover and ITV after grazing abandonment by using a specific statistical methodology.

#### 4.1. Community response to grazing abandonment and effects on forage quality

The present study showed that the plant community had low aggregated values of H and high aggregated values of SLA under grazing conditions; however, this trend was reversed after grazing abandonment. These results were in agreement with those reported in previous studies (e.g., Cingolani *et al.*, 2005; Cruz *et al.*, 2010; Evju *et al.*, 2009; Moreno García *et al.*, 2014; Peco *et al.*, 2017), suggesting that tolerance to grazing is the main strategy against defoliation by herbivores in productive grasslands with a long history of grazing (Cingolani *et al.*, 2005; Díaz *et al.*, 2007). Response traits H and SLA were strongly associated with the effect traits LNC and CN, revealing that the shift in trait composition following the change in grassland strategy after grazing abandonment (from tolerance to grazing, to aboveground competition) explains the decline in forage quality reported in these grassland sites (Odriozola *et al.*, 2014). Theoretically, grazing tolerance requires high SLA, which increases shoot regrowth capacity (Westoby, 1999), and high LNC, which improves leaf quality and selectivity by herbivores (Cingolani *et al.*, 2005). However, light competition requires increased H to capture the light and a conservative resource utilization (i.e., low SLA) for a higher investment in structural components (i.e., high CN) (Cingolani *et al.*, 2005).

The production of forage of high quality under grazing conditions has been also reported in other sub-humid and humid grasslands where tolerance is the plant community strategy against herbivores (Cingolani *et al.*, 2005; Cruz *et al.*, 2010; Deléglise *et al.*, 2015). This has also been observed in the semi-arid grasslands of South Africa (Moreno García *et al.*, 2014), although intense grazing areas coincided with water points in this case. By contrast, in the mesic grasslands of France, where tolerance is combined with avoidance, some species showed reduced SLA and LNC with cutting (Pontes *et al.*, 2010, 2007). Our results were in agreement with those of humid grasslands since the mean annual precipitation in Iberian Atlantic grasslands is 1,330 mm. Fertilization favors a resource acquisition strategy and may also improve forage quality (Pontes *et al.*, 2010, 2007). Since defoliation by herbivores is always coupled with fertilization by urine and feces (Lezama & Paruelo, 2016), community response is probably a combination of tolerance to defolia-

tion and response to fertilization, but these two effects cannot be disentangled in our study.

#### 4.2. Species turnover and ITV effects on the response to grazing abandonment

In agreement with the results of previous studies, the traits measured in the present study showed high ITV (Albert *et al.*, 2010; Cornelissen *et al.*, 2003; Lepš *et al.*, 2011; Westoby *et al.*, 2002). Pontes *et al.* (2007) observed higher between-species variation than within-species variation. We also found that species could be distinguished based on the mean values of traits; however, the exclusion of ITV resulted in a clear underestimation of community response to grazing abandonment for all traits. Similarly, Lee *et al.* (2017) claimed that intraspecific physiological response is an important driver of forage quality worldwide.

We observed a mismatch between species turnover and ITV effects on the response to grazing abandonment for H and SLA; the effects of species turnover were very weak, whereas those of ITV were very strong. The lack of clear association of the tall grasses *F. microphylla* and *A. capillaris* with E plots along with the abundance of the short dicot *G. saxatile* might explain the weak species turnover effect. Five years after grazing abandonment, opposite effects of species turnover and ITV were observed for SLA in Uzkuiti, as indicated by the negative covariance between species turnover and ITV (Figure 3B). This response was probably a result of the high abundance of *G. saxatile* (very high SLA) in the E plot. However, long-term changes in floristic composition were observed after grazing abandonment (nine years in both sites): *F. microphylla* and *A. capillaris* became the most abundant species in the E plots (Odriozola *et al.*, 2017). Our results are in agreement with those reported by Lepš *et al.* (2011), who suggested that ITV determines the resistance and stability of grasslands to short-term changes, while species turnover reflects processes associated with the resilience of grasslands to long-term changes.

The contributions of species turnover and ITV were more equilibrated for LNC and CN. *T. repens*, which showed very high LNC and very low CN (Table 2), was the most sensitive species to grazing abandonment and was clearly more abundant on G plots. This species is highly digestible and nutrient-rich, and is widely cultivated for animal nutrition (Parsons *et al.*, 2011). Our results demonstrated that *T. repens* is fundamental for maintaining the high nutritional value of Iberian Atlantic grasslands.

#### 4.3. Management implications

Previous studies have reported reductions in forage quantity along with improvement in quality under grazing conditions (Cruz *et al.*, 2010; Deléglise *et al.*, 2015; Moreno García *et al.*, 2014). Accordingly, an increase in



the annual aboveground net primary productivity has been observed in Iberian Atlantic grasslands after grazing abandonment (unpublished data). Cruz *et al.* (2010) claimed that the reduction in forage availability under grazing conditions is incompatible with the high animal productivity, whereas Moreno García *et al.* (2014) argued that the improved forage quality might compensate the reduction in quantity. It is widely accepted that both forage digestibility and nutritive value have direct effects on animal performance (Herrero *et al.*, 2015; Lee *et al.*, 2017). Additionally, although short-term grazing abandonment positively affects grassland productivity, long-term grazing abandonment has negative effects because litter accumulation inhibits plant growth (Patton *et al.*, 2007).

Our study revealed that ITV responded quickly to grazing abandonment and determined the short-term changes in forage quality. Strong species turnover effects may appear after long-term grazing abandonment when tall grasses with tissue of low quality outcompete high forage quality species (Odriozola *et al.*, 2017). The use of mountain grasslands by domestic livestock has declined slowly in most of the Pyrenean-Basque-Cantabrian grassland systems (Ruiz *et al.*, 2009), and significant management changes, including shorter duration in upland grasslands, lower stocking rate, and less shepherd control, have been identified (Aldezabal *et al.*, 2015). Our study suggested that an active management system of livestock herds is necessary to prevent damage to grasslands associated with long periods of grazing abandonment. Short-term ITV-based changes in forage nutritional value are easily reversible; however, recovery times are much longer when changes are caused by species turnover effects, and high tissue quality species may be reduced in abundance or eliminated. This study also identified *T. repens* as a key indicator of forage quality and successional status in Iberian Atlantic grasslands.

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## References

- Albert, C.H., Thuiller, W., Yoccoz, N.G., Soudant, A., Boucher, F., Saccone, P. & Lavorel, S., 2010. Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology*, 98: 604–613. <https://doi.org/10.1111/j.1365-2745.2010.01651.x>
- Aldezabal, A., Moragues, L., Odriozola, I. & Mijangos, I., 2015. Impact of grazing abandonment on plant and soil microbial communities in an Atlantic mountain grassland. *Applied Soil Ecology*, 96: 251–260. <https://doi.org/10.1016/j.apsoil.2015.08.013>
- AOAC, 1990. *Official Method of Analysis of the Association of Official Analytical Chemists*. 15<sup>th</sup> Edition, AOAC International Publisher, Washington DC.
- Batalla, I. 2015. *Opportunities and challenges of sheep milk system towards sustainability*. PhD Thesis, UPV/EHU, Bilbo.
- Cingolani, A.M., Posse, G. & Collantes, M.B., 2005. Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands. *Journal of Applied Ecology*, 42(1): 50–59. <https://doi.org/10.1111/j.1365-2664.2004.00978.x>
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G. & Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51(4): 335–380. <https://doi.org/10.1071/BT02124>
- Cruz, P., De Quadros, F.L.F., Theau, J.P., Frizzo, A., Jouany, C., Duru, M. & Carvalho, P.C.F., 2010. Leaf Traits as Functional Descriptors of the Intensity of Continuous Grazing in Native Grasslands in the South of Brazil. *Rangeland Ecology & Management*, 63(3): 350–358. <https://doi.org/10.2111/08-016.1>
- Deléglise, C., Meisser, M., Mosimann, E., Spiegelberger, T., Signarbieux, C., Jeangros, B. & Buttler, A., 2015. Drought-induced shifts in plants traits, yields and nutritive value under realistic grazing and mowing managements in a mountain grassland. *Agriculture, Ecosystems and Environment*, 213: 94–104. <https://doi.org/10.1016/j.agee.2015.07.020>
- Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D. & Gorné, L.D., 2016. The global spectrum of plant form and function. *Nature*, 529 (7585): 167–171. <https://doi.org/10.1038/nature16489>
- Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H. & Campbell, B.D., 2007. Plant trait responses to grazing – a global synthesis. *Global Change Biology*, 13(2): 313–341. <https://doi.org/10.1111/j.1365-2486.2006.01288.x>
- Díaz, S., Noy-Meir, I. & Cabido, M., 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits?. *Journal of Applied Ecology*, 38(3): 497–508. <https://doi.org/10.1046/j.1365-2664.2001.00635.x>
- European Commission, D.E. 2013. *Interpretation manual of European Union habitats*. EUR 28. DG-ENV, Luxemburg, LU.
- Evju, M., Austrheim, G., Halvorsen, R. & Mysterud, A., 2009. Grazing responses in herbs in relation to herbivore selectivity and plant traits in an alpine ecosystem. *Oecologia*, 161(1): 77–85. <https://doi.org/10.1007/s00442-009-1358-1>
- Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Doležal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V.P., Qested, H., Quéfier, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J.-P., Thébault, A., Vile, D. & Zarovali, M.P., 2007. Assessing the effects of land-use change on plant traits,

- communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Annals of Botany*, 99(5): 967–85. <https://doi.org/10.1093/aob/mcl215>
- Garnier, E., Ortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, J.-P., 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, 85(9): 2630–2637. <https://doi.org/10.1890/03-0799>
- Gibbons, W., Moreno, M.T., 2002. *The geology of Spain*. The Geological Society, London, UK.
- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, 86(6): 902–910. <https://doi.org/10.1046/j.1365-2745.1998.00306.x>
- Herrero, M., Havlik, P., Valin, H., Notenbaert, A., Rufino, M.C., Thornton, P.K., Blummel, M., Weiss, F., Grace, D. & Obersteiner, M., 2013. Biomass use, production, feed efficiencies, and greenhouse gas emissions from global livestock systems. *Proceedings of the National Academy of Sciences*, 110(52): 20888–20893. <https://doi.org/10.1073/pnas.1308149110>
- Herrero, M., Wiersenius, S., Henderson, B., Rigolot, C., Thornton, P., Havlik, P., de Boer, I. & Gerber, P.J., 2015. Livestock and the Environment: What Have We Learned in the Past Decade?. *Annual Review of Environment and Resources*, 40(1): 177–202. <https://doi.org/10.1146/annurev-environ-031113-093503>
- Lavorel, S. & Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, 16(5): 545–556.
- Lee, M.A., Davis, A.P., Chagunda, M.G.G. & Manning, P., 2017. Forage quality declines with rising temperatures, with implications for livestock production and methane emissions. *Biogeosciences*, 14(6): 1403–1417. <https://doi.org/10.5194/bg-14-1403-2017>
- Legendre, P. & Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129: 271–280. <https://doi.org/10.1007/s004420100716>
- Legendre, P. & Legendre, L., 2012. *Numerical Ecology*, 3rd English Edition, 3rd ed. Elsevier science, Amsterdam.
- Lepš, J., de Bello, F., Šmilauer, P. & Doležal, J., 2011. Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. *Ecography*, 34(5): 856–863. <https://doi.org/10.1111/j.1600-0587.2010.06904.x>
- Lezama, F. & Paruelo, J., 2016. Disentangling grazing effects: trampling, defoliation and urine deposition. *Applied Vegetation Science*, 19(4): 557–566. <https://doi.org/10.1111/avsc.12250>
- Loidi, J., 1982. Datos sobre la vegetación de Guipúzcoa (País Vasco). *Lazaroa*, 4: 1085–1093.
- McNaughton, S.J., 1984. Grazing lawns: Animals in herds, plant form and coevolution. *American Naturalist*, 124(6): 863–886. <https://doi.org/10.1086/284321>
- Milchunas, D.G., Sala, O.E. & Lauenroth, W.K., 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist*, 132(1): 87–106.
- Moreno García, C.A., Schellberg, J., Ewert, F., Brüser, K., Canales-Prati, P., Linstädter, A., Oomen, R.J., Ruppert, J.C. & Perelman, S.B., 2014. Response of community-aggregated plant functional traits along grazing gradients: Insights from African semi-arid grasslands. *Applied Vegetation Science*, 17(3): 470–481. <https://doi.org/10.1111/avsc.12092>
- Odrizola, I., García-Baquero, G., Fortin, M.-J., Laskurain, N.A. & Aldezabal, A., 2017. Grazing exclusion unleashes competitive plant responses in Iberian Atlantic mountain grasslands. *Applied Vegetation Science*, 20(1): 50–61. <https://doi.org/10.1111/avsc.12277>
- Odrizola, I., García-Baquero, G., Laskurain, N.A. & Aldezabal, A., 2014. Livestock grazing modifies the effect of environmental factors on soil temperature and water content in a temperate grassland. *Geoderma*, 235–236: 347–354. <https://doi.org/10.1016/j.geoderma.2014.08.002>
- Parsons, A.J., Edwards, G.R., Newton, P.C.D., Chapman, D.F., Caradus, J.R., Rasmussen, S. & Rowarth, J.S., 2011. Past lessons and future prospects: Plant breeding for yield and persistence in cool-temperate pastures. *Grass and Forage Science*, 66(2): 153–172. <https://doi.org/10.1111/j.1365-2494.2011.00785.x>
- Patton, B.D., Dong, X., Nyren, P.E. & Nyren, A., 2007. Effects of Grazing Intensity, Precipitation, and Temperature on Forage Production. *Rangeland Ecology & Management*, 60(6): 656–665. <https://doi.org/10.2111/07-008R2.1>
- Peco, B., Navarro, E., Carmona, C.P., Medina, N.G. & Marques, M.J., 2017. Effects of grazing abandonment on soil multifunctionality: The role of plant functional traits. *Agriculture, Ecosystems & Environment*, 249: 215–225. <https://doi.org/10.1016/j.agee.2017.08.013>
- Pontes, L.D.S., Louault, F., Carrère, P., Maire, V., Andueza, D. & Soussana, J.F., 2010. The role of plant traits and their plasticity in the response of pasture grasses to nutrients and cutting frequency. *Annals of Botany*, 105(6): 957–965. <https://doi.org/10.1093/aob/mcq066>
- Pontes, L.D.S., Maire, V., Schellberg, J. & Louault, F., 2015. Grass strategies and grassland community responses to environmental drivers: a review. *Agronomy for Sustainable Development*, 35(4): 1297–1318. <https://doi.org/10.1007/s13593-015-0314-1>
- Pontes, L.D.S., Soussana, J.F., Louault, F., Andueza, D. & Carrère, P., 2007. Leaf traits affect the above-ground productivity and quality of pasture grasses. *Functional Ecology*, 21(5): 844–853. <https://doi.org/10.1111/j.1365-2435.2007.01316.x>
- Quétier, F., Thébaud, A. & Lavorel, S., 2007. Plant traits in a state and transition framework as markers of ecosystem response to land-use change. *Ecological Monographs*, 77(1): 33–52. <https://doi.org/10.1890/06-0054>
- Ruiz, R., Diez-Unquera, B., Beltrán de Heredia, I., Mandaluniz, N., Arranz, J., Ugarte, E., 2009. The challenge of sustainability for local breeds and traditional systems: dairy sheep in the Basque Country. Proceedings of the 60<sup>th</sup> Annual Meeting of the European Association for Animal production, pp. 73. Barcelona.
- Van Der Meijden, E., Wijn, M. & Verkaar, H.J., 1988. Defence and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos*, 51: 355–363.
- Waghorn, G.C. & Clark, D.A., 2004. Feeding value of pastures for ruminants. *New Zealand Veterinary Journal*, 52(6): 320–331. <https://doi.org/10.1080/00480169.2004.36449>
- Westoby, M., 1999. The LHS strategy scheme in relation to grazing and fire. In: Eldridge, D. & Freudenberger, D. (Eds.), *People and Rangelands Building the Future*. VI International Rangeland Congress INC, pp. 893–896.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J., 2002. Plant Ecological Strategies: Some Leading Dimensions of Variation Between Species. *Annual Review of Ecology and Systematics*, 33(1): 125–159. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150452>

### Supplementary material

- Appendix A.
- Appendix B.
- Appendix C.