



# Decoupling of traditional burnings and grazing regimes alters plant diversity and dominant species competition in high-mountain grasslands

Leire Múgica<sup>a,\*</sup>, Rosa M. Canals<sup>a</sup>, Leticia San Emeterio<sup>a</sup>, Javier Peralta<sup>b</sup>

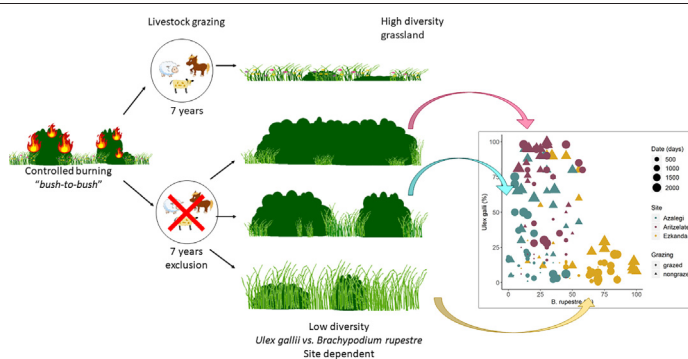
<sup>a</sup> Institute for Innovation & Sustainable Development in Food Chain (IS-FOOD), Departamento de Agronomía, Biotecnología y Alimentación, Universidad Pública de Navarra. Campus de Arrosadía 31006, Pamplona, Spain

<sup>b</sup> Departamento de Ciencias, Universidad Pública de Navarra. Campus de Arrosadía 31006, Pamplona, Spain

## HIGHLIGHTS

- Decoupling of controlled burns and traditional grazing occurs in many pasturelands.
- After traditional burns, the occurrence of herbivory influences grassland evolution.
- Regular extensive grazing decreases the competition among shrubs and tall-grasses.
- Regular extensive grazing significantly increases plant diversity in grasslands.
- Without grazing, site features define dominant species and community evolution.

## GRAPHICAL ABSTRACT



## ARTICLE INFO

### Article history:

Received 8 February 2021

Received in revised form 14 May 2021

Accepted 16 May 2021

Available online 23 May 2021

Editor: Manuel Esteban Lucas-Borja

### Keywords:

Land-use changes  
Pyric herbivory  
Grazing cessation  
Shrub encroachment  
Tall-grass dominance  
Grassland diversity

## ABSTRACT

Over millennia, the combination of controlled burnings and extensive grazing has maintained mosaic landscapes and preserved mountain grasslands in southern Europe. In the last century, deep socio-economic changes have led to an abandonment of traditional uses, to a general decline of the domestic herbivory and to a misuse of burning practices. This study aims to quantify how the decoupling of burning and grazing regimes affects in the long-term the structure, diversity and dynamics of high-mountain, shrub-encroached grasslands. In spring 2012, four treatments (burned-grazed, burned-ungrazed, unburned-grazed and unburned-ungrazed) were set up at three sites in the Special Area of Conservation Roncesvalles-Selva de Irati, in southwest Pyrenees. During seven years, we monitored floristic composition and the height of the native tall-grass *Brachypodium rupestre* in four plots at each site. In the burned plots, we surveyed the resprout of the dominant shrub *Ulex gallii* and the dynamics of recovering of the herbaceous vegetation. Plant communities evolved differently in grazed and ungrazed plots. Extensive grazing, despite being lower than in previous decades, maintained plant diversity and limited shrub encroachment. The total absence of grazing fostered the encroachment of *U. gallii* at two sites and the expansion of *B. rupestre* at the other site. When *B. rupestre* cover was >60%, the encroachment of *U. gallii* was reduced. This research highlights the competition that occurs between shrubs and tall-grasses in the absence of grazing, and the modulating effect exerted by the burnings and the site-specific features. Understanding local plant dynamics is the first step to design the most appropriate practices that help to preserve diversity at the landscape and the community level in high-mountain grasslands of south Europe.

© 2021 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

\* Corresponding author.

E-mail address: [leire.mugica@unavarra.es](mailto:leire.mugica@unavarra.es) (L. Múgica).

## 1. Introduction

The combination of fires and herbivory is at the origin of most natural grasslands worldwide: fire is a main abiotic disturbance of grasslands, and herbivores their primary consumers (Herrero and Thornton, 2013; Johansson et al., 2012; Leys et al., 2018; Limb et al., 2011). The spatial and temporal interaction between these two disturbances, pyric herbivory sensu Fuhlendorf et al. (2009), has historically originated and preserved complex landscapes that encompass open habitats of high ecological value (Fuhlendorf and Engle, 2004; Valkó et al., 2018; Vera, 2000; Zhang et al., 2018).

Vegetation dynamics in response to different regimes of pyric herbivory, interacting with other landscape drivers, generate various states of plant communities (Briske et al., 2005) such as different types of grasslands or woody plant communities assembled in heterogeneous and discontinuous patches (Van Langevelde et al., 2003). In some particular situations, non-reversible, alternate stable states may occur, as a response of crossing structural (e.g. disturbance suppression/intensification) or functional (e.g. soil erosion) thresholds (Briske et al., 2005; Pausas and Bond, 2019). The decoupling of traditional fire and grazing regimes may have negative consequences in diverse grasslands, and lead in the worse situations to alternate stable states of very complex recovery (Briggs et al., 2005; Suding et al., 2004).

The interaction between fire and herbivory has been studied in different ecosystems around the world. Firstly, in African savannas exposed to natural regimes of fires and wild herbivory (McNaughton, 1983). Latter, in North American rangelands and in Australian grassland ecosystems, leading to the development of a comprehensive theoretical framework to emulate the health of ecosystems managed by anthropogenic burnings and domestic herbivores (Bestelmeyer et al., 2017; Briggs et al., 2005; Briske et al., 2005; Fuhlendorf and Engle, 2004; Hill et al., 2005). In southern Europe, the most important surfaces of remaining natural grasslands occur in mountain areas, and the structuring role of burning and grazing has been much less studied (Alados et al., 2019; Komac et al., 2013), although it has been demonstrated that both disturbances have been crucial in their generation (Rius et al., 2009).

In the Pyrenees, traditional and sustainable land-use has maintained mosaic landscapes since Prehistory (Miras et al., 2010), and the use of pyric herbivory has persisted on the western side until recent years (Coughlan, 2014; Métaillé, 2006). However, rural societies have undergone deep changes during the last decades, altering the regime of pastoral burnings and grazing in mountains (Canals, 2019; Coughlan, 2013), associated with a loss of the traditional knowledge about the combination of these practices (Fernández-Giménez and Fillat, 2012). Nowadays, extensive livestock systems in the Pyrenees are characterized by a dominance of cattle versus sheep flocks, shorter residence times for herds, declining stocking rates, and less active shepherding compared to past centuries (Aldezabal et al., 2015; Coughlan, 2013). The relaxation of livestock grazing pressure on mountains has favoured shrub encroachment of grasslands and a misuse of fire, either increasing in frequency or disappearing completely. The changes in the traditional fire and grazing regimes have led to four different situations regarding grassland dynamics:

- (1) shrubland encroachment in the short term and forest regeneration in the long term (climax theory; Clements, 1936).
- (2) afforestation of open landscapes through tree expansion with little or no presence of associated shrubs (Dovčiak et al., 2015), such as pines in the subalpine grasslands (also associated with climate change, Battlori and Gutiérrez, 2008).
- (3) establishment of dense shrublands with low capability to evolve to other successional communities, such as dense gorselands of *Ulex gallii* Planch. (Múgica et al., 2018) and hedgehog-heaths of *Echinospartum horridum* (Vahl) Rothm. (Komac et al., 2013).
- (4) replacement of grazing-tolerant species by taller and more competitive native grasses (Pardo et al., 2015), such as *Agrostis curtisii*

Kerguelen (Amezaga et al., 2004) or *Brachypodium rupestre* (Host) Roem. & Schult., that constitute in the last stages monodominant, degraded covers highly stable in time (Canals et al., 2017; Niedrist et al., 2009).

All these situations are causing the reduction of the area of natural grasslands of high ecological value (Ascoli et al., 2013; Lasanta et al., 2015; Pe'er et al., 2014) and the loss of the ecosystem services provided by them, particularly those related to their diversity and provisioning value (Durán et al., 2020). In this scenario of climate change and shifting land-use, it is crucial to monitor the long-term evolution of plant communities and the guilds of species that may be favoured to establish the minimum threshold of traditional activities necessary to maintain the biodiversity and ecological value of the ecosystems. This research aims to evaluate how the decoupling of traditional burning and livestock grazing affects in the long term the floristic composition, structure, and diversity of grasslands with early signs of gorse encroachment, focusing particularly on the dynamics of two crucial species in western Pyrenees, the gorse *U. gallii* and the tall-grass *B. rupestre*. In order to determine whether management protocols for mountain grasslands conservation can be generalized or need to be fitted at local scale, we selected three close areas with particular site-specific characteristics that were described in detail with respect to topography, soils, vegetation and livestock grazing pressure. We hypothesize that the burning practice, when isolated and not combined with an extensive grazing, may conduct to a non-reversible alternate stable state, represented by a rapid loss of diversity and a dominance of a strong native competitor (*U. gallii* or *B. rupestre*). In certain circumstances, the current grazing regime, despite being lower than in previous decades, emerges as a crucial tool to preserve the ecological dynamics of high-valuable, inherited mountain grasslands.

## 2. Materials and methods

### 2.1. Study area and site characterization

The study area is situated in the Aezkoa Valley in the southwest Pyrenees (43°0'N, 1°10'W), located in the Special Area of Conservation Roncesvalles-Selva de Irati (Natura 2000 network, code ES0000126). The climate, influenced by the nearby Atlantic Ocean, is snowy and cold in winter and temperate and foggy in summer. The mean annual precipitation is 1990 mm and the mean annual temperature is 9.3 °C (see Supplementary material, Fig. S1). The vegetation of the area is a mosaic of beech forests, shrublands of gorse (*U. gallii*), and natural grasslands.

In early spring 2012, we selected three different sites (Ezkanda, Azalegi and Aritzelate) in a lightly shrub-encroached grassland area. The experimental sites were located relatively close to each other (<1 km linear distance) at similar altitudes (1080–1100 m a.s.l.) and comparable slopes (>15°), but with different exposures (S to NE). In March 2012, physical and chemical analyses of soils (0–10 cm depth) were conducted. Soils were deep and acidic, with loamy and clay-loam textural classes, high organic matter content, high cation exchange capacity and moderate total nutrient contents (Table 1).

A floristic survey was conducted in July 2012 to describe the preburning plant communities. The relative abundance of functional groups before burning was ≤5% shrubs (mainly *U. gallii*), 60–70% graminoids (perennial grasses such as *Festuca rubra* L., *B. rupestre* and *Agrostis capillaris* L.), <10% Fabaceae (*Trifolium repens* L.) and 20–30% other forbs (such as *Potentilla erecta* (L.) Rauschel and *Galium saxatile* L.).

Although stockbreeding has decreased in the Aezkoa valley during the recent decades, livestock still grazes the highlands (800–1500 m a.s.l.) and traditional land uses are maintained to some extent. Winter burns are frequent, and the traditional *shrub-to-shrub* burning technique is still used by local farmers in lightly shrub-encroached areas (San

**Table 1**

Site characteristics (*Infraestructura de Datos Espaciales de Navarra*, <https://idena.navarra.es>) and soil parameters (0–10 cm depth, Naserctic Official Laboratory, Pamplona, Spain).

Site data	Ezkanda	Azalegi	Aritzelate
Altitude (m a.s.l.)	1100	1080	1090
Exposure	S-SW	NE	N-NW
Slope (°)	15–20	10–20	15–20
Geology	Marl and siltstones	Calcarenites, limestones and limestone marls	Calcarenites, limestones and limestone marls/Marl and siltstones
Soil parameters			
Sand (0.05–2 mm) (%)	2.19	4.23	2.75
Silt (0.002–0.05 mm) (%)	50.16	46.65	47.04
Clay (<0.002 mm) (%)	44.59	45.07	47.94
pH in H <sub>2</sub> O (1:2.5)	5.23	4.58	4.53
Total CEC (cmol(+)·kg <sup>-1</sup> )	27.40	24.14	23.08
Organic matter (%)	16.45	17.61	15.77
C/N ratio	11.91	13.07	12.09
Total N (%)	0.81	0.78	0.76
Phosphorus (P <sub>2</sub> O <sub>5</sub> ) (mg·kg <sup>-1</sup> )	17.83	38.88	23.93
Potassium (K <sub>2</sub> O) (mg·kg <sup>-1</sup> )	306.73	257.70	255.85

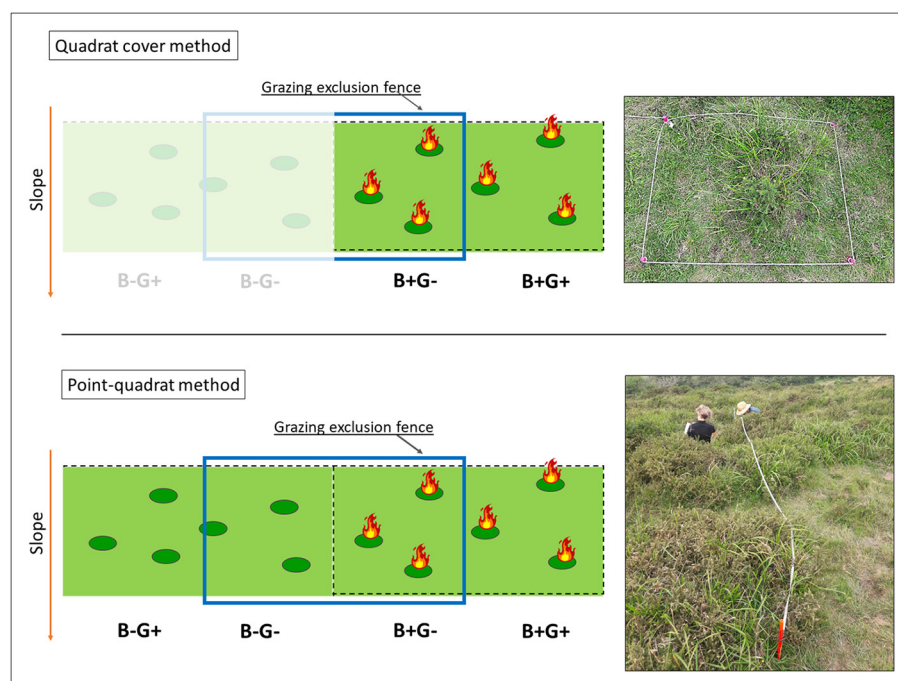
Emeterio et al., 2016). The area supports extensive, mixed herbivory of native breeds of sheep (*Latxa*), cattle (*Pirenaica*) and horses (*Burguete*) yearly, from early May to the last days of October. During the experiment, animal activity was detected in all the grazed plots (i.e. bitten plants, signs of trampling, faecal depositions, broken shrub branches, and presence of animals). According with the information provided by stakeholders, forest rangers and administrative officers of Aezkoa Valley, the estimated grazing pressure was site- and year- dependent and ranged from 1 to 3 LU·ha<sup>-1</sup>·6 months<sup>-1</sup>. Horses, cattle and sheep flocks graze in Ezkanda and Azalegi sites, while in Aritzelate grazing pressure is lower than in the other two sites and sheep presence is negligible (see Supp. Mat., Fig. S2).

## 2.2. Experimental set-up

In March 2012, each of the three sites was divided into two areas; one was burned while the other remained unburned. Local stakeholders applied the fire directly to each shrub with the help of a flammable fuel

(*shrub-to-shrub* technique). It was a low-intensity burning, creating a heterogeneous mosaic of patches of burned gorse shrubs (dark and grey ashes over the soil) and unburned herbaceous vegetation between them (see more detailed information about burnings in San Emeterio et al. (2016)). After the burning, a permanent fence (30 × 15 m) was installed at each site to exclude livestock grazing in the ungrazed plot. This procedure resulted in four treatments: burned and grazed (B<sup>+</sup>G<sup>+</sup>); burned and ungrazed (B<sup>+</sup>G<sup>-</sup>); unburned and grazed (B<sup>-</sup>G<sup>+</sup>); and unburned and ungrazed (B<sup>-</sup>G<sup>-</sup>) (Fig. 1; see experimental design in San Emeterio et al. (2016)).

The experimental design seeks to mimic the different situations currently occurring in these mountain grasslands: 1) maintenance of traditional extensive livestock grazing after *shrub-to-shrub* burnings (B<sup>+</sup>G<sup>+</sup>), and land use change situations as 2) reduction or cessation of grazing while maintaining the burnings (B<sup>+</sup>G<sup>-</sup>), 3) traditional grazing in unburned areas with early stages of shrub-encroachment (B<sup>-</sup>G<sup>+</sup>), and 4) abandonment of grazing and burnings (B<sup>-</sup>G<sup>-</sup>) (see Supp. Mat., Fig. S3).



**Fig. 1.** Experimental design and vegetation surveys at the three sites. Treatment combinations: burned and grazed (B<sup>+</sup>G<sup>+</sup>); burned and ungrazed (B<sup>+</sup>G<sup>-</sup>); unburned and grazed (B<sup>-</sup>G<sup>+</sup>); and unburned and ungrazed (B<sup>-</sup>G<sup>-</sup>). Survey methods: quadrat cover of burned shrubs (permanent quadrats) within burned plots and point-quadrat in all plots.

### 2.3. Vegetation surveys and data collection

Vegetation surveys were conducted every summer from 2012 to 2018. We used two types of non-destructive survey: 1) Quadrat cover method, to examine the regeneration dynamics of the plant community and diversity in the selected burned shrubs (subplots), and 2) Point-quadrat method (Daget and Poissonet, 1971), to examine the evolution of floristic composition in all four plots.

#### 2.3.1. Survey of the vegetation recover after burning in permanent quadrats

Six burned gorse shrubs (subplots) were randomly selected at each site and permanent quadrats were established around them (see Supp. Mat., Table S1), three in the grazed plot ( $B^+G^+$ ) and the other three in the ungrazed one ( $B^+G^-$ ). At each survey, we first identified at species level the vascular plants present within the quadrats and then we estimated their cover percentage as horizontal cover and bare soil proportion as ground vertically exposed to the sky. Only living branches of *U. gallii* were considered in the inventories. Due to plant stratification, total plant cover could attain values higher than 100%.

A total of eight surveys were conducted, one per year in July (2012–2018) and an extra survey in October 2012 to control the grazing effect during the first year, giving a total of 144 inventories (18 inventories per date, 8 dates in total). In the first survey (July 2012) we also recorded the number of new shoots of *U. gallii* in the 18 subplots, and in summer 2017 and 2018 we recorded at random seven measures of gorse height per subplot.

From the data recorded above, we estimated the plant cover by growth form: trees, shrubs (including the fern *Pteridium aquilinum*) and herbaceous plants, considering two plant guilds, graminoids (grasses, sedges and rushes) and forbs. *Ulex gallii* cover was analysed separately since it was the target of the burning. Three native perennial grasses were also individually analysed: (i) *B. rupestre*, a tall-grass exhibiting expansion in the area (Canals et al., 2017, 2014) and (ii) *F. rubra* and (iii) *A. capillaris*, two dominant grasses which are common components of high-diversity grasslands. Within the forbs, rosette-forming species, which are frequently related to the grazing activity of herbivores, were also studied separately.

We determined the species richness (total number of species in the permanent quadrats) and estimated the diversity by means of the Shannon diversity index ( $H'$ , a measure of alpha diversity) and the Pielou's evenness index ( $J$ , a measure of similarity among species cover).

#### 2.3.2. Floristic composition inventories by the point-quadrat method

According to the point-quadrat procedure, we established one line transect (7 m) on the diagonal of each plot ( $B^+G^-$ ,  $B^+G^+$ ,  $B^-G^-$  and  $B^-G^+$ ) at the three study sites, and we identified and recorded all the plant species that touched a narrow pin placed vertically at 20-cm intervals. We surveyed a total of 84 transects, 12 transects per 7 years. In each survey, we also measured the height (leaf length and maximum height) of ten plants of *B. rupestre* randomly selected in each plot.

We calculated the relative abundance of each plant species according to Daget and Poissonet (1971):

$$SRA_i = \frac{f_i}{\sum_{i=1}^n f_i} \times 100(\%)$$

where  $SRA_i$  and  $f_i$  are species relative abundance and frequency of occurrence of species  $i$ .

### 2.4. Statistical analyses

All statistical analyses were performed using R v.3.5.2. (R Core Team, 2018). We used the *mgcv* package (Wood, 2019) for generalized additive mixed models (GAMMs), *nlme* package (Pinheiro et al., 2015) for linear mixed-effect models, and *Vegan* (Oksanen et al., 2015) for multivariate analysis.

#### 2.4.1. Effects of grazing on plant cover and diversity after burning

We used Generalized Additive Mixed Models (GAMMs) to evaluate the effects of grazing and site on the evolution of plant cover after burning. Generalized additive models (GAMs) are a non-parametric extension of General Linear Models. The response curve of GAMs is more data-driven than model-driven. GAMs relate the mean of the response variable with non-linear predictors through a smooth link function (Yee and Mitchell, 1991). GAMMs are an extension of GAMs which allow the modelling of correlated data through the inclusion of random effects. The models included Site (S, three levels: Ezkanda, Azalegi and Aritzelate), Grazing (G, two levels: grazed and non-grazed) and Date (D) as fixed effects and Subplot as a random effect. We chose the optimal random and fixed effects structures of the models following a top-down strategy (Zuur et al., 2009). We fitted a beyond optimal model that included all the fixed effects and as many interactions as possible ( $S \times G + s(D \text{ by } S) + s(D \text{ by } G)$ , with "s" being a smooth function), and chose the optimal random effect structure using the likelihood ratio test (restricted maximum likelihood estimation procedures, REML). The fixed effects structure was chosen using a backward selection process and a likelihood ratio test (maximum likelihood estimation procedures, ML). Finally, the best model was re-fitted again using REML (see Supp. Mat.). The following response variables were analysed: cover of *U. gallii*, graminoids, *B. rupestre*, *F. rubra*, *A. capillaris*, forbs and rosettes, and percentage of bare soil (see Supp. Mat., Table S2).

To evaluate the effects of grazing and site on the evolution of the diversity indices (species richness, Shannon index and Pielou's index) after burning we followed the same approach as for the analysis of plant cover with data from the permanent quadrats (see Supp. Mat., Table S2).

#### 2.4.2. Effects of grazing on plant height

*Ulex gallii* height in the burned plots was analysed by linear mixed-effect models, including grazing (two levels), site (three levels) and the date of survey (two levels, 2017 and 2018) as fixed factors and subplot as a random effect (see Supp. Mat.). *Brachypodium rupestre* height from burned and unburned plots was analysed using GAMMs, including fire (F, two levels: burned and unburned), site and date as fixed effects, and plot as random effect (see Supp. Mat., Table S2). In both cases, we applied the procedure previously described for choosing the best model.

#### 2.4.3. Multivariate analysis of floristic composition

We performed a multivariate ordination approach to study the relationship between biotic and abiotic predictors and the floristic composition determined by the point quadrat method. In order to select the appropriate constrained ordination technique, the response matrix was examined using detrended correspondence analysis (DCA), with detrending-by-segments and non-linear rescaling of the axes. The length of the extracted gradients was less than three, which indicates a linear gradient, so we run a redundancy analysis (RDA) (Lepš and Šmilauer, 2003). We identified potential explanatory variables, abiotic and biotic, based on our observations and on peer-reviewed literature. The abiotic variables included in the full model were burning, site (exposure), bare ground (%), mean temperature (°C) and accumulated precipitation (mm) from the beginning of the plant growing period to the sampling date of each year (Fig. S1). The biotic variables included were grazing (presence or absence), grazing pressure ( $\text{LU} \cdot \text{ha}^{-1} \cdot 6 \text{ months}^{-1}$ ) (see Supp. Mat., Fig. S2), *B. rupestre* leaf length (cm), and grassland density (measured as number of total contacts in each linear transect). We used a forward selection procedure to determine the subset of explanatory variables explaining most variation in the floristic turn-over. The statistical power of the analysis was assessed by Monte Carlo permutation tests ( $n = 999$ ).



### 3. Results

#### 3.1. Grazing effects on plant community recovery after burning

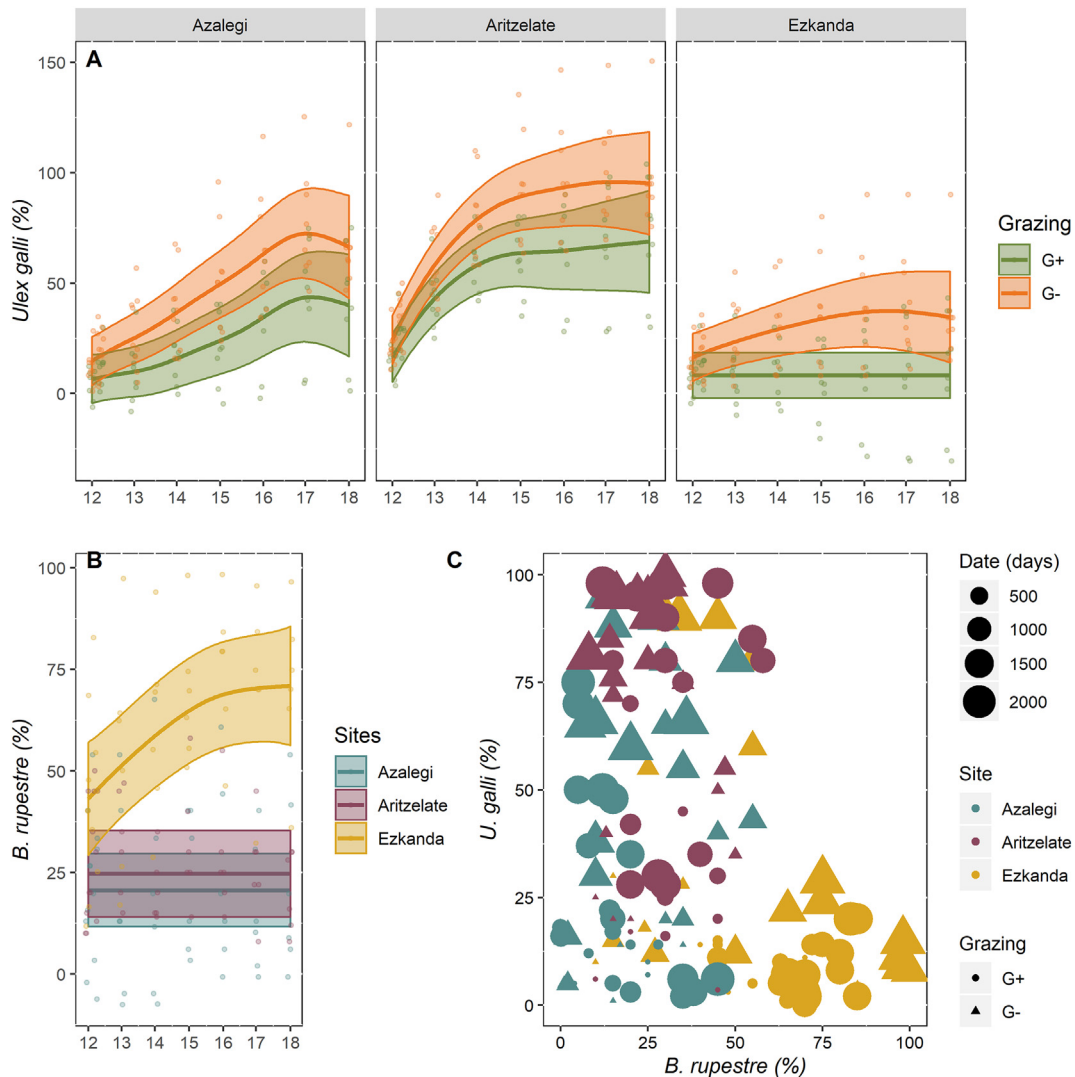
After burning, plant communities evolved differently depending on whether they were grazed or not. The exclusion of grazing increased the cover of *U. gallii* (Fig. 2) and, in the long term, decreased the cover of herbaceous species, graminoids and forbs (see Supp. Mat., Figs. S4 & S5). Shrub regeneration after burning was mostly due to *U. gallii* recovery, the most common shrub species. The absence of herbivores favoured the expansion of the gorse from 2012 to 2018, although this response was site-dependent, with greater cover at Aritzelate than at Ezkanda site at the end of the study (Fig. 2, Table 2). Although the first period of grazing did not affect gorse resprouting after burning (grazing,  $F = 1.569$   $p = 0.234$ ; site,  $F = 0.706$   $p = 0.513$ ), seven years of grazing reduced shrub growth. Gorse was 2.1 times taller in ungrazed than in grazed areas in 2017 and 2018 (grazing,  $LR = 17.432$   $p < 0.001$ ; site,  $LR = 3.157$   $p = 0.206$ ; date,  $LR = 43.031$ ,  $p < 0.001$ ) (Table 3).

Grazing increased the cover of graminoids, but the effect varied among sites and species (Fig. S4, Table 2): regarding the most dominant grasses, *F. rubra* attained the highest values in Azalegi and Aritzelate and *A. capillaris* in Ezkanda and Azalegi. In contrast, the cover of *B. rupestre*

was not significantly affected by grazing, but there were significant differences among sites, becoming the dominant grass in Ezkanda at the end of the study (Fig. 2, Table 2). Fig. 2-C shows that when *B. rupestre* cover was higher than 60%, the cover of *U. gallii* remained low, below 30%. The effect of fire on *B. rupestre* height was site and grazing-dependent. Leaf length and maximum height of this species were higher in ungrazed plots, but there was no burning effect, except in the grazed area of Azalegi, where *B. rupestre* height was greater in unburned plots (Fig. 3, Table 4).

Grazing did not significantly affect total forb cover but it tended to increase in later years in the grazed plots at Aritzelate and Azalegi compared to the ungrazed ones. Grazed plots contained similar proportions of forbs. The cover of rosette-forming species differed significantly between sites and treatments: it tended to a linear decrease in ungrazed plots, while in the grazed ones there was a peak in 2014, being 2.0, 2.6 and 1.7-fold higher than in ungrazed plots of Azalegi, Aritzelate and Ezkanda, respectively (see Supp. Mat., Fig. S5; Table 2).

The effect of grazing on bare soil was time-dependent (significant grazing  $\times$  date interaction): the first year it was similar in grazed and ungrazed areas, and then decreased following different trends in grazed and ungrazed plots. The presence of livestock maintained bare soil cover during the first years after burning, with values 3.5, 4.2 and 4.9-fold



**Fig. 2.** (A) Grazing exclusion effects on *Ulex gallii* cover and (B) site effects on *B. rupestre* cover in burned plots from 2012 to 2018. Expected values (line), partial residuals (dots) and the 95% confidence interval (shaded area). (C) *Ulex gallii* cover vs. *B. rupestre* cover in burned plots from 2012 to 2018 at the three study sites. Circles (grazed, G<sup>+</sup>) and triangles (ungrazed, G<sup>-</sup>) represent original values.

**Table 2**

Generalized additive mixed models (GAMMs) for growth form groups and subgroups, *U. gallii* and dominant grass cover, bare soil and diversity indices. Statistical outputs for parametric and smooth terms: *df*, degrees of freedom; *edf*, estimated degrees of freedom; variance ratio (*F*) and significance level (*p*). AIC, Akaike information criterion. S, Site; G, grazing; D, date. (\*) Square root transformed variables.

Variable	R <sup>2</sup>	AIC	Parametric terms			Smooth terms					
				<i>df</i>	<i>F</i>	<i>p</i>		<i>edf</i>	<i>F</i>	<i>p</i>	
Plant cover											
<i>U. gallii</i>	0.672	1082.7	S	2	15.73	<0.001	s(D:SAz)	3.840	3.52	<0.001	
			G	1	10.71	0.001	s(D:SAr)	2.950	8.23	<0.001	
Graminoids	0.515	1232.1	S	2	4.30	0.015	s(D:SEz)	0.000	0.00	0.591	
			G	1	11.18	0.001	s(D:G+)	0.000	0.00	0.440	
								s(D:G-)	2.142	1.68	0.005
								s(D:SAz)	0.000	0.00	0.763
								s(D:SAr)	0.861	0.35	0.093
								s(D:SEz)	1.949	1.54	0.004
<i>B. rupestre</i>	0.528	1125.4	S	2	15.21	<0.001	s(D:G+)	2.087	3.21	<0.001	
								s(D:G-)	0.000	0.00	0.719
								s(D:SAz)	0.000	0.00	1.000
								s(D:SAr)	0.000	0.00	0.525
								s(D:SEz)	1.826	2.14	<0.001
								s(D:G+)	2.126	3.16	<0.001
<i>F. rubra</i>	0.517	853.4	S	2	46.18	<0.001	s(D:G-)	0.845	0.21	0.207	
			G	1	10.57	0.001	s(D:G+)	0.676	0.21	0.207	
<i>A. capillaris</i>	0.346	944.9	S	2	8.20	<0.001	s(D:G+)	1.676	0.95	0.029	
			G	1	3.14	0.078	s(D:G-)	0.274	0.06	0.263	
			S × G	2	2.45	0.090					
Forbs	0.501	1095.1	S	2	0.44	0.646	s(D:G+)	2.999	4.31	<0.001	
			G	1	0.03	0.856	s(D:G-)	4.466	8.01	<0.001	
			S × G	2	2.27	0.107					
Rosette*	0.369	406.3	S	2	4.56	0.012	s(D:G+)	3.507	6.875	<0.001	
			G	1	5.76	0.018	s(D:G-)	1.543	1.968	0.001	
Bare soil*	0.764	486.4	S	2	17.50	<0.001	s(D:G+)	2.207	8.27	<0.001	
			G	1	25.94	<0.001	s(D:G-)	5.700	60.97	<0.001	
			S × G	2	5.17	0.007					
Diversity indices											
Species richness	0.713	661.3	S	2	4.58	0.012	s(D:G+)	3.003	12.25	<0.001	
			G	1	54.30	<0.001	s(D:G-)	2.527	3.25	<0.001	
Shannon index	0.680	13.2	S	2	7.05	0.001	s(D:SAz)	0.000	0.00	0.973	
			G	1	13.25	<0.001	s(D:SAr)	1.500	0.95	0.015	
								s(D:SEz)	0.881	0.24	0.167
								s(D:G+)	4.082	14.16	<0.001
Pielou's index	0.554	283.6	S	2	2.56	0.081	s(D:G-)	3.093	5.32	<0.001	
			G	1	2.13	0.147	s(D:SAz)	1.348	1.16	0.007	
			S × G	2	2.70	0.071	s(D:SAr)	2.614	5.88	<0.001	
								s(D:SEz)	0.526	0.14	0.198

higher in grazed areas than in ungrazed ones in Azalegi, Aritzelate and Ezkanda during 2013. In later years values were similar, except in Azalegi (see Supp. Mat., Fig. S5; Table 2).

3.2. Grazing effects on species richness and diversity after burning

The total number of species and the Shannon index increased in grazed and burned plots until 2016 and 2014, respectively, and afterwards they had a slight decrease or remained similar. In contrast, both parameters decreased with time in non-grazed areas. At the end of the study, grazed plots mostly doubled the number of species compared to non-grazed plots, and species richness was higher in Azalegi and Aritzelate than in Ezkanda. The Shannon diversity index was 1.7-fold greater in grazed than in non-grazed areas at

**Table 3**

*Ulex gallii* height (cm) in July 2017 and 2018, and the number of shoots after burning (July 2012) in burned-grazed and burned-ungrazed plots. Values are the mean ± standard error. Different letters indicate significant differences.

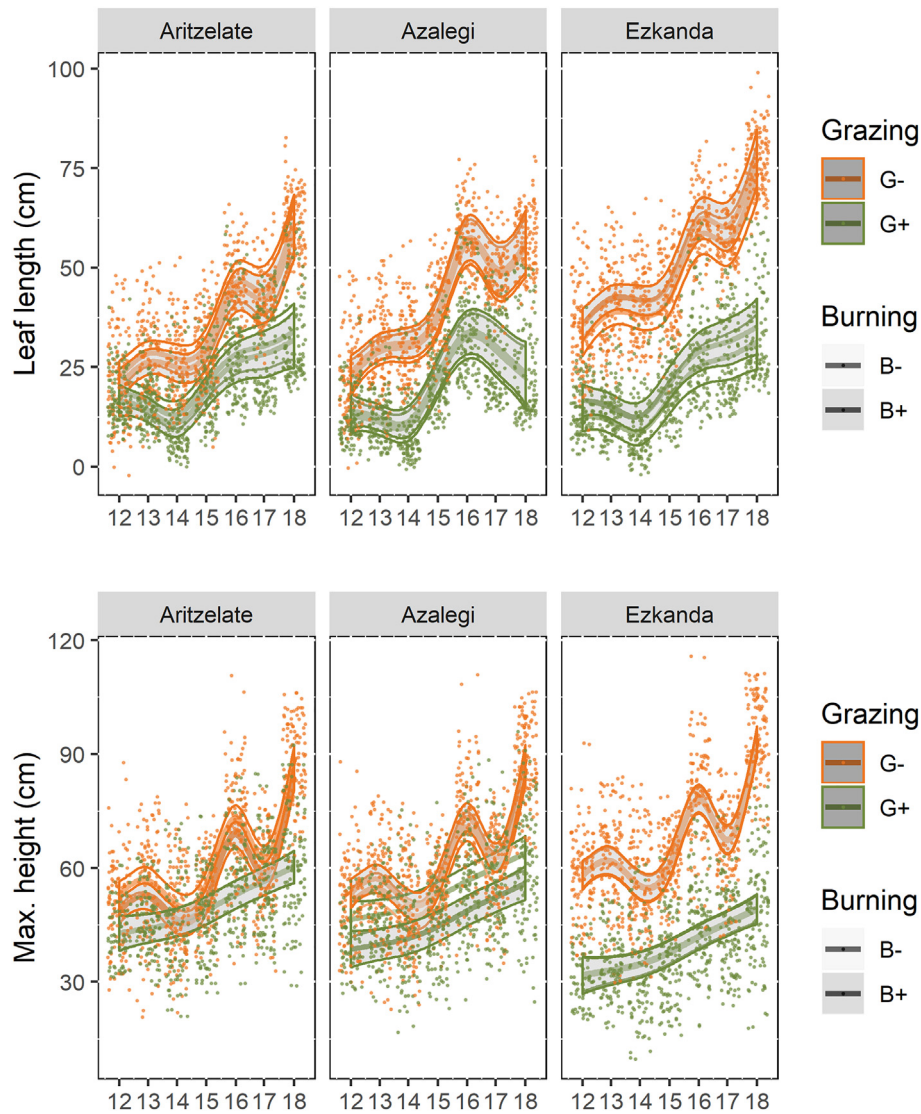
<i>Ulex gallii</i>	Year	Grazed	Ungrazed
Height (cm)	2017	23.8 ±1.6 d	51.0 ±1.5 b
	2018	28.9 ±2.0 c	61.7 ±1.8 a
Initial shoots (number)	2012	13.4 ±1.6	10.8 ±1.6

the end of the monitoring. The grazing effect on evenness was site-dependent: Pielou's index was greater in grazed than in non-grazed areas of Aritzelate (Fig. 4, Table 2).

3.3. The effects of the burning and grazing interaction on the evolution of floristic composition

According with the best fitting RDA model, the variability of plant communities evolution in the plots is mostly explained by the following explanatory variables: site, burning, grazing pressure (GP, livestock stocking rate), date, leaf length of *B. rupestre*, mean air temperature and vegetation density (Fs). The first and second axes of the RDA ordination explained 45.50 and 13.28% of the variation, respectively (Fig. 5).

The plant communities were similar at the beginning of the experiment (July 2012), but they diverged over time from grazing-tolerant herb-dominated communities (RDA ordination's lower-right side) to *B. rupestre*-dominated grasslands at Ezkanda (lower-left side, horizontal gradient) and to *U. gallii*-dominated plant communities at Aritzelate and Azalegi (upper-left side, diagonal gradient) (Fig. 5). Non-grazed plots, irrespective of the burning treatment, exhibited changes in their floristic composition over time depending on site. The absence of grazing mainly fostered the expansion of *B. rupestre* in Ezkanda, while in Azalegi and Aritzelate it favoured *U. gallii* encroachment (Fig. 5; see Supp. Mat., Fig. S6).



**Fig. 3.** *Brachypodium rupestre* leaf length and maximum height in the four plots (B<sup>+</sup>G<sup>+</sup>, burned and grazed; B<sup>+</sup>G<sup>-</sup>, burned and ungrazed; B<sup>-</sup>G<sup>+</sup>, unburned and grazed; B<sup>-</sup>G<sup>-</sup> unburned and ungrazed) from 2012 to 2018. Expected values (line), partial residuals (dots) and the 95% confidence interval (shaded area). Line colour: green, grazed plots (G<sup>+</sup>); orange, ungrazed plots (G<sup>-</sup>); background colour: white, unburned plots (B<sup>-</sup>); grey, burned plots (B<sup>+</sup>). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

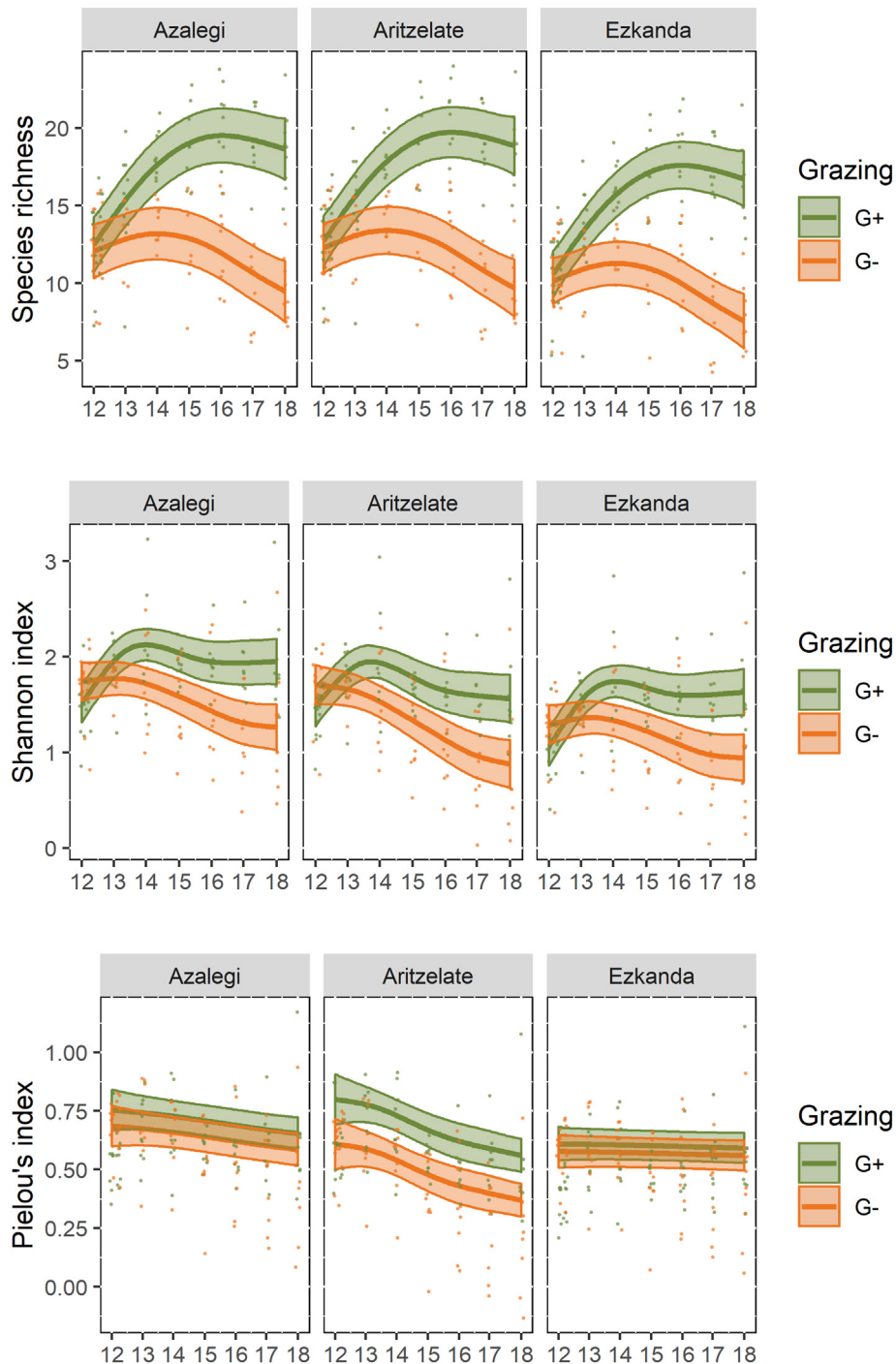
The occurrence of burnings were plotted in the diagonal, with burned treatment at the lower-left quadrant and unburned treatment at the upper-right. *Brachypodium rupestre* leaf length was positively

related to the year of sampling and mean temperature during the growing season (upper-left quadrant), but exhibited a negative correlation with grazing pressure (GP) (lower-right quadrant) (Fig. 5-B). Despite

**Table 4**

Generalized additive mixed models (GAMMs) for *B. rupestre* leaf length and maximum height. Statistical outputs for parametric and smooth terms: *df*, degrees of freedom; *edf*, estimated degrees of freedom; variance ratio (*F*) and significance level (*p*). AIC, Akaike information criterion. S, Site; G, grazing; B, burning.

Variable	R <sup>2</sup>	AIC	Parametric terms				Smooth terms			
				<i>df</i>	<i>F</i>	<i>p</i>		<i>edf</i>	<i>F</i>	<i>p</i>
Leaf length	0.708	6225.3	S	2	13.46	<0.001	s(D:SAz)	3.794	3.66	<0.001
			G	1	52.18	<0.001	s(D:SAr)	1.134	0.38	0.126
			B	1	1.64	0.201	s(D:SEz)	0.000	0.00	0.138
			S × G	2	21.59	<0.001	s(D:G+)	4.636	11.16	<0.001
			S × B	2	3.189	0.042	s(D:G-)	5.611	24.13	<0.001
Max. height	0.584	6131.5	S	2	6.68	0.001	s(D:G+)	2.672	13.58	<0.001
			G	1	39.42	<0.001	s(D:G-)	5.865	95.62	<0.001
			B	1	7.24	0.007				
			S × G	2	28.11	<0.001				
			S × B	2	3.81	0.022				
			G × B	1	2.21	0.136				
			S × G × B	2	5.67	0.003				



**Fig. 4.** Species richness, Shannon diversity index and Pielou's evenness index in burned plots from 2012 to 2018 at the three study sites. Expected values (line), partial residuals (dots) and the 95% confidence interval (shaded area). Grazed plots (G<sup>+</sup>); ungrazed plots (G<sup>-</sup>).

the grazed areas of the three sites being located around the centre of the RDA ordination, they had little in common (Fig. 5-C).

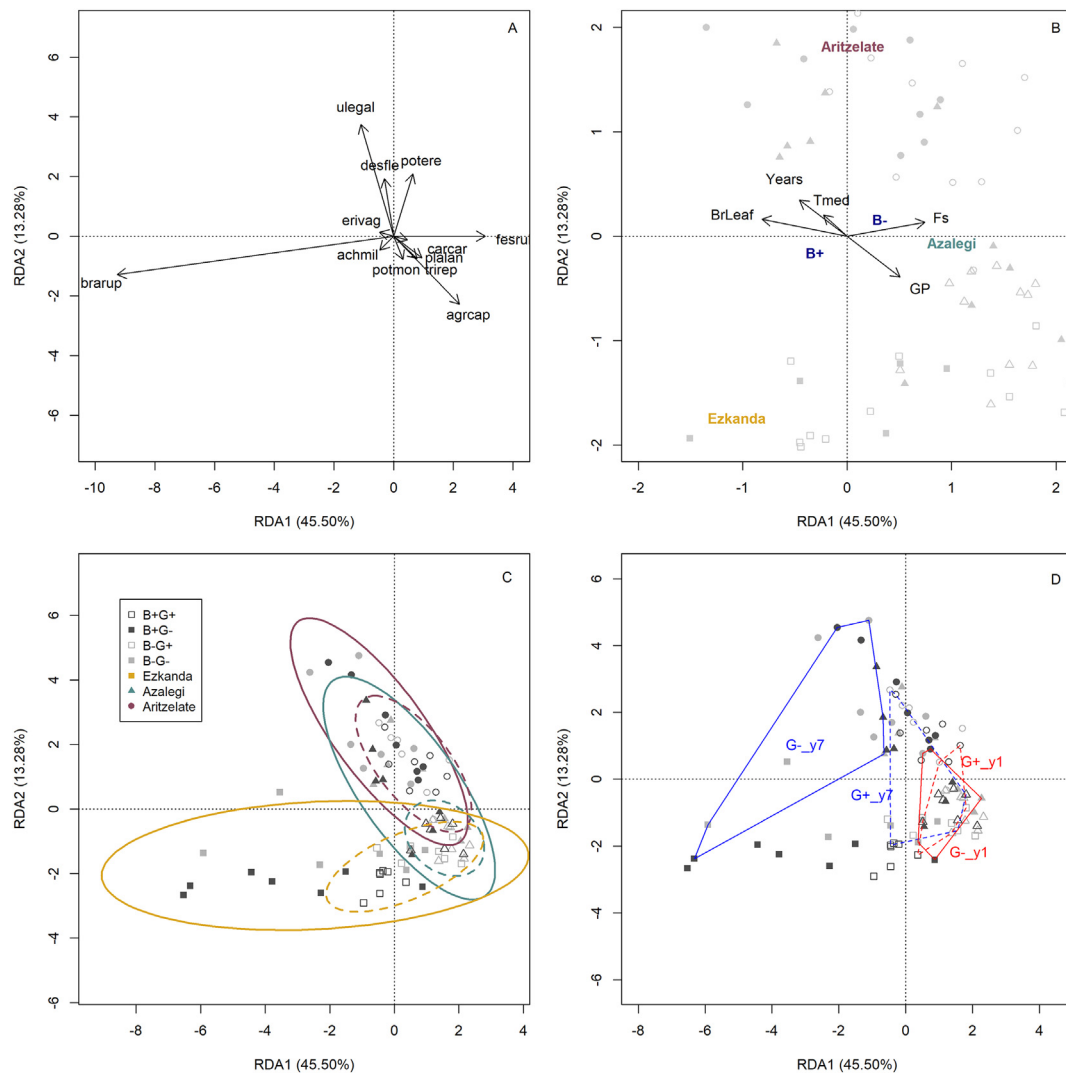
#### 4. Discussion

##### 4.1. Herbivory shapes the post-burning grassland evolution

The results of the study show that *U. gallii* resprout occurs consistently in both grazed and ungrazed areas, but the presence of grazers slows down its growth and expansion. According with previous works, domestic herbivores such as horses, sheep and goats browse

the tender shoots of gorse and cause severe mechanical damage by trampling (Jáuregui et al., 2009; López et al., 2017). Although the particular response to fire depends on the species of shrub and its regeneration strategy (Reyes and Casal, 2008), post-fire management is also decisive (Jáuregui et al., 2007). When extensive grazing delays the recovery and expansion of the gorse in grasslands, a low recurrence of burns is needed to control the resprout, allowing a sustainable burning regime (Gómez et al., 2019). Frequent burns can produce undesirable changes in soil functioning and nutrient pools (Girona-García et al., 2018; Godwin et al., 2017; San Emeterio et al., 2016), and also have negative impacts on plant communities.





**Fig. 5.** RDA ordination diagrams of the floristic composition of the four plots at the three sites measured by the Point Quadrat Method. (A) Ordination diagram showing the correlation vectors for the most abundant species. The species are labelled by the first three letters of their genus and species epithets (see Supp. Mat., Table S3). (B) Biplot diagram showing explanatory variables' vectors and centroids. BrLeaf, *B. rupestre* leaf length; Tmed, mean of air temperature; Fs, total species frequency (grassland density); GP, grazing pressure (stocking rate). (C) Ordination diagram showing inventories: burned ( $B^+$ ) and unburned ( $B^-$ ); grazed ( $G^+$ ) and ungrazed ( $G^-$ ); confidence ellipses (95%) for sites indicated by colours (yellow, Ezkanda; blue, Azalegi; pink, Aritzelate). (D) Ordination diagram showing grazed (dotted lines) and ungrazed (solid lines) areas in 2012 (red) and 2018 (blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The activity of herbivores (selective defoliation, dung deposition and gap generation) increases environmental heterogeneity and creates new opportunities for plant species as a result of changes in their competitive hierarchies (Adler et al., 2001; Gaujour et al., 2012; Piqueray et al., 2015). The revegetation process after burning is gradual in grazed areas, where livestock trampling and defoliation slow down recolonization, and increase micro-disturbances that provide space and opportunities for the establishment and growth of less abundant plant species (Canals and Sebastià, 2000). Although the effects of herbivores on plant diversity may differ depending on the environment (Davies and Bodart, 2015; Milchunas et al., 1988), measured diversity parameters in this research displayed consistent patterns at the three sites.

#### 4.2. Alternate stable states after the decoupling of burning and grazing

Our research also shows that, in the absence of herbivory, plant community recovery after burning is largely modulated by site-specific features, both abiotic (e.g. site exposure) and biotic characteristics (e.g.

preburning floristic composition). Resource availability and competitive interactions play a crucial role in the dynamics of plant communities when there are not dominant disturbances (Buckland et al., 2001; Odriozola et al., 2017).

*Ulex gallii* and *B. rupestre* are the two species that exploit their competitive traits (Table 5) to reach dominance in the grazing excluded areas. When *B. rupestre* reaches about 60% cover, *U. gallii* is outcompeted. This phenomenon was observed in Ezkanda, where abiotic factors (a higher soil pH and a southern exposure) may favour the development of *B. rupestre*, a species better adapted to a wider range of soil reaction and water balance than *U. gallii* (Rameau et al., 1989). It seems that the exposure and the water holding capacity of the soils at each study site, since the precipitation and the slopes are similar across the three sites, are key factors that may promote the growth of the tall-grass (measured as leaf length, maximum height, and plant cover) and increase its chances to outcompete the shrub in non-grazed areas. Therefore, the environmental variability may be decisive in plant community evolution in non-grazed areas (Deák et al., 2021), where abiotic factors allow the rapid growth of large

**Table 5**  
*Ulex gallii* and *Brachypodium rupestre* characteristics.

	<i>Ulex gallii</i>	<i>Brachypodium rupestre</i>
Life form	Shrub	Perennial tall-grass
Root system and nutrient uptake	Deep, with high nutrient uptake capacity (Hayati and Proctor, 1990). Symbiosis with N-fixing <i>Rhizobium</i> bacteria (Stokes and Bullock, 2003).	Robust rhizome (nutrients reservoir, clonal spread, buds protection) (Bobbink et al., 1998; de Kroon and Bobbink, 1997) and high N-uptake capacity (Canals et al., 2014; Ryser et al., 1997).
Propagation strategy	Mostly by seeds; germination in early autumn and spring. Also vegetative resprouting from root buds (Gloaguen, 1993; Jáuregui et al., 2007; Stokes and Bullock, 2003).	Sexual reproduction by seeds (Baba et al., 2012). Effective lateral clonal spreading and rapid propagation in early spring (Pignatti, 1982).
Palatability to herbivores	Dependent on the stage of development. Low for lignified branches and prickles (Ferreira et al., 2013).	Dependent on the stage of development. Low; rapid loss of digestibility compared to other temperate grasses (Illius and Gordon, 1993; Massey and Hartley, 2006).
Response to burns	Moderate regrowth from root buds (Gloaguen, 1993) and high seed germination response (Reyes and Casal, 2008).	Rapid vegetative spreading after surface fires (Canals et al., 2014).

clumps of native tall-grasses, hindering the development of shrubs by overshadowing (see Supp. Mat., Fig. S7).

Regarding diversity, the expansion of *U. gallii* or *B. rupestre* due to grazing exclusion leads to a loss of species richness and plant diversity over time. Both species, native to the area of study, benefit particularly from fires and decreased grazing (Table 5) and their relative covers influence plant diversity at different scales. At plant community level, dominance of either shrubs or tall-grasses leads to a reduction in  $\alpha$ -diversity, with a sharper decrease of the number of cohorts of herbaceous species when *B. rupestre* dominates the grasslands. On a landscape scale, shrub-encroachment by *U. gallii* and the subsequent loss of grasslands diminish vegetation mosaics, reducing  $\beta$ -diversity.

When the altered burning and grazing regimes persist over time, plant communities dominated by *U. gallii* or *B. rupestre* may become trap communities, constituting alternative stable states, with very low capability to evolve to other successional stages (Beisner et al., 2003; Pausas and Bond, 2019). After seven years of grazing exclusion, the spreading of both species in diverse grasslands not only leads to community degradation but also to the accumulation of great amounts of highly flammable above-ground biomass (Canals et al., 2017; Marino et al., 2011; Reyes et al., 2009). Consequently, given the current global warming scenario, these fuel accumulations increases the hazard of spontaneous wildfires in mountains (Galiana and Lázaro, 2010; Reyes et al., 2009). Therefore, it is advisable to design management plans of these plant communities to reverse the situation and maintain mosaic open areas.

#### 4.3. Management implications

Till the last century, the inherited traditional management related to fire and herbivory in mountain areas ensured the maintenance of cultural landscapes characterized by high  $\alpha$ - and  $\beta$ -biodiversity and proper ecological functioning (Galvnek and Lepš, 2008; Hillebrand et al., 2008; Johansson et al., 2018; Plieninger et al., 2006). In the last decades, a diversity loss and the development of alternate stable states are occurring, mainly due to the lack of grazers and to the misuse of burnings (Valko et al., 2014). Given the current global change scenario, it is more necessary than ever to preserve resilient landscapes, constituted by a complex mosaic of diverse habitats, and to promote the restoration of the already existing degraded areas (Guadilla-Saez et al., 2019;

Piqueray et al., 2011; Vandvik et al., 2005). The restoration of plant communities which have developed an alternate stable state aims to overcome the resilience of the degraded community favouring new states with greater potential to provide more ecosystem services (Wonkka et al., 2016).

The best approach for preserving and maintaining high-diversity communities developed with grazing and fire, is precisely, promoting the active application of both combined practices (Kohler et al., 2005). In mountain areas with a long history of fire management, burning is a necessary tool to preserve an optimal pastoral activity of grazed lands (Faerber, 1996), and it has become a valuable preventive method to reduce the risk of large wildfires (Johansson et al., 2018). Furthermore, maintaining the level of complexity of traditional management, that combines fire and grazing and applies them at adequate spatial scales, is crucial to preserve plant community diversity and complex mosaic landscapes (Vandvik et al., 2005).

## 5. Conclusion

Extensive livestock grazing after pastoral (*shrub-to-shrub*) burnings delays the encroachment of the shrub *U. gallii* and the expansion of the tall-grass *B. rupestre*, promoting high plant diversity in pasturelands. Nowadays, the activity of domestic herbivores in mountain areas must be understood and planned with the double purpose of satisfying the needs of animals (and farmers' productive needs) while promoting their crucial role as preservers of the inherited resilient landscapes (Alados et al., 2019; Fuhlendorf et al., 2009; Zhang et al., 2018). The results of this research show that the traditional management of domestic herbivores in western Pyrenees, characterized by a mixed grazing of sheep, cattle and horses, with limited animal guidance and stocking rates ranging from 1 to 3 LU · ha<sup>-1</sup> · 6 months<sup>-1</sup>, is adequate to preserve the high diversity and ecological value of grasslands, preventing the cascade of divergent degradative processes that occur in the total absence of herbivory.

## Funding information

Interreg Sudoe Programme, European Regional Development Fund, European-Union, Open2preserve Project (SOE2/P5/E0804). Spanish Ministry of Science and Innovation, Spain (CGL2010-21963 and CGL2011-29746 projects). L. Múgica was funded through a UPNA's Research Staff Training Grant. Leticia San Emeterio has received funding from "la Caixa" Foundation, Spain and CAN Foundation, Spain, under agreement LCF/PR/PR13/51080004.

## CRedit authorship contribution statement

**Leire Múgica:** Investigation, Formal analysis, Conceptualization, Writing – original draft. **Rosa M. Canals:** Funding acquisition, Conceptualization, Project administration, Methodology, Investigation, Writing – review & editing. **Leticia San Emeterio:** Methodology, Formal analysis, Writing – review & editing. **Javier Peralta:** Methodology, Investigation, Writing – review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

The authors are grateful to the Aezkoa Valley's administration, office staff, forest rangers (Roberto, Carlos, Mario and Asier) and stakeholders for allowing the establishment of this long-term experiment, for maintaining the exclusion fences for livestock animals and for the provided

information. Thanks to M. Durán, I. Rezola and S. Rebolé for their field collaboration in different years. The Institute for Innovation & Sustainable Development in Food Chain (IS-FOOD) funded the English editing service.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.147917>.

## References

- Adler, P., Raff, D., Lauenroth, W., 2001. The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128, 465–479. <https://doi.org/10.1007/s004420100737>.
- Alados, C.L., Saiz, H., Nucho, P., Gartzia, M., Komac, B., De Frutos, A., Pueyo, Y., 2019. Clearing vs. burning for restoring Pyrenean grasslands after shrub encroachment. *Cuad. Investig. Geogr.* 45. <https://doi.org/10.18172/cig.3589>.
- Aldezabal, A., Moragues, L., Odriozola, I., Mijangos, I., 2015. Impact of grazing abandonment on plant and soil microbial communities in an Atlantic mountain grassland. *Appl. Soil Ecol.* 96, 251–260. <https://doi.org/10.1016/j.apsoil.2015.08.013>.
- Amezaga, I., Mendarte, S., Albizu, I., Besga, G., Garbisu, C., Onaindia, M., 2004. Grazing intensity, aspect, and slope effects on limestone grassland structure. *J. Range Manag.* 57, 606–612.
- Ascoli, D., Lonati, M., Marzano, R., Bovio, G., Cavallero, A., Lombardi, G., 2013. Prescribed burning and browsing to control tree encroachment in southern European heathlands. *For. Ecol. Manag.* 289, 69–77. <https://doi.org/10.1016/j.foreco.2012.09.041>.
- Baba, W., Kurowska, M., Kompała-Baba, A., Wilczek, A., Długosz, J., Szarejko, I., 2012. Genetic diversity of the expansive grass *Brachypodium pinnatum* in a changing landscape: effect of habitat age. *Flora* 207, 346–353. <https://doi.org/10.1016/j.flora.2012.01.011>.
- Battlori, E., Gutiérrez, E., 2008. Regional tree line dynamics in response to global change in the Pyrenees. *J. Ecol.* 96, 1275–1288.
- Beisner, B.E., Haydon, D.T., Cuddington, K., 2003. Alternative stable states in ecology. *Front. Ecol. Environ.* 1, 376–382.
- Bestelmeyer, B.T., Ash, A., Brown, J.R., Densambuu, B., Fernández-Giménez, M., Johanson, J., Levi, M., Lopez, D., Peinetti, R., Rumpff, L., Shaver, P., 2017. State and Transition Models: Theory, Applications, and Challenges. [https://doi.org/10.1007/978-3-319-46709-2\\_9](https://doi.org/10.1007/978-3-319-46709-2_9).
- Bobbink, R., Hornung, M., Roelofs, J.G.M., 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *J. Ecol.* 86, 717–738.
- Briggs, J.M., Knapp, A.K., Blair, J.M., Heisler, J.L., Hoch, G.A., Lett, M.S., McCarron, J.K., 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. *Bioscience* 55, 243–254. [https://doi.org/10.1641/0006-3568\(2005\)055\[0243:AEITCA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0243:AEITCA]2.0.CO;2).
- Briske, D.D., Fuhlendorf, S.D., Smeins, F.E., 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Rangel. Ecol. Manag.* 58, 1–10. [https://doi.org/10.2111/1551-5028\(2005\)58<1:SMTARH>2.0.CO;2](https://doi.org/10.2111/1551-5028(2005)58<1:SMTARH>2.0.CO;2).
- Buckland, S.M., Thompson, K., Hodgson, Grime, J.P., 2001. Grassland invasions: effects of manipulations of climate and management. *J. Appl. Ecol.* 38, 301–309. <https://doi.org/10.1046/j.1365-2664.2001.00603.x>.
- Canals, R.M., 2019. Landscape in motion: revisiting the role of key disturbances for the preservation of mountain ecosystems. *Cuad. Investig. Geogr.* 45, 515–531.
- Canals, R.M., Sebastià, M.-T., 2000. Analyzing mechanisms regulating diversity in rangelands through comparative studies: a case in the southwestern Pyrenees. *Biodivers. Conserv.* 9, 965–984. <https://doi.org/10.1023/A>.
- Canals, R.M., Pedro, J., Rupérez, E., San Emeterio, L., 2014. Nutrient pulses after prescribed winter fires and preferential patterns of N uptake may contribute to the expansion of *Brachypodium pinnatum* (L.) P. Beauv. in highland grasslands. *Appl. Veg. Sci.* 17, 419–428. <https://doi.org/10.1111/avsc.12088>.
- Canals, R.M., San Emeterio, L., Durán, M., Múgica, L., 2017. Plant-herbivory feedbacks and selective allocation of a toxic metal are behind the stability of degraded covers dominated by *Brachypodium pinnatum* in acidic soils. *Plant Soil* 415, 373–386. <https://doi.org/10.1007/s11104-016-3153-1>.
- Clements, F.E., 1936. Nature and structure of the climax. *J. Ecol.* 24, 252–284. <https://doi.org/10.2307/2256278>.
- Coughlan, M.R., 2013. Errakina: pastoral fire use and landscape memory in the Basque region of the French Western Pyrenees. *J. Ethnobiol.* 33, 86–104. <https://doi.org/10.2993/0278-0771-33.1.86>.
- Coughlan, M.R., 2014. Farmers, flames, and forests: historical ecology of pastoral fire use and landscape change in the French Western Pyrenees, 1830–2011. *For. Ecol. Manag.* 312, 55–66. <https://doi.org/10.1016/j.foreco.2013.10.021>.
- Daget, P., Poissonet, J., 1971. Une méthode d'analyse phytologique des prairies. *Ann Agron.* 22 pp. 35–41.
- Davies, G.M., Bodart, J., 2015. Changes in vegetation diversity and composition following livestock removal along an upland elevational gradient. *IForest Biogeosci. For.* 8, 582–589. <https://doi.org/10.3832/ifer.1557-008>.
- de Kroon, H., Bobbink, R., 1997. Clonal plant dominance under elevated nitrogen deposition, with special reference to *Brachypodium pinnatum* in chalk grassland. In: De Kroon, H., van Groenendael, J. (Eds.), *The Ecology and Evolution of Clonal Plants*. Backhuys Publishers, pp. 359–379.
- Deák, B., Kovács, B., Rádai, Z., Apostolova, I., Kelemen, A., Kiss, R., Lukács, K., Palpurina, S., Sopotlieva, D., Báthori, F., Valkó, O., 2021. Linking environmental heterogeneity and plant diversity: the ecological role of small natural features in homogeneous landscapes. *Sci. Total Environ.* 763. <https://doi.org/10.1016/j.scitotenv.2020.144199>.
- Dovčiak, M., Hrivnák, R., Ujházy, K., Gömöry, D., 2015. Patterns of grassland invasions by trees: insights from demographic and genetic spatial analyses. 8, 468–479. <https://doi.org/10.1093/jpe/rtu038>.
- Durán, M., Canals, R.M., Sáez, J.L., Ferrer, V., Lera, F., 2020. Disruption of traditional land use regimes causes an economic loss of provisioning services in high-mountain grasslands. *Ecosyst. Serv.* 46. <https://doi.org/10.1016/j.ecoser.2020.101200>.
- Faerber, J., 1996. Impact of fire on vegetation communities of rangelands in the Central French Pyrenees. Rangelands in a Sustainable Biosphere. Proceedings of Th Fifth International Rangeland Congress, pp. 138–139.
- Fernández-Giménez, M.E., Fillat, F., 2012. Pyrenean pastoralists' ecological knowledge: documentation and application to natural resource management and adaptation. *Hum. Ecol.* 40, 287–300. <https://doi.org/10.1007/s10745-012-9463-x>.
- Ferreira, L.M.M., Celaya, R., Benavides, R., Jáuregui, B.M., García, U., Santos, A.S., García, R.R., Rodrigues, M.A.M., Osoro, K., 2013. Foraging behaviour of domestic herbivore species grazing on heathlands associated with improved pasture areas. *Livest. Sci.* 155, 373–383. <https://doi.org/10.1016/j.livsci.2013.05.007>.
- Fuhlendorf, S.D., Engle, D.M., 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *J. Appl. Ecol.* 41, 604–614. <https://doi.org/10.1111/j.0021-8901.2004.00937.x>.
- Fuhlendorf, S.D., Engle, D.M., Kerby, J., Hamilton, R., 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conserv. Biol.* 23, 588–598. <https://doi.org/10.1111/j.1523-1739.2008.01139.x>.
- Galiana, L., Lázaro, A., 2010. Potential barriers and factors for success. In: Montiel, C., Kraus, D. (Eds.), *Best Practices of Fire Use - Prescribed Burning and Suppression Fire Programmes in Selected Case-study Regions in Europe*. European Forest Institute, Porvoo, Finland, pp. 153–164.
- Galvánek, D., Lepš, J., 2008. Changes of species richness pattern in mountain grasslands: abandonment versus restoration. *Biodivers. Conserv.* 17, 3241–3253. <https://doi.org/10.1007/s10531-008-9424-2>.
- Gaujour, E., Amiaud, B., Mignolet, C., Patureux, S., 2012. Factors and processes affecting plant biodiversity in permanent grasslands. A review. *Agron. Sustain. Dev.* 32, 133–160. <https://doi.org/10.1007/s13593-011-0015-3>.
- Girona-García, A., Zufiaurre Galarza, R., Mora, J.L., Armas-Herrera, C.M., Martí, C., Ortiz-Perpiñá, O., Badía-Villas, D., 2018. Effects of prescribed burning for pasture reclamation on soil chemical properties in subalpine shrublands of the Central Pyrenees (NE-Spain). *Sci. Total Environ.* 644, 583–593. <https://doi.org/10.1016/j.scitotenv.2018.06.363>.
- Gloaguen, J.C., 1993. Spatio-temporal patterns in post-burn succession on Brittany heathlands. *J. Veg. Sci.* 4, 561–566.
- Godwin, D.R., Kobzar, L.N., Robertson, K.M., 2017. Effects of fire frequency and soil temperature on soil CO<sub>2</sub> efflux rates in old-field pine-grassland forests. *Forests* 8, 1–14. <https://doi.org/10.3390/f8080274>.
- Gómez, D., Aguirre, A., Lizaur, X., Lorda, M., Remón, J., 2019. Evolution of argoma shrubland (*Ulex gallii* Planch.) after clearing and burning treatments in Sierra de Aralar and Belate (Navarra). *Cuad. Investig. Geogr.* 45, 469–486.
- Guadilla-Sáez, S., Pardo-de-Santayana, M., Reyes-García, V., 2019. The role of traditional management practices in shaping a diverse habitat mosaic in a mountain region of Northern Spain. *Land Use Policy* 89, 104235. <https://doi.org/10.1016/j.landusepol.2019.104235>.
- Hayati, A.A., Proctor, M.C.F., 1990. Plant distribution in relation to mineral nutrient availability and uptake on a wet-heath site in south-west England. *J. Ecol.* 78, 134–151.
- Herrero, M., Thornton, P.K., 2013. Livestock and global change: emerging issues for sustainable food systems. *Proc. Natl. Acad. Sci. U. S. A.* 110, 20878–20881. <https://doi.org/10.1073/pnas.1321844111>.
- Hill, M., Roxburgh, S., Carter, J., McKeon, G., 2005. Vegetation state change and consequent carbon dynamics in savanna woodlands of Australia in response to grazing, drought and fire: a scenario approach using 113 years of synthetic annual fire and grassland growth. *Aust. J. Bot.* 53, 715–739. <https://doi.org/10.1071/BT04106>.
- Hillebrand, H., Bennett, D.M., Cadotte, M.W., 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* 89, 1510–1520.
- Illiou, A., Gordon, I., 1993. Diet selection on mammalian herbivores: constraints and tactics. In: Hughes, R. (Ed.), *Diet Selection: An Interdisciplinary Approach to Foraging Behaviour*. Blackwell, London.
- Jáuregui, B.M., Celaya, R., García, U., Osoro, K., 2007. Vegetation dynamics in burnt heather-gorse shrublands under different grazing management with sheep and goats. *Agrofor. Syst.* 70, 103–111. <https://doi.org/10.1007/s10457-007-9045-x>.
- Jáuregui, B.M., García, U., Osoro, K., Celaya, R., 2009. Sheep and goat grazing effects on three Atlantic heathland types. *Rangel. Ecol. Manag.* 62, 119–126. <https://doi.org/10.2111/07-120.1>.
- Johansson, M.U., Fetene, M., Malmer, A., Granström, A., 2012. Tending for cattle: traditional fire management in Ethiopian montane heathlands. *Ecol. Soc.* 17. <https://doi.org/10.5751/ES-04881-170319>.
- Johansson, M.U., Frisk, C.A., Nemomissa, S., Hylander, K., 2018. Disturbance from traditional fire management in subalpine heathlands increases Afro-alpine plant resilience to climate change. *Glob. Chang. Biol.* 24, 2952–2964. <https://doi.org/10.1111/gcb.14121>.
- Köhler, B., Gigon, A., Edwards, P.J., Krüsi, B., Langenauer, R., Lüscher, A., Ryser, P., 2005. Changes in the species composition and conservation value of limestone grasslands in Northern Switzerland after 22 years of contrasting managements. *Perspect. Plant Ecol. Evol. Syst.* 7, 51–67. <https://doi.org/10.1016/j.ppees.2004.11.003>.



- Komac, B., Kefi, S., Nuche, P., Escós, J., Alados, C.L., 2013. Modeling shrub encroachment in subalpine grasslands under different environmental and management scenarios. *J. Environ. Manag.* 121, 160–169. <https://doi.org/10.1016/j.jenvman.2013.01.038>.
- Lasanta, T., Nadal-Romero, E., Arnáez, J., 2015. Managing abandoned farmland to control the impact of re-vegetation on the environment. The state of the art in Europe. *Environ. Sci. Pol.* 52, 99–109. <https://doi.org/10.1016/j.envsci.2015.05.012>.
- Lepš, J., Šmilauer, P., 2003. *Multivariate Analysis of Ecological Data Using CANOCO*. Cambridge Press.
- Leys, B.A., Marlon, J.R., Umbanhowar, C., Vannièrè, B., 2018. Global fire history of grassland biomes. *Ecol. Evol.* 8, 8831–8852. <https://doi.org/10.1002/ece3.4394>.
- Limb, R.F., Fuhlendorff, S.D., Engle, D.M., Weir, J.R., Elmore, R.D., Bidwell, T.G., 2011. Pyric-herbivory and cattle performance in grassland ecosystems. *Rangel. Ecol. Manag.* 64, 659–663. <https://doi.org/10.2111/REM-D-10-00192.1>.
- López, C.L., García, R.R., Ferreira, L.M.M., García, U., Osoro, K., Celaya, R., 2017. Impacts of horse grazing on botanical composition and diversity in different types of heathland. *Rangel. J.* 39, 375–385. <https://doi.org/10.1071/RJ17079>.
- Marino, E., Guijarro, M., Hernando, C., Madrigal, J., Díez, C., 2011. Fire hazard after prescribed burning in a gorse shrubland: implications for fuel management. *J. Environ. Manag.* 92, 1003–1011. <https://doi.org/10.1016/j.jenvman.2010.11.006>.
- Massey, F., Hartley, S., 2006. Experimental demonstration of the antiherbivore effects of silica in grasses: impacts on foliage digestibility and vole growth rates. *Proc. R. Soc. B Biol. Sci.* 273, 2299–2304. <https://doi.org/10.1098/rspb.2006.3586>.
- McNaughton, S., 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. *Ecol. Monogr.* 53, 291–320.
- Métailié, J.P., 2006. Mountain landscape, pastoral management and traditional practices in the northern Pyrenees (France). In: Agnoletti, M. (Ed.), *The Conservation of Cultural Landscapes*. CAB International, pp. 108–124.
- 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. *Am. Nat.* 132, 87–106. <https://doi.org/10.1086/284839>.
- Miras, Y., Ejarque, A., Orengo, H., Mora, S.R., Palet, J.M., Poiraud, A., 2010. Prehistoric impact on landscape and vegetation at high altitudes: an integrated palaeoecological and archaeological approach in the eastern Pyrenees (Perafita valley, Andorra). *Plant Biosyst.* 144, 924–939. <https://doi.org/10.1080/11263504.2010.491980>.
- Múgica, L., Canals, R.M., San Emeterio, L., 2018. Changes in soil nitrogen dynamics caused by prescribed fires in dense gorse lands in SW Pyrenees. *Sci. Total Environ.* 639, 175–185. <https://doi.org/10.1016/j.scitotenv.2018.05.139>.
- Niedrist, G., Tasser, E., Luth, C., Dalla Via, J., Tappeiner, U., 2009. Plant diversity declines with recent land use changes in European Alps. *Plant Ecol.* 202, 195–210.
- 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. *Appl. Veg. Sci.* 20, 50–61. <https://doi.org/10.1111/avsc.12277>.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2015. *vegan: Community Ecology Package*.
- Pardo, I., Doak, D.F., García-González, R., Gómez, D., García, M.B., 2015. Long-term response of plant communities to herbivore exclusion at high elevation grasslands. *Biodivers. Conserv.* 24, 3033–3047. <https://doi.org/10.1007/s10531-015-0996-3>.
- Pausas, J.G., Bond, W.J., 2019. Alternative biome states in terrestrial ecosystems. *Trends Plant Sci.*, 1–14 <https://doi.org/10.1016/j.tplants.2019.11.003>.
- Pe'er, G., Dicks, L.V., Visconti, P., Arlettaz, R., Baldi, A., Benton, T.G., Collins, S., Dieterich, M., Gregory, R.D., Hartig, F., Henle, K., Hobson, P.R., Kleijn, D., Neumann, R.K., Robijns, T., Schmidt, J., Schwartz, A., Sutherland, W.J., Turbé, A., Wulf, F., Scott, A.V., 2014. EU agricultural reform fails on biodiversity. *Science* 344 (6188), 1090–1092. <https://doi.org/10.1126/science.1253425>.
- Pignatti, S., 1982. Flora d'Italia [Flora of Italy]. I-III. *Bol. Edagricole. Ital.*
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2015. *The R Core Team, R Core Team*, 2015. *nlme: Linear and Nonlinear Mixed Effects Models*.
- Piqueray, J., Bottin, G., Delescaillie, L.M., Bisteau, E., Colinet, G., Mahy, G., 2011. Rapid restoration of a species-rich ecosystem assessed from soil and vegetation indicators: the case of calcareous grasslands restored from forest stands. *Ecol. Indic.* 11, 724–733. <https://doi.org/10.1016/j.ecolind.2010.06.007>.
- Piqueray, J., Ferroni, L., Delescaillie, L.M., Speranza, M., Mahy, G., Poschold, P., 2015. Response of plant functional traits during the restoration of calcareous grasslands from forest stands. *Ecol. Indic.* 48, 408–416. <https://doi.org/10.1016/j.ecolind.2014.08.039>.
- Plieninger, T., Höchtl, F., Spek, T., 2006. Traditional land-use and nature conservation in European rural landscapes. *Environ. Sci. Pol.* 9, 317–321. <https://doi.org/10.1016/j.envsci.2006.03.001>.
- R Core Team, 2018. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rameau, J.C., Mansion, D., Dumé, G., Coll, 1989. *Flore Forestière Française, Guide écologique illustré. Plaines et collines*. Vol. 1. Institut pour le Développement Forestier, Ministère de l'Agriculture et de la Forêt, Paris.
- Reyes, O., Casal, M., 2008. Regeneration models and plant regenerative types related to the intensity of fire in Atlantic shrubland and woodland species. *J. Veg. Sci.* 19, 575–583. <https://doi.org/10.3170/2008-8-18412>.
- Reyes, O., Casal, M., Rego, F.C., 2009. Resprouting ability of six Atlantic shrub species. *Folia Geobot.* 44, 19–29. <https://doi.org/10.1007/s12224-009-9029-x>.
- Rius, D., Vannièrè, B., Galop, D., Vannièrè, B., Galop, D., 2009. Fire frequency and landscape management in the northwestern Pyrenean piedmont, France, since the early Neolithic (8000 cal. BP). *The Holocene* 19, 847–859. <https://doi.org/10.1177/0959683609105299>.
- Ryser, P., Verduyn, B., Lambers, H., 1997. Phosphorus allocation and utilisation in three grass species with contrasting response to N and P supply. *New Phytol.* 137, 293–302.
- San Emeterio, L., Múgica, L., Ugarte, M.D., Goicoa, T., Canals, R.M., 2016. Sustainability of traditional pastoral fires in highlands under global change: effects on soil function and nutrient cycling. *Agric. Ecosyst. Environ.* 235, 155–163. <https://doi.org/10.1016/j.agee.2016.10.009>.
- Stokes, K., Bullock, J., 2003. *Ulex gallii* Planch. and *Ulex minor* Roth. *J. Ecol.* 91, 1106–1124.
- Suding, K.N., Gross, K.L., Houseman, G.R., 2004. Alternative states and positive feedbacks in restoration ecology. *Trends Ecol. Evol.* 19, 46–53. <https://doi.org/10.1016/j.tree.2003.10.005>.
- Valkó, O., Török, P., Deák, B., Tóthmérész, B., 2014. Review: prospects and limitations of prescribed burning as a management tool in European grasslands. *Basic Appl. Ecol.* 15, 26–33. <https://doi.org/10.1016/j.baee.2013.11.002>.
- Valkó, O., Kelemen, A., Migléc, T., Török, P., Deák, B., Tóth, K., Tóth, J.P., Tóthmérész, B., 2018. Litter removal does not compensate detrimental fire effects on biodiversity in regularly burned semi-natural grasslands. *Sci. Total Environ.* 622–623, 783–789. <https://doi.org/10.1016/j.scitotenv.2017.11.356>.
- Van Langevelde, F., Van De Vijver, C.A.D.M., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., Prins, H.H.T., Rietkerk, M., 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84, 337–350. [https://doi.org/10.1890/0012-9658\(2003\)084\[0337:EOFAHO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0337:EOFAHO]2.0.CO;2).
- Vandvik, V., Heegaard, E., Måren, I.E., Aarrestad, P.A., 2005. Managing heterogeneity: the importance of grazing and environmental variation on post-fire succession in heathlands. *J. Appl. Ecol.* 42, 139–149. <https://doi.org/10.1111/j.1365-2664.2005.00982.x>.
- Vera, F.W.M., 2000. *Grazing Ecology and Forest History*. CABI.
- Wonkka, C.L., Twidwell, D., West, J.B., Rogers, W.E., 2016. Shrubland resilience varies across soil types: implications for operationalizing resilience in ecological restoration. *Ecol. Appl.* 26, 128–145. <https://doi.org/10.1890/15-0066.1>.
- Wood, S.N., 2019. Package “mgcv”: Mixed GAM Computation Vehicle With Automatic Smoothness Estimation. <https://doi.org/10.1201/9781315370279>.
- Yee, T.W., Mitchell, N.D., 1991. Generalized additive models in plant ecology. *J. Veg. Sci.* 2, 587–602.
- Zhang, C., Dong, Q., Chu, H., Shi, J., Li, S., Wang, Y., Yang, X., 2018. Grassland community composition response to grazing intensity under different grazing regimes. *Rangel. Ecol. Manag.* 71, 196–204. <https://doi.org/10.1016/j.rama.2017.09.007>.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology With R*. Springer, New York.