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Original Research Article

Plant diversity and botanical composition in an Atlantic heather-gorse dominated understory after horse grazing suspension: Comparison of a continuous and rotational management



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ABSTRACT

Floristic diversity changes substantially depending on the type of land management. We evaluated the impact of a continuous (CG) and rotational (RG) grazing system on the dynamics of plant diversity and community composition in a heather-gorse understory after a two and six-year pause from horse grazing. Previously grazed sites had higher total and rare species richness and diversity than ungrazed (UN), regardless the type of grazing system. The positive impact of previous grazing on species richness was higher in CG and continued after six years in both grazing systems. Seven species of high conservation interest in heathlands were present in the studied areas. Most of them were associated to CG management and none was exclusively in RG. The reduction of the shrub component by previous horse grazing led to a decrease of gorse dominance, thus potentially reducing fire risk and increasing plant diversity. The extent of the positive effect of horse grazing controlling excessive accumulation of combustible material and favoring species richness differed when relative abundance of species, and not solely the number of species, was taken into account (Simpson's dominance increased and Pielou's evenness decreased after six years). Overall, the effects of previous rotational and continuous grazing on plant diversity in an Atlantic heather-gorse dominated plant community were still apparent 2 or 6 years after grazing interruption, although declined after the six-year grazing interlude. Rotational management revealed a slight advantage upon the control of gorse biomass long term, and assisted to maintain the relative abundance of species more evenly over time. The alpha and beta diversity indices confirmed that plant diversity similarity between rotational and continuous management increased after six years.

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1. Introduction

Atlantic heathlands, dwarf-shrub plant communities dominated by heather species such as *Erica* spp. and *Calluna vulgaris*, are prized for their biodiversity, aesthetic and cultural value. Their distribution include Atlantic countries throughout Europe,

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from central Norway to Northern Morocco, and cover Atlantic portions of Denmark, NW Germany, The Netherlands, Belgium, Western France, The British Isles and NW Iberian Peninsula (Loidi et al., 2007). Although many regions of Western Europe lost up to 80–90% of their heaths over the last century, Iberian heathlands still cover wide areas and represent almost a quarter of the total European coverage (Rosa García et al., 2013). They are also the most biodiverse in Europe, as they are in the boundary between the Mediterranean and Atlantic biogeographical regions (Loidi et al., 2010), and are included in distinctive habitats listed in the European Habitats Directive (Thompson et al., 1995; Ramil Rego et al., 2013).

Land use practices as cutting, cultural burning and grazing have led to the formation of European heathlands, and their conservation is associated to a certain degree of moderate anthropic activity, therefore they are ecosystems supported by the European Union (EU) within the high nature value farming framework. Nonetheless, the rural depopulation and abandonment of management practices since the 1950s have contributed to large accumulations of highly flammable phytomass in heathlands of NW Spain, making them susceptible to wildfires that can cause big social, economic and environmental losses (Rosa García et al., 2013; López López et al., 2017). The EU is advocating for conservation plans that contemplate their sustainable management and efforts are invested in their preservation or restoration.

On the other hand, in European temperate ecosystems, grazing by livestock is a management strategy that can improve rural sustainability while controlling the accumulation of flammable woody vegetation (Osoro et al., 1999; Rigueiro-Rodríguez et al., 2009, 2012). It can also be a sustainable and successful management tool for shaping and maintaining semi-natural habitats, and promoting greater biodiversity and multifunctionality (Silva-Pando et al., 2002; McAdam and McEvoy, 2009; Fagúndez, 2016; López López et al., 2017). However, although the benefits of grazing on heathlands conservation provide a greater biodiversity than other interventions such as burning or cutting (Rosa García et al., 2013), grazing alone cannot maintain heathland in good conservation status and a combination of management is necessary (Bartolomé et al., 2000; Lake et al., 2001).

A higher plant diversity leads in general to greater productivity, better nutrient retention and more stability in plant communities; in contrast, the reduction of 50% in the number of plant species can conduct to a loss up to 10 or 20% of productivity (Tilman, 2000). In grazing systems, the dynamics of plant diversity greatly depends on the type of vegetation community, and is often influenced by animal grazing species or breed, stocking rates, and type of grazing system, among others (González-Hernández et al., 1998; Rook et al., 2004; Briske et al., 2008; Mosquera-Losada et al., 2009; Fagúndez, 2016). The analysis of Briske et al. (2008) provides an extensive evaluation of the controversy on rotational and continuous grazing systems as strategy in rangelands management and reports on the bias of most studies, focused on evaluating plant and livestock production given the economic importance of grazing. Thus, insufficient studies report on the effect of continuous and rotational grazing upon plant biodiversity in heathland communities (McEvoy et al., 2006; Mosquera-Losada et al., 2009; Rigueiro-Rodríguez et al., 2012). An analysis of the repercussion of different managed grazing systems on conservation of natural resources (i.e. plant diversity among others) would contribute useful information towards those agricultural policies that currently are contemplating to promote reduced stocking rates to achieve a balance between animal production and plant resources, as well as reducing greenhouse gas emissions (EUROSTAT, 2019).

Free ranging horses are compatible to heathland conservation management, maintaining biodiversity values and animal production in Europe (Putman et al., 1987; Celaya et al., 2012; Rosa García et al., 2013; Fagúndez, 2016; López López et al., 2017b; Fraser et al., 2019). Horse grazing is abundant in the mountainous areas of the NW of the Iberian Peninsula due to their easier management and lower care needs compared to other herbivore species, and it is known to provide relevant ecosystem services and habitat conservation (Silva-Pando et al., 2002; Izco et al., 2006; Fagúndez, 2016; López López et al., 2017a). Yet, in general, knowledge of how to manage heathlands by grazing is hampered by poor information on how different grazing regimes may affect the range of vegetation structures and habitats present on heathlands, and thus how to best provide habitat for a diversity of taxa (Lake et al., 2001). In this regard, continuous and rotational horse grazing management in a heather-gorse dominated understory were useful tools for reducing gorse (*Ulex europaeus*) biomass and, therefore, fire risk during a two-year grazing and post-grazing period (Rigueiro-Rodríguez et al., 2012). In that study, biomass reduction was not affected by the type of grazing system used; however, in the rotational grazing system, gorse biomass was reduced more efficiently by horse grazing, with a faster recovery for this species in the continuous system and, therefore the different grazing management affecting plant diversity at short-term in different ways. In the current study, we sought to assess the magnitude of change of floristic composition and plant diversity during a pause from a two-year horse grazing and its possible relation with the type of management used. More specifically, the objectives of this research were to: (1) examine short-term (2 years) and long-term (6 years) responses of a heathland plant community (i.e. dynamics of plant diversity and of community composition) after horse grazing suspension and (2) examine the impact of previous continuous (CG) and rotational (RG) management on such dynamics.

2. Material and methods

2.1. Site description

The experiment was conducted in a pinewood stand with an understory formed by gorse and heather species at San Estevo de Parga, Lugo, NW Spain, (43°09' N, 7°48' W) located 500 m a.s.l. Tree density comprised 833 trees ha⁻¹ of *Pinus*

radiata in a 3 × 4 m spatial arrangement. No thinning or pruning had taken place since the stand was established in 1970. The initial understory vegetation was a dense shrubland dominated by *U. europaeus* (over 80% of plant cover, approximately 2.5 t ha⁻¹; see Rigueiro-Rodríguez et al., 2012), and heathers (*Calluna vulgaris*, *Erica cinerea* and *Erica umbellata*, among others). The most common herbaceous species were grasses such as *Agrostis curtisii* and *Agrostis capillaris*.

Climate is temperate oceanic with mean annual precipitation and temperature of 1300 mm and 12.2 °C, respectively. Soils are classified as Umbrisol (FAO, 1998), acid (pH 4.51) and nutrient poor with a sandy-clay texture (63% sand, 20% clay and 17% silt).

2.2. Study design and animal management

The experimental design consisted of two fenced areas of 6 ha that were previously designated to continuous (CG) and rotational (RG) horse grazing. CG and RG enclosures were chosen as experimental units before grazing based on their homogeneous and similar vegetation structure. For rotational management, RG enclosure was sub-divided into four paddocks of 1.5 ha. Each grazing system was grazed by two mature mares (8–10 years old, 300 ± 20 kg) of the protected Galician Mountain Horse breed (i.e. Cabalo Galego de Monte), a small horse with rustic feeding habits, whose populations are under recovery (Xunta de Galicia, 2001). Thus, horses were managed at stocking densities of 0.33 and 1.33 animals ha⁻¹ in the CG and RG, respectively. Each paddock (1.5 ha) in the RG system was grazed by two horses during 30 days in sequence, each followed by a rest period of 90 days until next grazing occurred. The horse density was selected based on previous studies that reported the efficiency of one horse every 4 ha to reduce combustible biomass and therefore fire risk (Rigueiro-Rodríguez et al., 1999). Grazing started in July 2000 and ceased in December 2002 (for more details of grazing period see Rigueiro-Rodríguez et al., 2012). In addition, eleven 10 m × 10 m fenced plots established before grazing (hereafter ungrazed: UN) and located adjacent to the CG and RG enclosures were used to look at vegetation successional trends.

2.3. Study of plant diversity

In June of 2004 and 2008 (i.e. after 2 and 6 years of horse grazing suspension) we conducted floristic inventories in a set of four circular plots of 20 m diameter (each plot about 314 m² visually estimated) per grazing system. Inventoried plots were positioned to capture representative areas of pasture in both grazed systems. For that purpose, CG enclosure was visually divided into quarters (the RG system was physically divided in four paddocks), and circular plots placed randomly and sufficiently separated from each other. Thus, 16 floristic inventories of 314 m² were accomplished in the grazed systems. In addition, we carried out eleven floristic inventories in the UN fenced plots in June of 2004 (surveying an area of 1100 m²). We used this data set as a baseline to compare never grazed vegetation with the successional trends after grazing (i.e. how long the positive impact of grazing on plant diversity maintained after grazing ceased).

Vascular plant species presence and estimated visual cover to the nearest 5% were recorded in all plots. From those 27 floristic inventories, species richness (total number of species), and alpha and beta diversity indices (Whittaker, 1972) were determined to assess the impact of each grazing system on plant diversity dynamics along a two and six year interval after grazing. Both alpha and beta diversity indices were determined as Magurran (2004), except beta complementarity estimated by Colwell and Coddington (1994). Simpson dominance index was calculated as $D = \sum p_i^2$, where p_i is the proportional abundance of each i species, Shannon diversity index was calculated as $H' = -\sum (p_i \ln p_i)$, Pielou's evenness was calculated as $J = H'/\ln \text{spp.}$, where spp. is the number of species. Beta diversity represents the extent of species replacement or biotic change along environmental gradients. Several beta diversity indices were studied to explain the degree of gain or loss of species among treatments. For that purpose, coefficients of similarity, replacement and complementarity were calculated using qualitative data (presence-absence of species) to look at the degree of similarity in the vegetation dynamics between the grazing systems. Similarity indices widely used such as Jaccard's and Sorensen's were calculated as $I_J = c/(a + b - c)$ and $I_S = 2c/(a + b)$, respectively. Other similarity estimates used were Sokal and Sneath's as $I_{SS} = c/[2(a + b + c) - c]$, Braun-Blanquet as $I_{B-B} = c/(b + c)$, and Ochiai-Barkman as $I_{OB} = c/\sqrt{[(c + b)(c + a)]}$. In all of them, a is the number of species in Site A, b is the number of species in Site B and c is the number of species found in both sites (Magurran, 2004). These indices are designed to equal 1 in cases of complete similarity (that is where the two sets of species are identical) and 0 if the sites are dissimilar and have no species in common. On the other hand, replacement coefficients take into account substitution of species. We used one of the most straightforward measures (Magurran, 1988), Whittaker's, calculated as $\beta = (S/\alpha) - 1$, where S = the total number of species recorded in the system and α is the average sample diversity where each sample is a standard size and diversity is measured as species richness. Cody's replacement index is a good intuitive measure of species turnover (Magurran, 1988), and simply adds the number of new species encountered to the number of species that are lost: $\beta_C = 1 - (c(a + b)/2ab)$. Routledge's takes overall species richness and the degree of species overlap into consideration and is expressed as $\beta_R = (S^2/2r + S) - 1$, where S is the total number of species in all samples and r is the number of species pairs with overlapping distributions (if only 2 sites, then $r = c$). Magurran's beta diversity index, as $\beta = (a + b)(1 - I_J)$, explains how beta diversity value raises when number of species in both sites increases and also when they become more different.

Complementarity was estimated as $C_{AB} = U_{AB}/S_{AB}$, where $U_{AB} = a + b - 2c$ and $S_{AB} = a + b - c$. This index explains the degree of dissimilarity on species composition between biota pairs (Colwell and Coddington, 1994).

Because at a local scale, plant functional traits can be useful tools in predicting species' responses to grazing (de Bello et al., 2005), we pooled cover percentages from the same inventories and analyzed the following items: grasses, herbaceous non-graminoids (forbs and a small amount of ferns), shrubs and tree seedlings (as an estimate of the effect of previous grazing system on tree natural regeneration). Finally, a set of distinctive species were also selected for discussion based on their high fidelity to the community and/or with a high conservation interest (Loidi et al., 2007; Fagúndez, 2016; Online Atlas of the British and Irish Flora, 2018).

Table 1

Presence (●) of plant species in a heather-gorse dominated understory. Continuous grazing (C), rotational grazing (R) after two and six years of grazing suspension, and ungrazed plots (UN). G: Grasses, HNG: Herbaceous non-graminoids, S: Shrubs, TS: Tree seedlings. Plant species present solely in C (■) and R (▲), exclusively 2 years after grazing (blue) and 6 years after grazing (red). Species marked with (*) have been reported as of high fidelity to heathland communities or rare species with a high conservation interest.

Plant species	Family	Group	2yC	2yR	6yC	6yR	UN
* <i>Laserpitium prutenicum</i>	Apiaceae	HNG	■		■		
<i>Achillea millefolium</i>	Asteraceae	HNG	■				
* <i>Cirsium filipendulum</i>	Asteraceae	HNG	●			●	●
<i>Hypochoeris radicata</i>	Asteraceae	HNG		●	●	●	
* <i>Scorzonera humilis</i>	Asteraceae	HNG	●		●	●	
<i>Betula pubescens</i>	Betulaceae	TS	●		●	●	●
<i>Blechnum spicant</i>	Blechnaceae	HNG	●	●	●	●	
<i>Glandora prostrata</i>	Boraginaceae	S	●		●		●
* <i>Jasione montana</i>	Campanulaceae	HNG	●				●
<i>Halimium lasianthum</i>	Cistaceae	S	●	●	●	●	
<i>Xolantha globularifolia</i>	Cistaceae	HNG	●	●	●		
<i>Hypericum humifusum</i>	Clusiaceae	HNG		●	●	●	
<i>Dryopteris affinis</i>	Dryopteridaceae	HNG		▲			
<i>Dryopteris dilatata</i>	Dryopteridaceae	HNG				▲	
<i>Calluna vulgaris</i>	Ericaceae	S	●	●	●	●	●
<i>Daboecia cantabrica</i>	Ericaceae	S	●		●	●	●
<i>Erica ciliaris</i>	Ericaceae	S		●	●	●	●
<i>Erica cinerea</i>	Ericaceae	S	●	●	●	●	●
<i>Erica tetralix</i>	Ericaceae	S			●	●	
<i>Erica umbellata</i>	Ericaceae	S	●	●	●	●	●
<i>Adenocarpus complicatus</i>	Fabaceae	S				▲	
<i>Cytisus scoparius</i>	Fabaceae	S	●	●	●	●	●
<i>Cytisus striatus</i>	Fabaceae	S		●	●	●	●
* <i>Genista anglica</i>	Fabaceae	S			●		●
<i>Genista florida</i>	Fabaceae	S		●		●	●
<i>Lotus corniculatus</i>	Fabaceae	HNG	■		■		
<i>Pterospartum tridentatum</i>	Fabaceae	S	●	●	●	●	●
<i>Ulex europaeus</i>	Fabaceae	S	●	●	●	●	●
<i>Castanea sativa</i>	Fagaceae	TS	●		●	●	
<i>Quercus pyrenaica</i>	Fagaceae	TS		●	●	●	
<i>Quercus robur</i>	Fagaceae	TS	●	●	●	●	●
* <i>Gladiolus illyricus</i>	Iridaceae	HNG	■				
<i>Luzula multiflora</i>	Juncaceae	HNG	■				
<i>Simethis mattiazzi</i>	Liliaceae	HNG		●	●	●	●
<i>Pinus radiata</i>	Pinaceae	TS	●	●	●	●	●
<i>Veronica serpyllifolia</i>	Plantaginaceae	HNG			■		
<i>Agrostis capillaris</i>	Poaceae	G	●	●	●	●	●
<i>Agrostis curtisii</i>	Poaceae	G	●	●	●	●	●
<i>Agrostis hesperica</i>	Poaceae	G			■		
<i>Agrostis truncatula</i>	Poaceae	G	●	●			●
<i>Avenula sulcata</i>	Poaceae	G			●	●	
<i>Dactylis glomerata</i>	Poaceae	G			●	●	
<i>Danthonia decumbens</i>	Poaceae	G				▲	
<i>Holcus lanatus</i>	Poaceae	G	■		■		
<i>Holcus mollis</i>	Poaceae	G		●	●	●	●
<i>Pseudarrhenatherum</i>	Poaceae	G	●	●	●	●	●
<i>Polygala vulgaris</i>	Polygalaceae	HNG			■		
<i>Rumex acetosa</i>	Polygonaceae	HNG	■				
<i>Sesamoides purpurascens</i>	Resedaceae	HNG		●	●	●	
<i>Frangula alnus</i>	Rhamnaceae	TS			■		
<i>Potentilla erecta</i>	Rosaceae	HNG	●	●	●	●	●
<i>Rubus sp.</i>	Rosaceae	S		●	●	●	●
<i>Galium saxatile</i>	Rubiaceae	HNG	■				
<i>Salix atrocinerea</i>	Salicaceae	TS	●			●	
<i>Digitalis purpurea</i>	Scrophulariaceae	HNG		●		●	●
<i>Linaria triornithophora</i>	Scrophulariaceae	HNG		▲			
* <i>Thymelaea coridifolia</i>	Thymelaeaceae	HNG	■				
<i>Viola canina</i>	Violaceae	HNG			■		

2.4. Data analysis

We used two-way ANOVA to test for differences in the impact of grazing system on plant community dynamics following livestock removal. The type of management (CG, RG) and time following livestock removal (2 and 6 years) were entered as fixed factors (independent variables). The species richness, diversity indices and relative proportions of plant groups (grasses, herbaceous non-graminoids, tree seedlings and shrubs) were entered as dependent variables. The homogeneity of variance was checked for each data set by plotting the residuals. Natural log transformations were used to obtain constant variance for Simpson's dominance, shrubs and herbaceous non-graminoids. Fisher's test (Least Significant Difference, LSD) was applied for comparisons. Statgraphics Centurion XVI v.16.1.18 was used for all tests.

Differences in plant community composition were evaluated by visualizing the two first axes of a non-metric multidimensional scaling (NMDS) analysis choosing Bray-Curtis dissimilarity as a distance measure between post-grazing regimes using PAST (Hammer et al., 2001). In this analysis, the statistical units were grouped in their five experimental conditions: ungrazed (UN), rotational grazing after 2 years (2 yR), continuous grazing after 2 years (2 yC), rotational grazing after 6 years (6 yR), and continuous grazing after 6 years (6 yC). Species that occurred in at least two experimental conditions, and at least in two plots, were included in a contingency table using Pearson's chi-square statistic to test for positive or negative significant association with previous grazing. We used data of relative proportions of species in both analyses.

3. Results

3.1. Species richness and diversity

A total of 58 plant species from 28 families were recorded in the studied sites (Table 1). Of the 16 species that occurred in all the experimental conditions (UN, 2 yR, 2 yC, 6 yR, 6 yC), shrubs were the most abundant (50%), followed by herbaceous (37.5%) and tree seedlings (12.5%). Shortly after grazing cessation (i.e. two years), the average in the number of species was lower than six years following removal of horses, and the mean number of species in the UN area was lower than in the previously grazed systems (Fig. 1a). The two-way ANOVA showed a higher species richness in CG than in RG, and a significant increase six years from grazing ($P < 0.01$ for grazing system (Gr) and years after grazing interruption (Y), respectively) (Table 2).

Unlike species richness, the Simpson's dominance index did not show differences between grazing systems. Higher values of this index after six years of grazing abandonment ($P < 0.05$ for Y) (Table 2) revealed an increase of dominance (opposite to diversity) over time since the cessation of disturbance in both continuous and rotational grazing systems, in accordance with a higher dominance in the undisturbed ungrazed plots (Fig. 1b). On the other hand, Shannon-Wiener's index (H') measure of diversity was the lowest in the UN area in agreement with Simpson's and species richness indices (Fig. 1c). Nevertheless, this estimate showed no differences of plant diversity between grazing systems or as a result of time (Table 2). Pielou index (J) revealed a higher evenness shortly after grazing suspension ($P < 0.01$ for Y) (Table 2). Beta diversity estimates confirmed that the differences between the rotational and continuous management after grazing weaken over time (Table 3). Most β similarity indices were higher after six years of grazing cessation than after two years. On the other hand, β replacement estimates showed the opposite trend, as they measure species turnover. For example, Magurran's index, which explains how beta diversity value becomes higher when number of species in both sites increases and when they become more different, revealed that the differences between the two types of management on plant diversity were less evident six years after grazing ceased. This index showed a 1.7-fold decrease from the value found only two years after grazing cessation. In line with this, complementarity index, which reflects the degree of dissimilarity on species composition, decreased after six years.

3.2. Relative abundance of plant species and plant groups

European gorse dominated in the UN area, followed by ericoids and *Rubus* sp. (Fig. 2). Previously grazed systems revealed a more balanced proportion of gorse, heathers and herbaceous plants. Two years after grazing ceased, gorse was still 40% less abundant than in the UN area, and the ericoid component hardly changed. Four years later heathers dominated over gorse in the previously grazed areas. Grasses was the plant group that primarily balanced the abundance of shrubs two years after grazing interruption, and especially in continuous management (Fig. 3). The abundance of *Agrostis curtisii*, *Agrostis truncatula* and *Pseudarrhenatherum longifolium* continued to be higher in CG than in ungrazed sites 2 years after grazing ceased, whereas *Agrostis capillaris* proportions showed twice higher in RG (Fig. 2). Grasses abundance dropped 4 years later when the cover of shrubs such as *Ulex europaeus*, *Erica* spp. and *Calluna vulgaris* increased (Fig. 2).

The analysis of diversity by biological types (i.e. herbaceous, shrubs or tree seedlings) showed that relative proportions of the herbaceous component were higher in grazed than in ungrazed sites only after a grazing interruption of two years (Fig. 3). Overall, a decrease of herbaceous plants occurred over time (Table 2). Finally, relative abundance of shrubs increased during the four-year interval ($P < 0.05$ for Y), but did not differ between grazing systems (Table 2). Only after 2 years of grazing suspension, the proportion of shrubs was lower than in the UN areas (Fig. 3).

The two-way ANOVA confirmed the absence of interaction between the independent variables (time after grazing interruption and grazing system). Overall, the significant differences in the diversity indices and in the plant groups were only attributable to the time since the end of grazing and not to a particular grazing system.

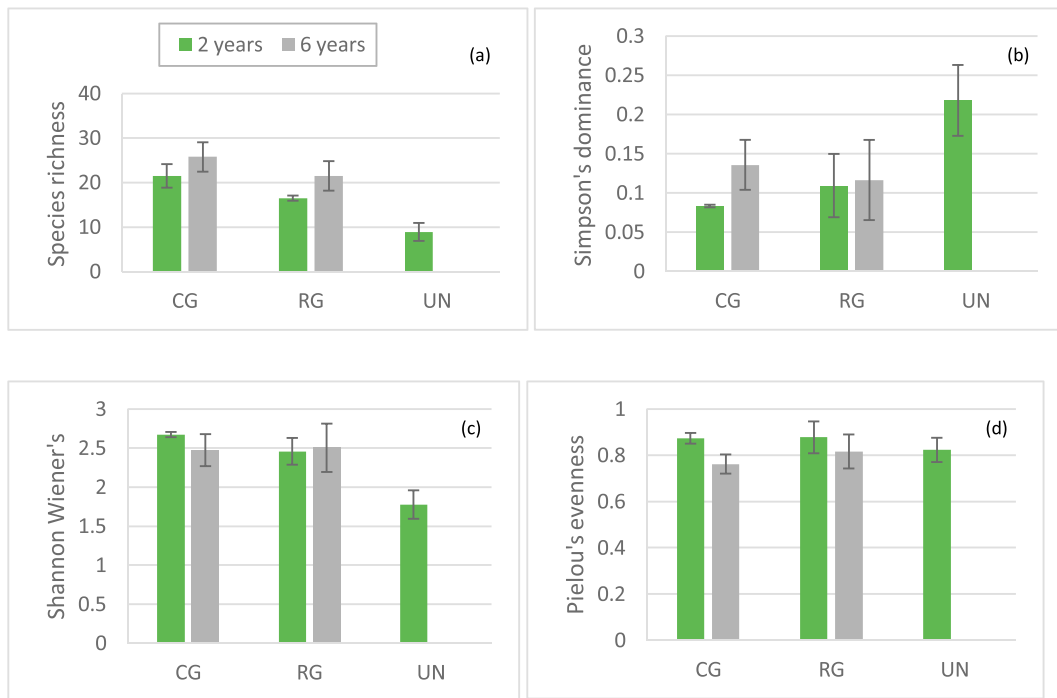


Fig. 1. Mean ± standard deviation of diversity indices in ungrazed (UN) plots, continuous (CG) and rotational (RG) grazing systems of a heather-gorse dominated understory after 2 and 6 years of grazing suspension.

Table 2

Results of two-way ANOVA performed on diversity parameters and relative abundance of plant groups at a heather-gorse dominated understory. *P*-value in bold indicates a significant effect.

Data	Env ^a	<i>F</i> -ratio	<i>P</i> -value
Plant diversity index			
Species richness	Gr	11.44	0.0055
	Y	7.23	0.0197
	Gr x Y	0.01	0.9323
Simpson's dominance	Gr	0.01	0.9426
	Y	6.63	0.0243
	Gr x Y	1.14	0.3069
Shannon Wiener's <i>H'</i>	Gr	0.82	0.3816
	Y	1.84	0.2002
	Gr x Y	0.53	0.4803
Pielou's evenness	Gr	1.47	0.2490
	Y	12.60	0.0040
	Gr x Y	0.40	0.5371
Relative abundance			
Grasses	Gr	2.49	0.1408
	Y	14.58	0.0024
	Gr x Y	0.65	0.4344
Herbaceous non-graminoids	Gr	1.02	0.3321
	Y	8.24	0.0141
	Gr x Y	1.70	0.2162
Tree seedlings	Gr	3.02	0.1078
	Y	1.68	0.2196
	Gr x Y	0.75	0.4038
Shrubs	Gr	0.56	0.4694
	Y	5.95	0.0312
	Gr x Y	0.19	0.6709

^a Environmental variables: Gr: previous grazing treatment (continuous vs rotational), Y: year (2 years or 6 after the grazing interruption).

Table 3

Summary of β diversity indices in a heather-gorse dominated understory explaining plant diversity similarities between continuous (C) and rotational (R) management following grazing removal (2 and 6 years after grazing ceased).

β - diversity estimates	Indices		2yC-2yR	6yC-6yR
β Similarity ^a	Jaccard	I_j	0.2292	0.5882
	Sorensen	I_S	0.5946	0.7407
	Sokal & Sneath	I_{SS}	0.1294	0.1563
	Braun-Blanquet	I_{B-B}	0.3548	0.4054
	Ochiai-Barkman	I_{OB}	0.3734	0.4261
β Replacement ^a	Cody (1993)	β_C	0.4015	0.2537
	Routledge (1977)	β_R	27.167	22.432
	Magurran (1988)	β	57.042	33.353
	Whittaker (1972)	β	0.2857	0.2400
	Complementarity ^b	Complementarity	C_{A-B}	0.58

^a Indices determined as Magurran (2004).

^b Index by Colwell and Coddington (1994).

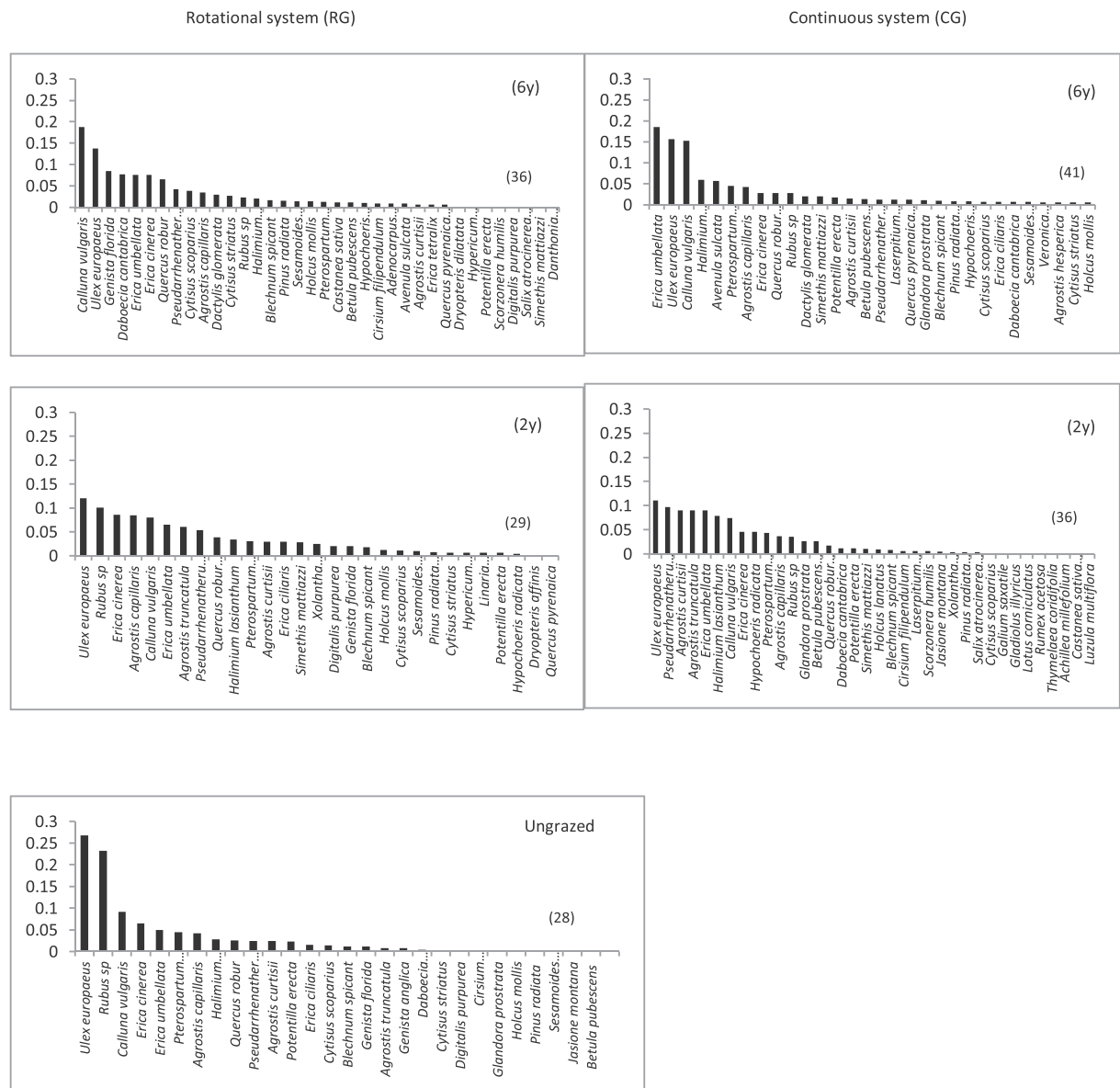


Fig. 2. Relative abundance of plant species in a heather-gorse dominated understory: rotational (left) and continuous (right) grazing systems displaying 6 years (6y), 2 years (2y) after grazing, and ungrazed (control). Numbers in brackets indicate total number of plant species found in each site.

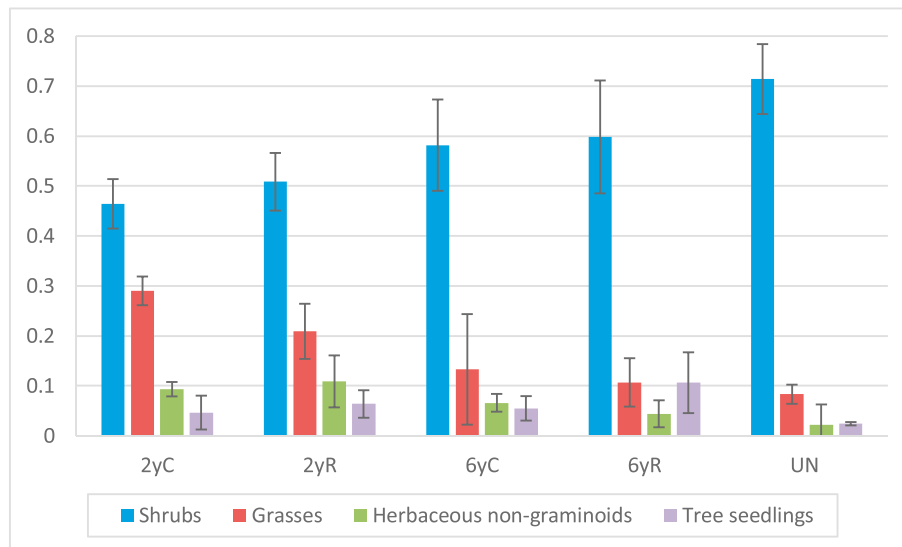


Fig. 3. Mean \pm standard deviation of relative proportions of shrubs, grasses, forbs and tree seedlings in continuous (C), rotational (R) and ungrazed (UN) sites of a heather-gorse dominated understory after 2 and 6 years of grazing suspension.

3.3. Plant community composition

The resulting two-dimensional NMDS (Stress = 0.15) overlapped the two grazing systems and discriminated the 2-year and 6-year lapse of time since grazing cessation (Fig. 4). Therefore, this additional analysis confirmed the previous results on the resemblance of plant diversity in both types of management and the dissimilarities that occurred mainly as a result of the time interval since grazing. The area representing the composition of the plant community after a six-year grazing interruption from continuous grazing (6 yC) intersected to some extent with that of the ungrazed areas (UN).

Nearly 16% of species (9/58) showed a significant ($P < 0.05$) positive or negative association with some of the five experimental conditions (Table 4). Shrubs such as *Ulex europaeus* and *Rubus* sp. were negatively associated with previous grazing. In contrast, *Calluna vulgaris*, *Genista florida* and *Daboecia cantabrica* had a positive association with rotational management after six years. Two grasses had a significant positive association with continuous grazing after two years of cessation (Table 4): *Agrostis truncatula* and *Pseudarrhenatherum longifolium*.

A few distinctive species were associated to the grazed system and/or time after grazing interruption. Five species were exclusively related with RG, and 14 were restricted to CG. Among the seven species found of high conservation interest, and with high fidelity to the community (species marked with * in Table 1), three were associated exclusively to CG: *Laserpitium*

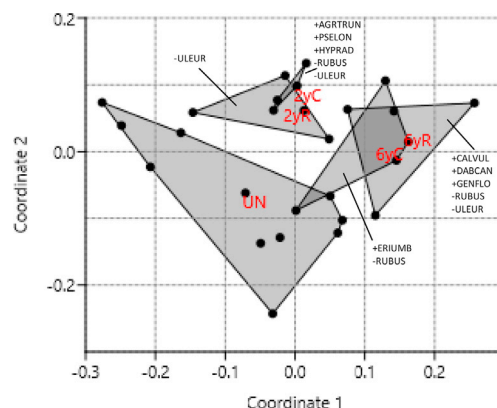


Fig. 4. Non-metric multidimensional distance scaling (NMDS) analysis of plant community composition of 27 floristic inventories plotted for the first two coordinates and calculated from Bray-Curtis dissimilarity index. Stress value = 0.15, which indicates an acceptable representation (i.e. in the scale of 0.05 excellent to 0.3 poor). Polygons represent the coherent area of the different experimental conditions: rotational (R) and continuous (C) grazing management after 2 and 6 years of grazing cessation (2y, 6y). UN represents the ungrazed sites. The species positively (+) or negatively (-) associated to each of the experimental conditions are shown (see Table 4 for details on degree of association and species acronyms).

Table 4

Species associations with the experimental conditions using Pearson's chi-square statistic. Phi coefficient (values between 0 and 1, + or -) indicates the degree and type of association with previous grazing management (UN: ungrazed, continuous: C, rotational: R) after 2 or 6 years following grazing removal.

Plant species	χ^2	P value	Phi	Association
Grasses				
<i>Agrostis truncatula</i> (AGRTRUN)	6.737	0.009	0.184	UN*2 yC
<i>Pseudarrhenatherum longifolium</i> (PSELON)	4.031	0.045	0.142	UN*2 yC
Shrubs				
<i>Calluna vulgaris</i> (CALVUL)	4.153	0.042	0.144	UN*6 yR
<i>Daboecia cantabrica</i> (DABCAN)	7.254	0.007	0.190	UN*6 yR
<i>Genista florida</i> (GENFLO)	5.701	0.017	0.161	UN*6 yR
<i>Rubus</i> sp. (RUBUS)	13.211	0.000	-0.257	UN*2 yC
	15.341	0.000	-0.277	UN*6 yC
	17.735	0.000	-0.298	UN*6 yR
<i>Ulex europaeus</i> (ULEUR)	6.640	0.010	-0.182	UN*2 yC
	5.604	0.018	-0.167	UN*2 yR
	3.854	0.050	-0.139	UN*6 yR
<i>Erica umbellata</i> (ERUM)	10.286	0.001	0.227	UN*6 yC
Herbaceous non-graminoids				
<i>Hypochoeris radicata</i> (HYPRAD)	5.128	0.024	0.160	UN*2 yC

prutenicum, *Thymelaea coridifolia* and *Gladiolus illyricus*, and none was exclusive of RG. *Scorzonera humilis* was present in CG in the two lapses of time studied, but occurred in RG only after the long pause from grazing. Two species present in the ungrazed areas, *Jasione montana* and *Genista anglica*, only occurred in the CG system, after 2 and six years of grazing cessation, respectively.

4. Discussion

4.1. Influence of previous grazing management on plant diversity

In our study, previously grazed sites showed higher plant diversity than ungrazed sites. Horse grazing increased species richness and diversity, as well as numbers of rare species in heathlands (Bullock and Pakeman, 1997; Rigueiro-Rodríguez et al., 2012; Fagúndez, 2016; López López et al., 2017b). This positive impact of horse grazing on plant diversity did not translate equally over time for all the diversity indices here studied. In general, plant diversity in continuous and rotational management developed after grazing cessation similarly, and only the species richness index was significantly higher in continuous management. This is coherent with reports on the potential damage associated with excessive grazing stocking rates in rotational management (Heitschmidt et al., 1987), or the significant raise in the viability of some species population when the stock load is reduced by 50% or more (McGraw and Furedi, 2005). More specifically, in temperate European heathlands, whereas moderate grazing positively influences biodiversity (Bullock and Pakeman, 1997), the type of herbivore and stocking rate can be critical for the conservation of plant diversity in heathlands dominated by *Erica mackaiana* (Fagúndez, 2016). In the case of our study, a 4 times higher instantaneous stocking rate in RG, in one of every 4 months, could have determined the superior number of species found in the CG system. Nevertheless, studies on grazed heathlands in UK concluded that stocking density does not always accurately reflect the effects of grazing intensity, and that utilization rate of dominant plants may be the best measure (Lake et al., 2001). Disturbances may increase species richness by lowering the dominance of a few species, freeing resources for early successional plants, and providing opportunities for herbaceous species to spread rapidly. Thus, the speed of regeneration of the dominant shrub species can be a major factor affecting structural parameters in these communities, and the moment when the maximum value in species diversity appears is highly related, among other factors, to whether the site is dominated by resprouters, which recover more rapidly, or seeders (Calvo et al., 2012). Dominant heathers in our study: *Calluna vulgaris*, *Erica umbellata* and *Erica cinerea*, are germination dependent after disturbances, and their slower regeneration could allow other woody species and herbaceous species to spread. The slow renewal rate of heathers (González-Hernández et al., 1998; Calvo et al., 2012; Muñoz et al., 2012) could have induced in our study a longer positive effect of previous grazing on species richness that lasted throughout the six years interval. Yet, the number of species is the oldest and simplest concept of estimating biodiversity, and it does not take into consideration the existing uniformity that occurs naturally in plant communities. Thus, considering various plant diversity indicators together might have advantages, as single indicators are incomplete surrogates of biodiversity (Wilsey et al., 2005).

The analysis of other diversity indices, which are influenced by the underlying species abundance distribution, disclosed additional information indicating that plant diversity within the same post-grazing period was not influenced by the grazing system, and confirming (in accordance with species richness) that previous grazed systems maintained higher plant diversity compared to ungrazed sites. In contrast with the species richness estimate, Simpson's dominance and Pielou's evenness indices showed a decrease of plant diversity from the 2 years lapse from grazing to the six years interlude. As a consequence of the extent of the grazing pause, is expected that dominant shrubs proceed to cover existing gaps from previous grazing, which could increase shading conditions at ground level and compromise the permanence of light-demanding species (mainly

herbaceous), and modify the values of diversity indices (Jáuregui et al., 2007; Celaya et al., 2010; Calvo et al., 2012; Rigueiro-Rodríguez et al., 2012). The information from Shannon Wiener's index (which encloses both species richness and evenness) confirmed the uniformity of plant diversity between the two grazing systems after both intervals of grazing interruption. The values of this index in our study (1.8 for ungrazed sites and around 2.5 for previously grazed) were in the usual range, which is between 1.5 and 3.5, and only rarely surpasses 4.5 (Magurran, 2004).

The interrelationships between the diversity metrics are complex as they are differently influenced by species richness and abundance, so it is unrealistic to expect them to display similar response patterns to disturbance (Li et al., 2004; Yuan et al., 2016). Many studies on the response of vegetation to disturbance focus on species richness and diversity, often with reference to the 'intermediate disturbance hypothesis' (IDH) (Connell, 1978). Yuan et al. (2016) reported unimodal curves describing vascular plant species richness peaks at an intermediate level of grazing disturbance, although when they expressed the species diversity using Shannon-Weiner and Simpson indices, both metrics had lower R-square values than species richness. In our study, only the response of species richness to the low-to-high disturbance gradient of grazing (from UN to CG and to RG), showed some consistency with the predictions of IDH.

Overall, plant diversity was mainly influenced by the interval of time since grazing interruption, and less by the type of management. The beta diversity increase on similarity confirmed that the plant diversity differences between the rotational and continuous zones weakened over time and, coherently, beta replacement and complementarity estimates showed the opposite trend. This negative effect on plant diversity due to the interruption of grazing is consistent with studies where grazers increased species replacement. Oldén and Halme (2016) found that grazers had positive effects on plant β -diversities within mesic wood-pastures, creating and maintaining high species replacement by increasing heterogeneity of areas where different species can colonize, grow, dominate or go extinct.

4.2. Effects on plant community composition

The abundance of species is of primary importance in linking species diversity with ecosystem functioning (Wilsey et al., 2005). Nevertheless, biodiversity indices do ignore the identity of the species (Magurran, 2004), and the ecosystem functions (e.g. stability, productivity) are likely more dependent on the dominant species' traits (Grime, 2001; Lepš, 2005). In the present study, the post-grazing plant composition showed some distinctive species and plant groups associated with the grazing system and/or time since grazing interruption.

In grazing conditions, herbs/woody plants ratio and different renewal rates of plant groups are relevant in vegetation dynamics (González-Hernández et al., 1998; Calvo et al., 2012; Muñoz et al., 2012). Thus, at a local scale, plant functional traits are useful tools in predicting species' responses to grazing and, for conservation purposes, in identifying species vulnerable to land-use changes (de Bello et al., 2005). The analysis of the relative abundance of plant groups revealed that grasses was the biological type that primarily contributed to maintain plant diversity in previously grazed sites. This is coherent with the fact that horse grazing in heath communities promotes grasses and that light grazing helps establishment of herbaceous species (Rosa García, 2013; Fagúndez, 2016). However, the grasses abundance increase by previous grazing (Rigueiro-Rodríguez et al., 2012), was only maintained during the short interval after grazing cessation (2 years), and decreased after six years. The same tendency occurred for other herbaceous non-graminoids. It is likely that the distribution of excreta in the previously grazed sites could have also contributed interactively with grazing to favor herbaceous species. The interactive effects of disturbances such as overgrazing and increased nitrogen atmospheric deposition in heathlands showed to favor perennial herbaceous species competing with ericoid species after 2 years (Alonso and Hartley, 1998; in Calvo et al., 2005). Our results agree with reports for similar heathlands where herbaceous species, which dominated during the first year of the secondary succession, are gradually replaced by woody species as the community age after disturbance (Calvo et al., 2012).

Horses are mainly grass consumers (López López et al., 2017a), but may also act as browsers of other less nutritious species such as *Rubus* sp., *Ulex europaeus* and *Calluna vulgaris* (Putman et al., 1987; González-Hernández et al., 2001; Kuiters and Slim, 2003; Rigueiro-Rodríguez et al., 2012). In our study, the first two were negatively associated with previously grazed sites, but the degree of such association differed depending on species. For example, *U. europaeus* remained negatively associated with rotational management after six years of grazing removal and not with the continuous grazing after such lapse of time. This negative association of *U. europaeus* with previously grazed sites is consistent with studies suggesting that horse grazing could be beneficial to reduce gorse dominance and fire risk (Rigueiro-Rodríguez et al., 2012; López López et al., 2017b). On the other hand, *C. vulgaris* showed a positive association with rotational management after six years of grazing cessation, as it corresponds to a heath that benefits from reduced grazing (Hulme et al., 2002) and is hardly palatable for horse in Atlantic heathlands (Silva-Pando et al., 2002; López López et al., 2017a).

Unlike heath, gorse is highly selected by horses in heathlands (Putman et al., 1987; Rigueiro-Rodríguez et al., 2012; López López et al., 2017a). The reasons seem to be related to the greater protein content and absence of tannins for this legume, therefore with opposite nutritional attributes to heather species (González-Hernández and Silva-Pando, 1999; González-Hernández et al., 2003). Moreover, nutrition in horses may be more constrained by the presence of plant secondary compounds than in ruminants (Menard et al., 2002; López López et al., 2017a). Gorse recovery after horse grazing was similar in both types of management systems after two years of grazing interruption, and decelerated after six years in the rotational management. This reveals an advantage of the higher grazing pressure that occurred in RG upon the control of gorse biomass, which, based on the NMDS results, it also translated after six years in a higher resemblance of vegetation composition between the continuous grazing system and the ungrazed areas.

A positive association of *D. cantabrica* with rotational management after the longer pause from grazing is in agreement with the evidence that this species benefits from the absence of grazing in similar heathlands (López López et al., 2017b). This heliophile plant could have been favored by an increased spatial heterogeneity in the availability of light associated with a more open and heterogeneous spatial distribution of the vegetation after previous rotational grazing (Adler et al., 2001; Peco et al., 2006).

Horses are the most efficient in reducing gorse dominance among the common domestic herbivores, and promoted grasses when shrub cover decreased in other Atlantic heathlands (López López et al., 2017a,b). Unlike sheep, they do not preferentially graze flower heads (Oates, 1994), and may be better in maintaining flower-rich swards (Lake et al., 2001). This synergic effect could translate short time after grazing in the positive association of *Agrostis trunquatula* and *Pseudarrhenatherum longifolium* with previously managed systems. In heathlands of NW Spain, horse grazing favored the proliferation of *Pseudarrhenatherum longifolium*, *Agrostis curtisii*, and other grasses with rapid regrowth capability under high grazing pressure such as *Agrostis capillaris* (Silva-Pando et al., 2002; López López et al., 2017b). Yet, after six years of grazing interruption, those two grasses showed no association with previous grazing management, in agreement with the expansion of shrubs whose relative proportions turn similar to those in ungrazed areas. Pavlů et al. (2003) found that plant diversity differences between continuous and rotational managed grasslands disappeared after five years of grazing abandonment.

Although the presence of endemic, rare or endangered species is not a measure of the diversity of the community, it does reflect components of community interest in terms of conservation (de Bello et al., 2006). Horse grazing favored the presence of rare species such as *Cirsium filipendulum*, *Gentiana pneumonanthe*, *Serratula tinctoria*, *Scorzonera humilis*, and *Thymelaea coridifolia*, which have a high conservation interest in heathlands communities (Silva-Pando et al., 2002; Fagúndez, 2016; López López et al., 2017b). In line with these studies, we found four species of high conservation interest in our study that were exclusively present in the grazed sites: *Laserpitium prutenicum*, *Gladiolus illyricus*, *Thymelaea coridifolia*, and *Scorzonera humilis*. They were mostly associated to the continuous management, except for the latter, which also appeared in RG after 6 years. From our results, we can hypothesize that continuous grazing management favored the species of high conservation interest to a higher extent than rotational management. For example, *Laserpitium prutenicum*, a plant sensitive to grazing (Stammel et al., 2003, in Fagúndez, 2016), occurred associated to the successional trend in CG, but not in RG (where a more intense grazing occurred). In *Erica mackaiana* heathlands, *Thymelaea coridifolia*, a narrowly endemic species to North Spain, was positively associated to horse grazing (Fagúndez, 2016), and it appeared exclusively in CG after the two-year interval since grazing. *Scorzonera humilis* was observed following successional trends after continuous grazing in the two intervals of time considered in our study, but it took 6 years to occur after rotational management. However, it is difficult to discern at community level how some of the species of conservation concern may have benefited from previous grazing, and more studies on the dynamics of the single species in heathlands after disturbances are necessary to conclude with coherence about their successional trends.

Tree natural regeneration, as an expression of plant dynamics towards a different successional stage, was higher in previously grazed systems than in ungrazed sites. However, the impact of the type of grazing system on this group was similar. McEvoy et al. (2006), in the same study area, found no differences to suggest one grazing system over the other for minimizing sapling damage and density of natural regeneration of oak (*Quercus robur*).

From the environmental point of view, our results showed that the positive effects of previous rotational and continuous horse grazing on plant diversity in an Atlantic heather-gorse dominated plant community were still apparent 2 or 6 years after grazing interruption. Of relevance to forestry managers is the finding that rotational and continuous horse grazing systems, as presented here, can be suitable management strategies to preserve Atlantic heathlands, at least for the period of grazing and post-grazing here studied. The larger variability found after six years of grazing removal in the mean values of plant diversity, and the decrease of evenness, suggest a greater heterogeneity compared with the short time interval. This could be of relevance in future management decisions, as shifting mosaics can be critical for the maintenance of structural heterogeneity and the biological diversity of pasture lands (Fuhlendorf et al., 2006). Horse grazing was beneficial before in gorse-dominated heathlands to reduce gorse dominance and fire risk, and enhance biodiversity levels (Rigueiro-Rodríguez et al., 2012; López López et al., 2017b), and other studies recognize the potential role of native ponies in conservation management (Fagúndez, 2016; Fraser et al., 2019). Our results are in agreement with those that conclude that horse grazing deserves a conservation status to preserve and restore plant diversity in Atlantic heathlands, as well as to promote the populations of the endangered breeds of wild ponies.

Declaration of competing interest

The authors declare no competing interests, including financial and non-financial interests.

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