



Fire does not transform shrublands of *Echinospartum horridum* (Vahl) Rothm. into grasslands in the Pyrenees: Development of community structure and nutritive value after single prescribed burns

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ABSTRACT

Prescribed fire has been extensively used in recent years to control woody encroachment into mountain and other grassland-dominated landscapes. In the Aragon Pyrenees, prescribed burns have been mainly used to remove the native thorny shrub *Echinospartum horridum* (Vahl) Rothm., whose populations are spreading to the detriment of grasslands. To study the effectiveness of the burning of *E. horridum* to preserve grasslands for livestock grazing, the vegetation of six sites burned 0.5, 2, 3, 6, 15 and 35 years ago was sampled and compared with that of nearby unburned shrubland (control) and grassland (reference). In addition, the nutritional quality of *E. horridum* was examined and compared to that of the reference grassland to evaluate to what extent shrub growth can be controlled by herbivores after burning. Initial shrub cover recovered as early as 15 years after fire, with *E. horridum* being dominant. Plant diversity was greatest at intermediate number of years after fire. Initial floristic composition and life-form spectrum were restored 15–35 years after burning. *Echinospartum horridum* exhibited early lignification that restricts its availability as a palatable forage for the first two years after burning and makes it unlikely to be consumed thereafter, highlighting the difficulty in controlling the expansion of this species by livestock herbivory. The analysis of the nutrient levels suggested an increased shortage of limiting elements, such as phosphorus or sulfur, in the mid-term after burning due to substantial nutrient losses and exports during and after the burn. Our results question the suitability and sustainability of a single prescribed burn as management tool alone to control the expansion of *E. horridum* and call for caution in its application for fighting shrub encroachment in the Central Pyrenees.

1. Introduction

As in other European mountain ranges, many of the grasslands below the alpine belt in the Pyrenees are secondary communities (i.e., resulting from arrested succession after forest removal) (Ninot et al., 2017; García-Ruiz et al., 2020). Hence, their sustainability requires on-going disturbance, whether by grazing, mowing or fire, to prevent the transition to shrubland and forest (López-i-Gelats, 2015; Lasanta, 2019; Múgica et al., 2021). For decades, livestock decline or other changes in grazing patterns have favored the encroachment of various shrub species (Nuche and Alados, 2018; García-Ruiz et al., 2021; Gelabert et al., 2021). Apart from the loss of mountain grassland, its negative

consequences also include decreased biodiversity and water resources and increased risk of wildfires (Fanlo et al., 2015; Lasanta et al., 2018; Khorchani et al., 2021; Múgica et al., 2021). Controlling woody encroachment is therefore a challenge in grazing management and the ecological preservation of grasslands (Canals, 2019). In recent years, prescribed burning, consisting of the controlled application of fire under favorable atmospheric conditions by fire professionals, has gained renewed importance as a tool for shrub removal (Valkó and Deák, 2021). This procedure is more cost-effective for initial reduction in shrub cover than mechanical clearing (Goldammer and Montiel, 2010; Bidwell and Woods, 2017) and is considered less risky and less harmful to soil than traditional pastoral fires (Fernandes et al., 2013).

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In the southern Central Pyrenees (Aragon, Spain), the abandonment of traditional pastoralism since circa 1960 has been followed by extensive shrub encroachment, which transformed 21% of previous croplands and 20% of previous rangelands into shrublands from the mid-1980s to the mid-2000s (Gartzia et al., 2014). The most important encroaching shrub in the subalpine belt is *Echinopartum horridum* (Vahl) Rothm. (Fabaceae), a long-lived cushion-shaped bush native to the French Central Massif and the Pyrenees that can reach over 50 cm in height and 1 m in diameter. Its primary habitat in the southern Pyrenees is on calcareous ridges where this shrub constitutes permanent vegetation mainly between 1000 m and 1700 m altitude, although its extreme altitudinal limits are 390 m.a.s.l. and 2344 m.a.s.l. (Instituto Pirenaico de Ecología y Gobierno de Aragón, 2005). In contrast to French populations, where it occurs as a rare relict species (Denninger, 2005; Gaudillat, 2010), *E. horridum* has spread in the southern Pyrenees from its core locations on slopes with shallow, stony ground (Montserrat et al., 1984; Komac et al., 2011b) and into grasslands (Komac et al., 2011a; Nuche and Alados, 2018). This colonization can occur either by the dispersal of its numerous seeds and/or by the ability of the stems to root, which allows for rapid expansion. *Echinopartum horridum* shows good primary production and moderate-low nutritional quality (Marinas et al., 2003, 2004; Martín-Ramos et al., 2020), and it is occasionally consumed by domestic goats and wild ungulates, particularly during spring regrowth and blooming (Aldezabal and Garin, 2000; Garin et al., 2001). Nevertheless, the sharp tips of the stems that give the plant a thorny morphology and the high lignin content diminish the attractiveness to the cattle and sheep that make up the bulk of livestock farming (Palacio and Montserrat-Martí, 2006), making the expansion of *E. horridum* a serious risk to grassland conservation and livestock management.

Echinopartum horridum does not resprout after fire but exhibits high seed regeneration, being regarded as an obligate seeder (Palacio et al., 2007) and a pyrophyte (Montserrat et al., 1984; Alados et al., 2019). Prescribed burns—or alternatively, mechanical clearings—have often been used to control shrublands dominated by this shrub in the southern Central Pyrenees (region of Aragon, Spain). Previous studies by Nuche et al. (2018) and Alados et al. (2019) compared the initial effectiveness of prescribed burning versus mechanical cutting of *E. horridum* shrubs in terms of demography and seed bank. These studies concluded that burning was less suitable than cutting because it leads to higher germination of *E. horridum* and to communities more dissimilar to the original grasslands. However, it has not been ascertained whether shrub clearance either by prescribed burning or mechanical removal and subsequent grazing can facilitate grass recovery in the longer term (that is, whether the shrubland can be eventually turned into grassland).

In this work, we evaluated the effectiveness of the burning of *E. horridum* to restore pasture grasslands. To this aim, the vegetation of six sites burned at different times over a 35-year period was sampled and compared with that of nearby unburned shrublands and grasslands. We assessed the changes in the coverage, diversity and structure of vegetation (biological forms and abundance of the functional types). In addition, the forage quality of *E. horridum* was analyzed and compared to that of the reference grassland to evaluate to what extent shrub growth can be controlled by herbivores after burning. Our research attempts to answer the following questions: Can we control the encroachment by *E. horridum* in the Pyrenees by the current prescribed burning practices? How does burning affect nutrient availability in the postburn environment? Does the postburn vegetation serve as pasture for livestock? Can the evolution of vegetation toward grasslands be expected after burning and subsequent grazing?

2. Material and methods

2.1. Study areas and field work

The field work was performed in September 2016 and June–August

2017 in three localities of the southern Central Pyrenees (Huesca, Spain): Yebra de Basa, Tella, and Chía. These areas include a mosaic of grasslands and shrublands that are extensively grazed in summer (early June–late September), mostly by sheep but also by cattle and goats. The intensity of grazing ranges 0.5–1.0 livestock units (1 LU = 1 adult cattle = 2 sheep) per hectare on average, but is null in the shrublands due to the lack of palatable grasses and the thorny nature of *E. horridum*. The livestock densities and the guidelines of pastoral management have been relatively constant in recent decades. Fire was traditionally used in these areas in a timely manner until the mid-20th Century to keep the grasslands free of undesired plants, often removing the shrubs one by one. Unplanned burns were banned in 1968, and since then, fire has been applied to small areas (<10 ha) at request of local shepherds according to a burn plan with permission of the local authorities. Currently, the Wildfire Prevention Teams (EPRIF by their Spanish acronym) are responsible for planning and executing the prescribed burns. Burns are performed in spring or autumn using different firing techniques (point source, head, backing fires) depending on the topography and the wind direction and speed. According to the EPRIF, the prescribed burns are planned as single burns, not intended to be repeated for a foreseeable period.

In these areas, a total of six sites were selected that had been subjected to burns for the removal of shrublands at different times in the period 1982–2016, composing a chronosequence with the following ages: 0.5, 1–2, 3, 6, 15, and 35 yr (years) after burning (Table 1). The burned area was identified by visual survey in those sites more recently burned, and with the help of the local Nature Protection officers (APN by their Spanish acronym) in those sites burned longer ago. According to the EPRIF, these sites had not burned in the preceding decades, at least for the last 50 yr, and the canopy closure and coverage of *E. horridum* before burning was equal or close to 100% in all cases, which is in agreement with our own observation of the burns in 2015 and 2016 (Armas-Herrera et al., 2018; Girona-García et al., 2019).

The field work was performed in summer 2016 and 2017 (see Table 1 for the exact dates). Within each burned area, a representative area in terms of slope, exposure and soil and the physiognomy and general coverage of vegetation was chosen and within it four 30 m long transects were delineated. The first transect began at a random point and ran downslope for easier moving through the shrub thickets, and the other three transects were placed parallel to the first, separated by approximately 20 m. In each transect, the percentage ground-cover was assessed by the line-intercept method. This method allows calculating the cover of each ground-cover category along the line transect by adding the intercept distances and then expressing the proportion of the total line length. The following categories were recorded: bare soil, stones, burned plant material, or the name of the intercepted living plant. Wherever possible, similar samplings were performed in the vicinity of each site in unburned shrubland (control) areas (n = 4) and grassland areas [chalk grasslands and *Nardus stricta* L.–mat grasslands, respectively related to the alliances *Bromion erecti* and *Nardion strictae* (Gómez, 2008b), n = 5], which we considered to be the “target” grasslands of reference, i.e., those that are intended to be recovered through shrubland removal.

In eight of the shrubland sites (five burned and three unburned), material was collected from a minimum of 12 individuals of *E. horridum* chosen at random, picking one twig per plant. From this material, the grazable fraction (i.e., leaves, flowers, buds, and green stems with diameters less than 0.5 mm) were separated for analysis. At the Tella site, burned 1.4 yr before sampling, two types of material from *E. horridum* were collected separately: soft material from plants germinated in the same growing season (i.e., aged a few months), and an already slightly lignified material from plants germinated during the previous growing season (i.e., aged about 1 yr). Samples were also collected from the reference grasslands by cutting the above-ground herbage within a square of 30 × 30 cm randomly located.

Table 1
Location and characteristics of the study areas.

Locality	Yebra de Basa		Tella	Chía		
UTM coordinates (31T: X, Y)	72,486	72,388	26,899	26,830	29,049	29,053
	471,070	471,167	472,046	472,076	471,137	471,134
Elevation (m.a.s.l.)	1575	1600	1875	1800	1480	1460
Mean rainfall (mm y ⁻¹)	1030	1015	1280	1280	1075	1075
Mean temperature (°C)	8.4	8.4	7.0	7.0	7.2	7.2
Slope (%)	8	8	20	20	35	35
Exposure	E	E	S	S	E	E
Soil type (IUSS Working Group WRB, 2015)	Eutric Endoleptic Cambisols (Loamic, Humic)		Eutric Epileptic Cambisols (Loamic, Humic)		Calcaric Epileptic Cambisols (Loamic, Humic)	
Date of burning	Dec 2016	Apr 2014	Apr 2015	Feb 2011	2002	1982
Date of ground–cover assessment	Jun 2017	Jun 2017	Jun 2017	Jul 2017	Aug 2017	Aug 2017
Date of sampling for chemical analysis	Jun 2017	Jun 2017	Sep 2016	–	Aug 2017	Aug 2017
Years since burning	0.5	3.2	1.4 (sampling) 2.2 (inventory)	6.3	15	35
Including control (unburned shrubland)	Yes	Yes	Yes	Yes	No	No
Including reference grassland	Yes	Yes	Yes	Yes	Yes	No

2.2. Laboratory procedures

The samples of the grazable fraction of *E. horridum* and of the herbage of the reference grasslands were dried in a forced-air oven at 60 °C for 48 h and then ground to <1 mm. The organic composition was assessed by the Weende procedure (AOAC, 2006), including the determinations of gravimetric moisture at 103 °C, crude protein by the Kjeldahl method, crude fiber by acid–basic hydrolysis, crude fat by Soxhlet extraction, crude ash by ashing at 550 °C, and the calculation of the nitrogen–free extractives (NFE). In addition, the fiber was analyzed using the method of Van Soest et al. (1991) using an Ankom 200 fiber analyzer (Ankom Technol., Fairport NY, USA), where the neutral detergent fiber (NDF) and the acid detergent fiber (ADF) were sequentially obtained. The remaining acid–insoluble residue was ashed to determine the concentration of acid–detergent ash (ADA), which was subtracted from that of the residue to obtain the acid–detergent lignin (ADL).

For the study of the mineral composition, crude ash was dissolved with aqua regia and distilled water, and the solution obtained was analyzed for the concentrations of phosphorus (P) by the molybdate–blue method (Murphy and Riley, 1962), calcium (Ca) by complexometry with EDTA, and potassium (K) and sodium (Na) by flame spectrophotometry. For the analysis of sulfur (S), a sample was pre-treated with magnesium nitrate to prevent S losses (Kalra and Maynard, 1991), ashed at 550 °C, and dissolved with aqua regia and water, and then the concentration of dissolved S was determined by turbidimetry with barium chloride (AOAC, 2006).

2.3. Statistical analysis

From the line intercept data, the cover of the various ground–cover categories (bare soil, stones, burned plant material, and living plant cover) and of the individual plant species was calculated, and the diversity was assessed in terms of the number of species and Shannon index. The plant species were categorized into shrubs (i.e., *E. horridum*, *Buxus sempervirens* L., *Genista scorpius* (L.) DC., and young, still shrub–sized *Pinus sylvestris* L.), herbaceous legumes (Fabaceae), graminoids (Poaceae and Cyperaceae), and forbs (all other herbaceous species) and according to their life forms following Raunkiaer (1934) into therophytes, geophytes, hemicryptophytes, chamaephytes, and phanerophytes. The cover for each group was calculated by summing the cover values of all species in that group.

The cover of the different ground–cover categories and functional groups was analyzed in relation to the time elapsed since burning and with respect to the control shrubland and to the reference grassland. Their values were compared by nonparametric analysis of variance (Kruskal–Wallis) followed by Mann–Whitney tests in case of significance

($P < 0.05$). No correction was made for multiple comparisons because comparisons were considered descriptive, intended only to outline the trends in the post–fire regrowth of vegetation. Additionally, the cover values of the plant species were analyzed overall using detrended correspondence analysis (DCA) (Hill and Gauch, 1980) to examine the floristic composition across the burned and unburned areas and the reference grasslands.

Based on the laboratory results, calculations were made to determine the concentrations of cell content ($CC = 100 - NDF$), hemicellulose ($HEM = NDF - ADF$), cellulose ($CEL = ADF - \text{acid-insoluble residue}$), and acid–detergent lignin ($ADL = \text{acid-insoluble residue} - ADA$) and to estimate the dry matter digestibility (DMD) using the formula by Van Soest and Jones (1968):

$$DMD = 0.98 \times CC + NDF \times \left(1.473 - 0.789 \times \log_{10} \frac{100 \times ADL}{ADF} \right) - 3 \times ADA$$

To provide a synthetic view of the composition of *E. horridum* in the burned areas compared to unburned areas and to the reference grasslands, a principal component analysis (PCA) was performed on the values of crude protein, crude fiber, crude fat, crude ash, NFE, CC, HEM, CEL, ADL, ADA, Na, P, S, K, and Ca (other variables were excluded because they were implicit or depended on the variables included).

Statistical tests were performed using IBM SPSS Statistics v. 22 (IBM Corporation, Armonk NY, USA). DCA and PCA were performed using Canoco 4.5 (Microcomputer Power, Ithaca NY, USA).

3. Results

3.1. Plant recovery after burning

Prior to burning, the shrublands exhibited closed, uniform covers close to 100% (excluding rocky outcrops), mostly made up of *E. horridum*. After burning, the ground–cover became heterogeneous due to uneven combustion resulting in patches of plant fuel remaining largely untouched by the fire, as reported by Mora et al. (2021). Half a year after fire application in the 0.5–yr site, approximately 50% of the ground was covered by burned material, about 30% by vegetation and about 20% by bare ground (Fig. 1a). The vegetation cover increased across sites with time since burning (Fig. 1a): in the 3–yr site, vegetation was already predominant, and in the 15–yr site, the vegetation coverage was almost complete and equal to that of the unburned shrubland. In the 2–yr site, a massive germination of *E. horridum* was observed with a high abundance of seedlings, which were replaced in the 3–yr site by a similar coverage of young plants with lignified and hooked twigs. The cover of *E. horridum* was already considerable in the 6–yr site, and in the 35–yr site it approached the coverage of control shrubland, sometimes with the

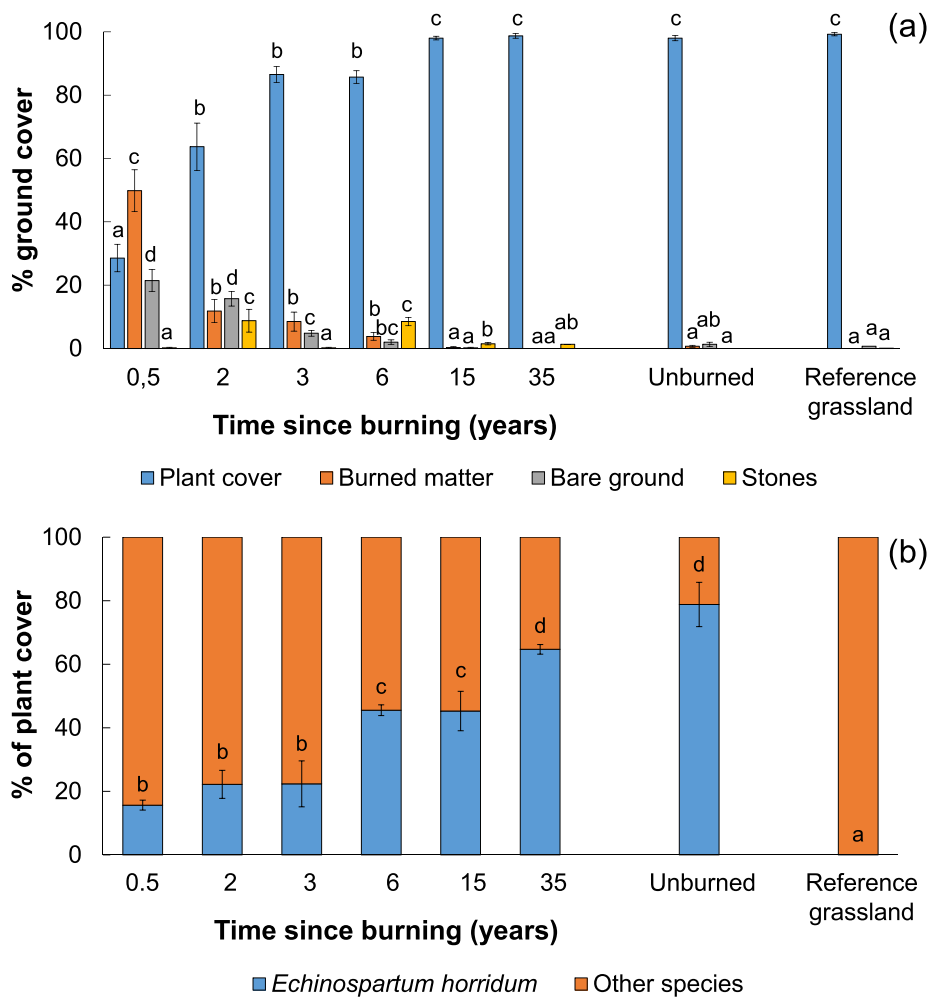


Fig. 1. Average values (mean ± standard error) of (a) the ground cover (%) of vegetation, burned debris, bare ground and stones and (b) the cover of *Echinospartum horridum* relative to total plant cover (%) across the sites burned at different times, the unburned shrublands and the reference grasslands. Within each ground-cover category, values followed by the same letter in the columns do not differ among them.

presence of the shrub *B. sempervirens*, which vigorously re-sprouted after fire and often accompanied the mature shrubland.

The number of species in the burned areas varied considerably along the chronosequence (Fig. 2): it was similar to that of the control

shrubland in the 0.5-yr site, then it markedly increased up to values similar to those of the reference grassland in the 3-yr site, and it declined thereafter down to values not significantly different from the unburned shrubland in the 15-yr and 25-yr sites. In turn, the diversity

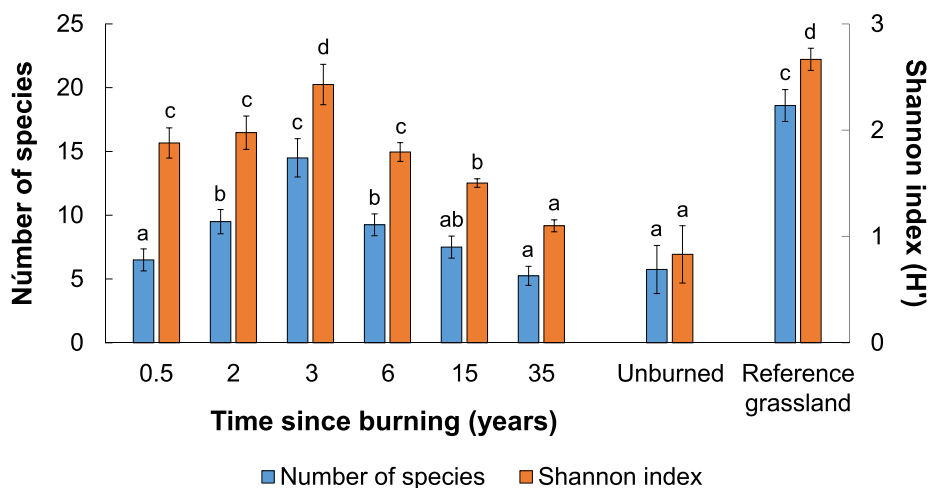


Fig. 2. Average values (mean ± standard error) of the species richness (number of species) and diversity (Shannon index) across the sites burned at different times, the unburned shrublands and the reference grasslands. Values followed by the same letter in the columns do not differ among them.

(Shannon index) (Fig. 2) was already high in the 0.5-yr site, then increased in the 2-yr and 3-yr sites, and strongly decreased thereafter to low values not significantly different from those of the control shrubland and very far from the reference grassland.

The life-form plant spectrum at the various post-fire stages, as shown in Fig. 3a, indicates that the increase in the cover of *E. horridum* was accompanied in the later stages by variable presence of *B. sempervirens* and other shrubs and even pines (phanerophytes). Chamaephytes other than *E. horridum* increased initially, peaking in the 2-yr site, and then decreased afterward. Hemicryptophytes increased until being predominant in the 3-yr site, gradually decreasing thereafter to a minimum below their representation in the unburned shrubland and very far from that for grassland. Geophytes exhibited highly variable covers in the various stages after fire, being quite frequent in the 0.5-yr site. Therophytes were not abundant in the more recently burned sites and became absent at later stages, just as they were residual in the unburned shrubland.

Fig. 3b depicts the post-fire development of vegetation in terms of pastoral taxonomic groups of species. Shrub species (including *E. horridum*) were absent in the reference grasslands but were significantly present in the 0.5-yr site and increased with time since burning, becoming predominant in the 6-yr site, reaching values no longer different from those of unburned shrubland at 15 yr since fire. Graminoids were the dominant functional group during the first stages

post-fire, showing cover values close to those of the reference grassland in the sites burned ≤ 3 yr before. Although the frequency of graminoids was very high until the sixth yr after burning, it should be noted that the grasses *Brachypodium pinnatum* (L.) Beauv. and *Bromus erectus* Huds. were strongly dominant (80–90% coverage combined). In contrast, other species that were more frequent in the reference grassland and that have higher pastoral values, such as *Festuca* gr. *rubra* L., *Poa pratensis* L., *Koeleria pyramidata* (Lam.) P. Beauv. and *Briza media* L. were barely present or showed very low coverage in the burned areas and occurred only in the patches of vegetation not affected by fire. Among the Gramineae characteristic of the reference grassland, only *Agrostis capillaris* L. was well-represented in the burned sites. Afterward, the coverage of graminoids decreased, reaching values in the 15-yr site that were not different from those of unburned shrubland. Legumes followed a similar pattern, but their presence was very limited at all stages. The leguminosae of the burned areas coincided with those of the reference grassland (*Trifolium* sp. pl. and *Lotus corniculatus* L.), but they did not result from resprouting after fire since they were only present in isolated patches not affected by fire. As a whole, the presence of graminoids and legumes provides an indication of the forage quality of the vegetation, which can be regarded as reaching its highest at 3-yr site and decreasing from the 6-yr site onwards. Other species (forbs) exhibited cover values similar to those in grasslands, and then they decreased until they reached a coverage that was not significantly different from that of

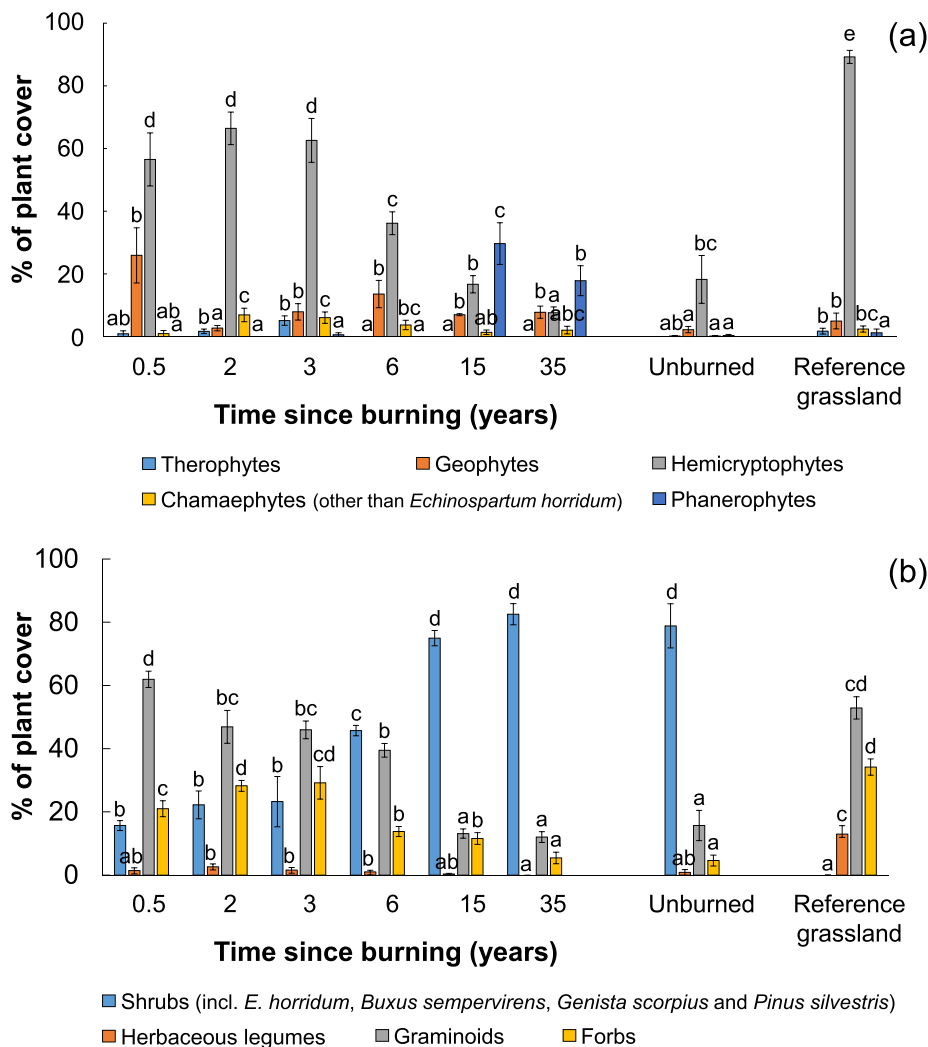


Fig. 3. Average values (mean \pm standard error) of the cover relative to total plant cover (%) of the various plant functional groups according to (a) the classification of Raunkiaer (1934) and (b) pastoral taxonomic criteria across the sites burned at different times, the unburned shrublands and the reference grasslands. Within each functional groups, values followed by the same letter in the columns do not differ among them.

unburned shrublands in the 35-yr site.

A list of the plant species identified in the burned areas, the unburned shrubland and the reference grasslands is presented in [Supplementary Table 1](#). [Fig. 4](#) shows the results of the overall DCA of the floristic composition of the various stages after burning, the control shrubland and the reference grassland. The first axis, accounting for 24.1% of the variance, was strongly related to the woody encroachment process, with the areas more recently burned (<6 yr) receiving lower scores ([Fig. 4](#), on the center) than those burned longer ago (on the center-right). The unburned shrubland (on the right) showed a position close to the sites burned longer ago on this axis, whereas the reference grassland (on the left) appeared as a distinct group distinct to the other sites.

3.2. Development of nutritional composition

The composition of the grazable fraction of *E. horridum* is shown in [Table 2](#) in comparison with the values of the herbage of the reference grasslands and those reported for *E. horridum* by [Marinas et al. \(2003\)](#). The PCA ([Fig. 5](#)) allows visual comparison of the overall composition of *E. horridum* at different times with those of the grassland herbage and of *E. horridum* in unburned shrublands. The first principal component (Axis 1), which explained 59.8% of the variance, was correlated with the levels of minerals and fiber. The samples of the reference grasslands, with the highest mineral and lowest fiber contents, were grouped on the positive side of this axis, and close to them were the samples of young *E. horridum* from the 0.5-yr and 2-yr sites. In contrast, the other samples of *E. horridum*, high in fiber and low in minerals, were located on the negative side of the first axis, showing few differences in composition between the shrubs over 1 yr of age from burned areas and those from unburned areas. The second component (Axis 2), with a lower explanatory power (19.2% of explained variance), separated the samples of reference grasslands, with higher contents of highly digestible carbohydrates (NFE), from those of young *E. horridum*, which were richer in crude protein, P, and ADA. In general terms, the composition of the *E. horridum* growing on burned areas substantially differed from that of the reference grasslands, and only the young *E. horridum* approximated the composition of grasslands to some extent.

[Fig. 6](#) illustrates the development of some compositional features with the age of *E. horridum* relative to the mean values in the reference grasslands. As shown, the levels of several components key to animal

feeding, such as crude protein, DMD, P, S, or K, exhibit continuous decreases with the age of *E. horridum*, with the most marked decreases displayed by 2 yr-old *E. horridum* for K and by 3 yr-old *E. horridum* for crude protein, DMD, P, and S. After fire, the levels of P decrease faster than those of protein, as shown in [Fig. 6](#) by the increasing N:P ratio. Notably, such increasing N:P ratios differentiate the *E. horridum* growing in burned areas from that of unburned areas, whose N:P values are close to those of the reference grasslands. The levels of S remained stable in the first yr and declined thereafter, which was inversely mirrored by the N:S ratio, which decreased initially but rose again after 3 yr after burning.

4. Discussion

4.1. Changes in vegetation

Despite the sites sharing similar vegetation prior to burning, early (<6 yr post fire) vegetation showed considerable floristic variation among sites that was not obviously related to burning chronology. Such differences may be related to factors other than time since fire, such as different patterns of burn severity, which are known to strongly influence early post-fire vegetation and can cause succession to start from different points ([Turner et al., 1999](#); [Kayes et al., 2010](#)). In terms of life forms, early post-fire succession involved a rapid spreading of hemi-cryptophytes, which have been reported as major colonizers after shrubland fires ([Trabaud, 1992](#); [Pérez et al., 2003](#)). Geophytes were also locally abundant during the first yr after burning, highlighting the high resilience of geophytes and some hemicryptophytes to prescribed fire as a result of the protected location of their perennating buds ([Chapman and Crow, 1981](#); [Pyke et al., 2010](#)). *Echinospartum horridum* did not resprout after being killed by burning, as was also reported by [Nuche et al. \(2018\)](#), but produced a large quantity of rapidly growing seedlings, as is typical for fire-adapted nonresprouter shrubs ([Lamont and Wiens, 2003](#); [Pausas et al., 2004](#)).

In a 5-yr study following the burn of an *E. horridum* shrubland, [Alados et al. \(2019\)](#) described increasing plant cover but decreasing species diversity over time. In the present study, plant cover was found to increase in parallel with species diversity until 3 yr after burning, when the plant cover reached values above 80% and the diversity was comparable to that of the reference grasslands. This 3-yr stage was,

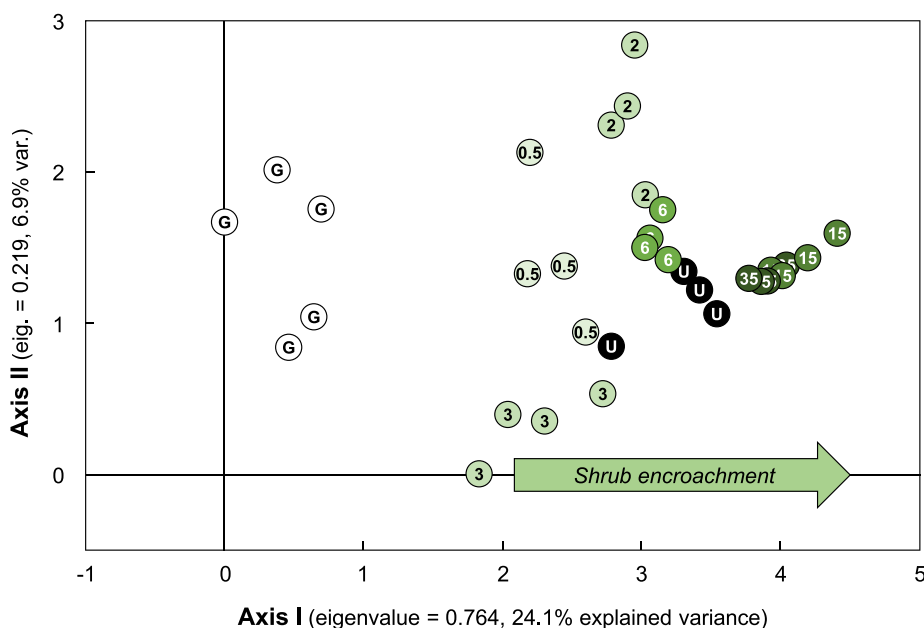


Fig. 4. Biplot of the results of the detrended correspondence analysis (DCA) of the species composition of the sites burned at different times, the unburned shrublands and the reference grasslands. 0.5, 2, 3, 6, 15, 25 = sites burned 0.5, 2, 3, 6, 15 and 35 yr before, U = unburned shrubland (control), G = grassland (reference).

Table 2

Nutritional–chemical composition (mg g⁻¹) of the grazable fraction of *Echinospartum horridum* in burned and unburned sites and of the reference grasslands. Average values for *E. horridum* reported by [Marinas et al. \(2003\)](#) are given as references.

	Time since fire (yr)					Unburned control	Reference grassland	Marinas et al. (2003)	
	0.5	1		3	15				35
		(a)	(b)						
Crude protein	190	121	151	105	98	105	109 ± 11	119 ± 6	74–155
Crude fiber	291	346	137	381	330	311	317 ± 20	120 ± 15	
Crude fat	12.9	14.3	14.6	15.8	16	15.6	14.7 ± 0.7	25.8 ± 4.0	
Crude ash	93.8	38.6	48.5	39.2	32.2	36.5	32.7 ± 8.0	108.8 ± 14.6	
NFE	412	480	649	460	524	616	526 ± 15	626 ± 9	
Cell content	431	371	491	367	337	322	351 ± 16	490 ± 49	429–302
NDF	569	629	509	633	663	678	649 ± 16	510 ± 49	571–698
Hemicellulose	165	170	146	140	158	177	164 ± 7	218 ± 41	162–217
ADF	404	459	363	493	504	501	485 ± 16	292 ± 9	354–515
Cellulose	281	345	275	350	323	321	320 ± 8	225 ± 19	189–300
ADL	88	106	79	132	169	166	149 ± 6	49 ± 11	139–218
ADA	34.4	7.9	7.9	11.2	12	13.2	15.7 ± 4.6	17.4 ± 2.7	
DMD	492	575	652	528	457	443	468 ± 26	612 ± 45	432–510
Na	0.63	0.43	0.86	0.42	0.23	0.29	0.38 ± 0.07	0.59 ± 0.11	
P	0.82	0.55	0.65	0.35	0.29	0.28	0.45 ± 0.06	0.54 ± 0.03	
S	0.51	0.37	0.49	0.32	0.24	0.25	0.30 ± 0.10	0.54 ± 0.16	
K	1.47	0.70	0.88	0.76	0.62	0.59	0.78 ± 0.08	1.38 ± 0.13	
Ca	0.71	0.68	0.85	0.52	0.47	0.63	0.54 ± 0.06	1.39 ± 0.46	

NFE = nitrogen–free extractives, NDF = neutral–detergent fiber, ADF = acid–detergent fiber, ADL = acid–detergent lignin, ADA = acid–detergent ash, DMD = dry matter digestibility.

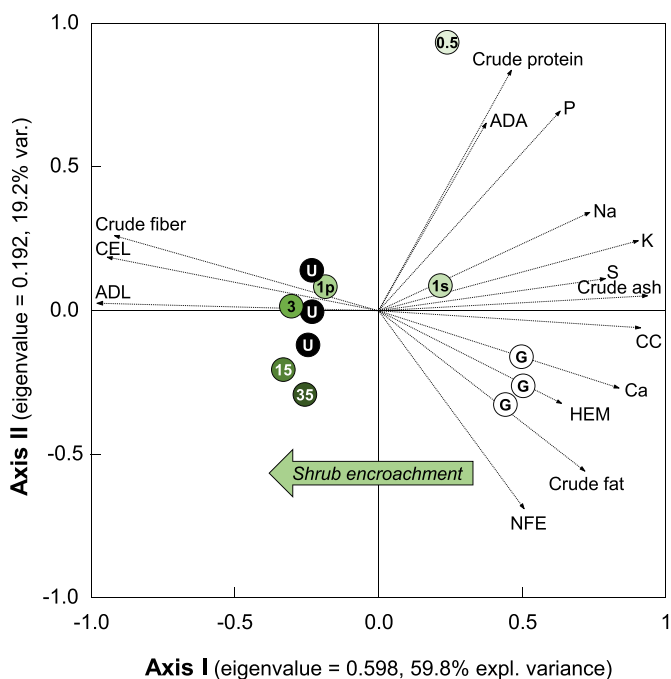


Fig. 5. Biplot of the results of the principal component analysis (PCA) of the chemical nutritional composition of *Echinospartum horridum* across the sites burned at different times and the unburned shrublands and of the herbage in reference grasslands. 0.5, 3, 15 and 35 = *E. horridum* from sites burned 0.5, 3, 15 and 35 yr before, 1p = *E. horridum* collected from site burned 1 yr before and germinated the previous year, 1s = *E. horridum* collected from site burned 1 yr before and germinated the same year, U = *E. horridum* from unburned shrubland (control), G = herbage from grassland (reference), CC = cell content, HEM = hemicellulose, CEL = cellulose, ADL = acid–detergent lignin, ADA = acid–detergent ash, NFE = nitrogen–free extractives.

among the stages studied, the one with the greatest pastoral interest and the best suited to use by grazing livestock, although the shrub, already spiky, can hardly be eradicated. At the following stage (6 yr after burning), the diversity declined, coinciding with a sharp rise in the abundance of *E. horridum*, which occurred mainly at the expense of

hemipterophytes–first of forbs, then of graminoids. At 15 yr since burning and thereafter, other shrubs and phanerophytes were established, such as *B. sempervirens*, whose entrance is facilitated by the growth of *E. horridum* ([Nuche and Alados, 2018](#)).

Noticeably, the floristic composition of the burned areas always remained far from that of the reference grassland. In terms of life forms, it is worth noting the practical absence in the reference grassland of species that are shrubs when grown, as also observed by [Alados et al. \(2019\)](#). Conversely, herbaceous legumes were practically absent from the burned areas but they were present in the reference grassland. These findings are consistent with previous literature reporting poor colonization by characteristic grassland species after shrub removal by fire (e. g., [Srinivasan, 2012](#); [Nota et al., 2021](#)). Many grassland species do not accumulate seedbanks that can be triggered to germinate by fire and have their surface–lying seeds killed by heat ([Thompson, 2000](#)). Hence, after fire, grassland species are outcompeted by ruderal species that produce abundant wind–dispersed seeds ([Whelan, 1986](#); [Halpern et al., 2014](#)). In the long term, the establishment of characteristic grassland species may be prevented by the rapid propagation of *E. horridum*, as they are heavily affected by the allelopathic, competitive and shading effects of the shrubs ([Srinivasan, 2012](#); [Nuche et al., 2018](#)).

4.2. Forage value and nutrient limitations

The reference grassland had values of crude protein, fat, ash and various fiber fractions that, according to [Ferrer Benimeli \(2016\)](#), are typical for young–to–medium age grasslands with a small presence of legumes. The composition of the grazable fraction of *E. horridum* was mostly within the ranges reported for this species by [Marinas et al. \(2003\)](#), although it showed somewhat higher values for the most labile components (crude protein, CC and HEM) during the early stages of post–fire regeneration and for those least digestible (CEL, ADL) during the late stages. According to general forage quality standards ([Rivera and Parish, 2010](#)), the forage value was only “acceptable” in the reference grasslands and for the young *E. horridum* (aged <1 yr) during the 2 yr following fire. From 3 yr after fire and onward, the intake and digestibility of *E. horridum* was substantially reduced by high values of NDF, ADF and, especially, ADL, although the levels of crude protein remained moderate. Lignification not only decreases the nutritional quality of *E. horridum* but also hardens the terminal spines of the stems,

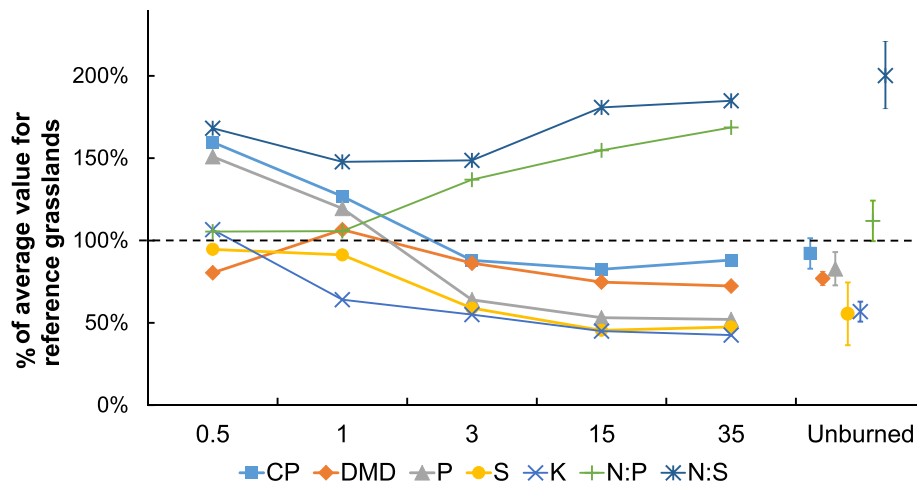


Fig. 6. Selected nutritional–chemical components [crude protein (CP), dry matter digestibility (DMD), P, S and K] and elemental mass–ratios (N:P and N:S) across the sites burned at different times and the unburned shrublands (mean \pm standard deviation) in relation to the values of the herbage of the reference grasslands (%).

which act as deterrents for grazers (Marinas et al., 2004; García-González et al., 2007).

In terms of mineral composition, the reference grassland and *E. horridum* at various ages contain adequate levels of Ca and K to meet the requirements of grazing livestock but lack sufficient amounts of P and S to fulfill the needs of livestock according to Ferrer Benimeli (2016). Indeed, the N:P ratios showed values ranging between 35 and 59 for *E. horridum* and 32–39 for the reference grasslands that were well above the threshold values of 16–20 (Koerselman and Meuleman, 1996; Güsewell, 2004), indicating a prevailing limitation of P over N at the community level. Such limitation is typical in soils developed on calcareous substrates due to the high Ca concentrations which precipitate P to insoluble phosphates making it unavailable for plants (Niinemets and Kull, 2005; Du et al., 2011). Furthermore, the N:S ratios showed values within the ranges of 49–66 for the burned areas and unburned shrublands and 29–57 for the reference grasslands, all well above the critical value of 16 that is generally used as diagnostic of S deficiency in grasslands (Ryant and Skládanka, 2009).

It is well known that fire creates a nutrient-rich ash layer from plant biomass that can alleviate nutrient limitations, e.g. of P in P-limited ecosystems (Toberman et al., 2014; Butler et al., 2018). On the other hand, fire can result in considerable volatilization of N and S and off-site removal of P- and S-rich ash by convection in the smoke during fire and by surface runoff and wind transport after fire (Raison et al., 1985a; Binkley and Fisher, 2019). The N losses can be replenished in the mid-term by N-fixation by the leguminous shrubs, but S and P losses are persistent and may be cumulative in case of frequent burning. Mora et al. (2021) found notable losses of S and P during the prescribed burning of an *E. horridum* shrubland and a gradual decline in the plant-available concentrations of both elements over the 2 yr following the burn, although the S levels were found to increase immediately after burning. In the present study, the levels of P were found to decrease after fire faster than those of protein, as shown in Fig. 6 by the increasing N:P ratio, which points to an exacerbation of P limitation with the aging of *E. horridum*. These findings suggest that in the mid-term exports and losses can lead to further P-limitation, which then ameliorates with time until they are not apparent in shrublands unburned in recent decades. On the other hand, the N:S ratio suggests a transient alleviation of S limitation during the first 3 yr after burning, then followed by a return to the initial deficiency level, once the immediate fertilizing effect of ash was over. The recovery rates of the stocks of nutrients lost off-site during and after fire should be taken into account to estimate a suitable burning frequency. For example, Raison et al. (1985b) calculated that prescribed

fire rotations of >10 and >20 yr would be required to permit natural inputs to replace the losses of N and P, respectively, after the burn of a subalpine *Eucalyptus* woodland.

4.3. Practical implications

Prescribed burning of shrubs temporarily increased the plant diversity and the grazing resources by replacing woody biomass with more palatable graminoids and forbs, as has also been shown for other mountain areas (Sachro et al., 2005; Wangchuk et al., 2013; Paudel et al., 2020). The increase in plant diversity cannot be seen as beneficial on its own because the gain was due to nitrophilous species of low quality for livestock. On the other hand, the increase in pasture availability occurred in a period when the ground was covered of burn residues (i.e. ash, charred twigs, etc.), which, under low livestock density, can cause the livestock to prefer grazing other green pastures available in the surrounding area. It was also short-lived (~3 yr), as *E. horridum* became rapidly predominant, after first having become thorny and ligneous (as soon as 2 yr after burning). The practice of single burns as described here temporarily cleared up the shrubs for apparently little benefit, at the risk of promoting erosion and even providing land to nitrophilous opportunistic species. Moreover, fire stimulated the activation of the seed bank and the rejuvenation of the shrublands, which took advantage of the transient increase in soil fertility resulting from burning.

The aim of prescribed burning should not be temporarily removing the shrubs only to bring them back in a short time with equal or even denser cover. Moreover, removing the shrubs of *E. horridum* is not a goal in itself because, although it is a poor pasture, it has some positive aspects such as increased nitrogen fixation into the soil and soil protection from erosion (Martín-Ramos et al., 2020). Furthermore, *E. horridum* is native to the area, therefore it is not an invasive species that must be removed at all costs. The intended purpose of burning is to attain long-term pastureland similar to the pasture grasslands of the area. This is what is intended by shepherds requesting the burns and which, according to our findings, was not achieved by burning. On the other hand, prescribed burns provide other services apart from the maintenance and improvement of pastures, most notably the prevention of wildfires through the elimination of vegetable fuels (Francos and Úbeda, 2021).

Prescribed burns of *E. horridum* were planned as single burns, and repeated burning was not considered in the present study. However, it is possible that frequent burning may contribute to the goal of restoring grasslands. Seedbanks of obligate seeders (such as *E. horridum*) may

require one to two decades to replenish after fire, so burning at a shorter interval can eliminate them from the community (Fairman et al., 2015; Syphard et al. 2018). The choice of the optimal burning frequency should be based not only on the seedbank response, but also consider the environmental drawbacks of repeated burning, such as increased chance of erosion (Cawson et al., 2012; Klimas et al., 2020) or cumulative adverse effects on soil properties and soil communities (Callaham et al., 2012; Fontúrbel et al., 2021). Armas-Herrera et al. (2018) found that the effects of burning an *E. horridum* shrubland on the dynamics and turnover of organic matter may linger in the soil for at least 5 yr after burning. The finding in the present study that burns decreased the availability of P for a period of up to 35 yr cautions advise against recurrent burns because the risk of depleting this limiting nutrient (Raison et al., 2009; Butler et al., 2018).

Moreover, although frequent burning can be expected to allow the persistence of ruderal grasses and forbs (Schaffhauser et al., 2012; Syphard et al. 2018), nothing in our findings suggests that the community will transform into a more typical grassland as result of subsequent burns in the mid-term. As in other mountain regions in Europe, the subalpine grasslands of the Pyrenees are not the direct result of burning or cutting but require centuries of sustained grazing and grass harvesting after land clearance, with a timely use of fire to keep the grasslands free of undesired plants (Gómez, 2008a; Canals, 2019).

5. Conclusions

The development of the vegetation after the burn of an *E. horridum* shrubland involved increasing richness and diversity, albeit still far from the pastoral value of the reference grasslands, during the first 3 yr after burning, and thereafter reverted back to the initial state in terms of structure and dominant species. Before that point, the regrowing *E. horridum* had already become thorny and ligneous, and its composition approached that of unburned areas, becoming unattractive to livestock. Based on our results, single prescribed burns cannot prevent *E. horridum* encroachment under the current burning and grazing regimes. Our study also showed the characteristic grassland species to be outcompeted by ruderals in early post-fire stages and by the rapid regrowth of *E. horridum* in later stages. Based on this, it is unlikely that the current burning practices will contribute to the evolution of vegetation toward the pastoral grasslands typical of the area. Our results challenge the suitability of the current practice of single prescribed burns for fighting the encroachment of *E. horridum* in the southern Central Pyrenees, except temporarily. It remains to be seen whether frequent burning or increased livestock pressure can contribute to more effective control of scrub recovery and the spread of higher quality grassland. However, our results suggest caution against frequent burning because of potential drawbacks such as the risk of depletion of limiting nutrients.

Credit author statement

Juan L. Mora, David Badía-Villas and Daniel Gómez: Conceptualization, Methodology, Investigation, Resources, Writing (Writing – original draft, Writing – review & editing). **Juan L. Mora:** Formal analysis, Visualization. **David Badía-Villas and Daniel Gómez:** Funding acquisition, Project administration.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2022.115125>.

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