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CLEARING VS. BURNING FOR RESTORING PYRENEAN GRASSLANDS AFTER SHRUB ENCROACHMENT

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ABSTRACT. *Anthropogenic activities have modified vegetation on subalpine belts for a long time, lowering the treeline ecotone and influencing the landscape mainly through grazing and fire. The abandonment of these traditional land use practices during the last decades and global warming are contributing largely to the colonization of woody species in subalpine grasslands, causing irreversible changes in ecosystem functioning. A variety of management strategies requiring the use of fire and/or clear-cutting are carried out to prevent the expansion of highly encroaching shrubs and improve the conservation status of subhumid high-productive grasslands ecosystems. However, it is still poorly understood how different management strategies affect the recovery of subalpine grasslands, which is influenced concurrently by the vegetation community involved. In this study we used field experiments to test the impact of management treatments on soil properties and vegetation responses in subalpine* Bromion erecti *grassland communities colonized by the pyrophyte shrub* Echinospartum horridum *(Vahl) Rothm. on the southern Pyrenees. Vegetation was monitored for 5 years in* E. horridum *plots (two plots per treatment) where the vegetation was removed by prescribed fire (Burnt treatment) or by mechanical removal (Clear-cut treatment). Undisturbed* E. horridum *plots were used as a control (C-Erizón) for shrub removal treatments and a* Bromion erecti *grassland community regularly grazed (C-Grass) was used as a control for subalpine grassland. Clear-cut treatment of* E. horridum *community was more effective to control* E. horridum *colonization than Burnt treatment and contributed to a higher extent to recover original grassland vegetation, because* E. horridum *seedling performed worse (lower germination rates) and plant species were more similar to the original grassland (legumes, non-legume forbs, and grasses). Shrubs and sub-shrubs cover in Burnt areas increased faster than in Clear-cut areas during the 5 years following the treatment, although it did not reach the level of C-Erizón. Species richness and diversity increased in comparison with C-Erizón in both treatments, but they were* *significantly lower than those in the C-Grass. Network connectivity was larger in well preserved grasslands, i.e, C-Grass, than in any other treatments, mainly dominated by negative plant-plant association. Soils nutrients declined in Burnt sites 4 years after the fire treatment and no difference was observed between Clear-cut and C-Erizón sites, although they did not reach the soil fertility values of C-Grass in terms of organic matter and C/N ratio. This study showed that grazing favors plant diversity and community complexity in subalpine grasslands. It also demonstrated that clearing is a better strategy than burning to restore grasslands after shrub encroachment because burning entails deeper soil degradation and faster recovering of the pyrophyte shrub,* E. horridum.

Desbroces frente a quemas para restaurar los pastos pirenaicos tras la expansion del matorral

RESUMEN. *Las actividades antrópicas han modificado la vegetación en los cinturones subalpinos durante mucho tiempo, disminuyendo el ecotono del límite del bosque e influyendo en el paisaje principalmente a través del pastoreo y el fuego. El abandono de estas prácticas tradicionales de uso de la tierra ocurrido durante las últimas décadas y el calentamiento global están contribuyendo en gran medida a la colonización de especies leñosas en pastos subalpinos, causando cambios irreversibles en el funcionamiento de los ecosistemas. Actualmente se están llevando a cabo diferentes estrategias de gestión que requieren el uso de fuego y / o desbroce para prevenir la expansión de arbustos altamente invasores y mejorar el estado de conservación de los ecosistemas de pastizales subhúmedos de alta productividad. Sin embargo, todavía desconocemos cómo las diferentes estrategias de gestión afectan la recuperación de los pastos subalpinos, la cual depende a su vez de la comunidad vegetal involucrada. En este estudio, utilizamos experimentos de campo para evaluar el impacto de los tratamientos de manejo sobre las propiedades del suelo y las respuestas de la vegetación en las comunidades de pastos subalpinos de* Bromion erecti *colonizados por el arbusto pirófito* Echinospartum horridum *(Vahl) Rothm. en el sur de los Pirineos. La vegetación fue monitoreada por 5 años en parcelas de* E. horridum *(dos parcelas por tratamiento) donde la vegetación fue eliminada por fuego prescrito (tratamiento de Quemado) o por desbroce mecánico (tratamiento de Desbroce). Se utilizaron parcelas no perturbadas de* E. horridum *como control (C-Erizón) para los tratamientos de eliminación de arbustos y se usó una comunidad de pastos* Bromion erecti *regularmente pastada (C-Grass) como control de pastos subalpinos. El tratamiento de Desbroce de la comunidad de* E. horridum *fue más eficaz para controlar la colonización de* E. horridum *que el tratamiento de Quemado y contribuyó en mayor medida a recuperar la vegetación original de pastizales, porque las plántulas de* E. horridum *tuvieron un peor rendimiento (menores tasas de germinación) y las especies de plantas fueron más similar al pasto original (leguminosas, hierbas no leguminosas y pastos). La cobertura de arbustos y sub-arbustos en las áreas quemadas aumentó más rápido que en las áreas desbrozadas durante los 5 años posteriores al tratamiento, aunque no alcanzó el nivel de C-Erizón. La riqueza* *de especies y la diversidad aumentaron en comparación con C-Erizón en ambos tratamientos, pero fueron significativamente más bajos que los de C-Grass. La conectividad de la red fue mayor en los pastos bien conservados, es decir, C-Grass, que en cualquier otro tratamiento, principalmente dominado por la asociación negativa planta-planta. Los nutrientes del suelo disminuyeron en sitios quemados 4 años después del tratamiento con fuego y no se observaron diferencias entre los sitios desbrozados y C-Erizón, aunque no alcanzaron los valores de fertilidad del suelo de C-Grass en términos de materia orgánica y relación C/N. Este estudio mostró que el pastoreo favorece la diversidad de plantas y la complejidad de la comunidad en los pastos subalpinos. También demostró que el desbroce es mejor estrategia que la quema para restaurar los pastos tras la invasión de los arbustos porque la quema implica una degradación más profunda del suelo y una recuperación más rápida del arbusto pirófito,* E. horridum.

Keywords: subalpine vegetation, diversity, *Echinospartum horridum*, grassland restoration, plant-plant association, soil fertility.

Palabras clave: vegetación subalpina, diversidad, *Echinospartum horridum*, restauración de pastos, asociación planta-planta, fertilidad del suelo.

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1. Introduction

The subhumid grassland communities in mountain regions are shifting from productive grasslands to high competitive shrubland communities as reported in several alpine and subalpine zones (Anthelme *et al*., 2002; Tasser and Tappeiner, 2002; Gellrich *et al*., 2007; Gartzia *et al*., 2014). This process commonly called shrub encroachment is rapidly increasing as a result of climate and land use change (Guisan and Theurillat, 2000; Gehrig-Fasel *et al*., 2007). Shrub encroachment has profound effects on natural ecosystems: produces irreversible changes in ecosystem functioning (Knapp *et al*., 2008) and services (Metzger *et al*., 2006), modifies landscape net primary production patterns (Moreno-de-las-Heras *et al*., 2015), reduces biodiversity (Price and Morgan, 2008) and changes soil and vegetation properties towards an increase of resistance to runoff related erosion processes, but a decrease of slope stability against shallow landslides (Caviezel *et al*., 2014). However, this vegetation shift is not constant across mountain regions and will depend upon different factors, such as land management history (Milchunas *et al*., 1988), climate conditions (Sankaran *et al*., 2005), or vegetation structure (Theurillat and Guisan, 2001).

There is large evidence of the influence of climate change on plant distribution in European alpine mountain areas (Guisan and Theurillat, 2000), where the growing-season temperature is the primary factor affecting the treeline ecotone (Körner and Paulsen, 2004). Nevertheless, different studies reported little changes in community composition in subalpine grasslands in response to warming (Price and Waser, 2000; Vittoz *et al*., 2009) because the invasion of new herbaceous species may be hampered by the density of local ones (e.g. Poaceae and Cyperaceae with high longevity), resulting in limited species replacement (Theurillat and Guisan, 2001) and suggesting the importance of biotic interactions as drivers of assemblage processes in these communities. On the other hand, several other non-climatic factors such as anthropogenic management are also reported to influence plant community changes in the European alpine mountains (Gehrig-Fasel *et al*., 2007). According to Körner´s hypothesis (Körner, 2005), future vegetation changes in mountain areas will be influenced more by anthropogenic management than by climate. Overall, anthropogenic activities have modified vegetation for a long time (Tinner and Theurillat, 2003). Grazing and fire have lowered the treeline ecotone and influenced species distribution in subalpine belts (Olofsson *et al*., 2009; Speed *et al*., 2012). Grazing by vertebrate herbivores reduces the impact of warming on plant communities in alpine ecosystems, maintaining the abundance of graminoids in contrast to the increase of woody vegetation in areas with no grazing (Post and Pedersen, 2008; Speed *et al*., 2012). For example, large herbivores such as reindeer enhance nutrient cycling and productivity, reduce shrub cover and promote graminoid vegetation in the Arctic tundra (van der Wal, 2006).

Socioeconomic changes in Europe are leading to emigration from rural areas to industrialized cities, causing substantial depopulation (Romano, 1995; André, 1998; Ayuda and Pinilla, 2002) and land abandonment of rural mountain areas (MacDonald *et al*., 2000; Gehrig-Fasel *et al*., 2007). The abandonment of pasturelands leads to a reduction of grazing and, consequently, the recolonization of subalpine grasslands by trees and shrubs (Vittoz *et al*., 2008; Peringer *et al*., 2013), which is further encouraged by fire suppression practices (Moreira *et al*., 2001; Pausas *et al*., 2008). Land use changes are considered the main driver in terrestrial ecosystems, whereas biodiversity of grassland and mountain ecosystems is expected to be especially sensitive to these changes (Sala *et al*., 2000).

Many of the European grassland ecosystems with high conservation value are threatened by the change of those land uses that created and maintained them over the time (WallisDeVries *et al*., 2002; Öckinger *et al*., 2006; Veen *et al*., 2009). Most rangelands are considered fire-dependent ecosystems, where historical fire regimen maintained under control woodland expansion (Limb *et al*., 2016). Prescribed fire has been used as a management tool in rangeland ecosystems, for regenerating pastures, because fire can promote forage production, quality and palatability, and also opens up new foraging areas where canopy closure by shrubs obstructed the access to grasslands areas (Hobbs and Spowart, 1984; Cook *et al*., 1994; Cubit, 1996; Collins *et al*., 1998; Fernandes *et al*., 2013; Clark *et al*., 2016; Santín and Doerr, 2016). Although there is large knowledge on the effects of fire on forests (Pausas *et al*., 2008; Fernandes *et al*., 2013; Santín and Doerr, 2016), the response of ecosystems to fire is still not fully understood because it depends on the spatial and temporal scale, the historical fire regime, and presence of other environmental stressors (e.g. drought and grazing) (Limb *et al.*, 2016). Moreover, the influence of fire on soil fertility showed contradictory results. Some authors reported soil nutrient decreases after prescribed fire events (Martínez-Mena *et al.*, 2001; San Emeterio *et al.*, 2016; Nuche *et al.*, 2018), while others reported neutral or even positive effects on soil nutrients (Fernandes *et al.*, 2013).

In recent time, clear-cut has been proposed as a management practice to control shrub cover expansion (Lasanta *et al.*, 2009) and improve plant diversity (Collins *et al.*, 1998), although little information exists concerning the effect of clearing on grasslands restoration (Pittarello *et al.*, 2016). Clear-cut is an appropriate management practice because it contributes to the recovery of herbaceous coverage and is less aggressive than fire (Fernández-Santos *et al.*, 1992), but it requires being along with active grazing (Álvarez-Martínez *et al.*, 2016; Kirkpatrick *et al.*, 2016) to control shrub expansion.

Optimal management of pastures requires the use of fire and/or clear-cutting, particularly for the conservation of grasslands in subhumid high productive ecosystems (Sankaran *et al.*, 2005). However, the optimal strategy that guarantees the sustainability of alpine and subalpine grasslands is still not known. The response of the plant community to a given management treatment is expected to depend on the characteristics of dominant species and on the disturbance regimen in the area (Pausas *et al.*, 2008). Most of the fire-prone communities are rich in shrubs and sub-shrubs able to resprout after a fire event, and majority of non-resprouting species growing in those ecosystems are post-fire recruiters (i.e., plants whose seeds are stimulated by the fire heat (Paula and Pausas, 2008), which increase their population size after a fire event (Vilà *et al.*, 2008). Different researchers have documented changes in resprouting capacity after experimental recurrent clipping (Canadell and López-Soria, 1998; Paula and Ojeda, 2006). On the other hand, biotic interactions between plant species can play an important role in post-fire successional processes. For example, after fire events shrub resprouter species can enhance the opportunities for seeding establishment (Raffaele and Veblen, 1998; Pausas and Keelay, 2014), while grasses can become more competitive (Melgoza *et al.*, 1990; Canals *et al.*, 2014). Finally, grazing interferes with fire/clear-cut. For instance, grazing after burning increases plant diversity even in periodically burnt grassland (Collins *et al.*, 1998). Therefore, grasslands restoration needs to evaluate rangeland management practices and incorporate temporal dynamics to support predictive inferences.

We focused this study in Pyrenees subalpine grasslands, where the expansion of woody species is a serious threat to grassland conservation (Komac *et al.*, 2011a; Gartzia *et al.*, 2014; Nadal-Romero *et al.*, 2018) and human activities have played a key role in maintaining these ecosystems for centuries (Montserrat and Fillat, 1990). *Echinospartum horridum* (Vahl) Rothm. (Erizón) is a strictly calcicolous chamaephyte, thorny cushion, endemic of the Pyrenees, which occurs mainly on south facing slopes (Benito Alonso, 2006). It is among the most aggressive species encroaching Pyrenean grasslands and it is spreading rapidly (Komac *et al*., 2011a). Empirical studies reported increased seed germination and seedling survival of *E. horridum* after burning and in less extent under clearing treatment (Nuche *et al*., 2018). Thus, it is of major importance to understand the dynamics of this species if optimal management practices are to be applied in the Pyrenees.

In this study we addressed the effects of two common management practices used to control shrub encroachment in grassland plant communities of Spanish Pyrenees (i.e., burning and clear-cutting). To do that, we run a 5-year manipulative experiment to monitor changes in vegetation structure and soil properties after prescribed fire and clear-cut events, comparing them against two control communities: the original *Bromion erecti* grasslands and the shrub encroached *E. horridum* community. Specifically, we (1) investigated the effect of burnt and clear-cut treatments in the vegetation structure and soil properties of the *E. horridum* community that invaded subalpine grassland; and (2) evaluated the suitability of the treatments to recover the original productive grasslands.

We predicted that (H1) *E. horridum*, as a pyrophytic species, would be more competitive and would recover faster after prescribed fire than after clear-cut, while the latter treatment would promote a faster recovery of grasses and forbs species by more efficient removal of the competitor *E. horridum*. We also expected (H2) a more similar vegetation composition to the original *Bromion erecti* grasslands in the clear-cut experiment than in the burnt treatment. We also predict that (H3) soil nutrient contents would be affected differently by rangeland management practices, such as burning and clear-cutting. Burning was expected to be associated with higher loss of soil nutrients and slower recovery of soil properties than clear-cutting.

2. Materials and Methods

2.1. Study Area

The study was conducted in the Central Pyrenees, at the Ordesa and Monte Perdido National Park and its peripheral zone, in northern Spain. The study included two locations with prescribed fire and clear-cutting areas: Torla (42º 38' 34''N, 0º 07' 36''W, 1720 m a.s.l.) and Tella (42º 36' 09''N, 0º 10' 53''W, 1960 m a.s.l.). The *Bromion erecti* regularly grazed grassland communities (C-Grass) used as a control for subalpine grassland were located in Góriz (42º 36' 25''N, 0º 01' 03'' E, 1904 m a.s.l.) and Sesa (42º 35' 56''N, 0º 04' 14'' E, 1735 m a.s.l.) (Fig. 1). The average mean minimum and maximum temperature at the nearest meteorological station between 1982 and 2012 (Refugio de Góriz at 2200 m a.s.l. 42º 39' 48''N, 0º 00' 54''E) was 1.5 and 8.7º C and the average annual precipitation was 1688 mm. The average slope in the study area ranged from approximately 10º to 30º.

Vegetation was originally a subalpine *Bromion erecti* grassland community over calcareous soil substrate dominated by herbaceous species such as *Bromus erectus* Huds., *Festuca rubra* L. or *Plantago lanceolata* L., and species with a high fodder value, such as *Trifolium* and *Medicago* spp. These grasslands have been colonized by *E. horridum*, a chamaephyte that reproduces asexually through clonal propagation of decumbent branches, forming dense monospecific patches (cover > 90% of the soil surface).

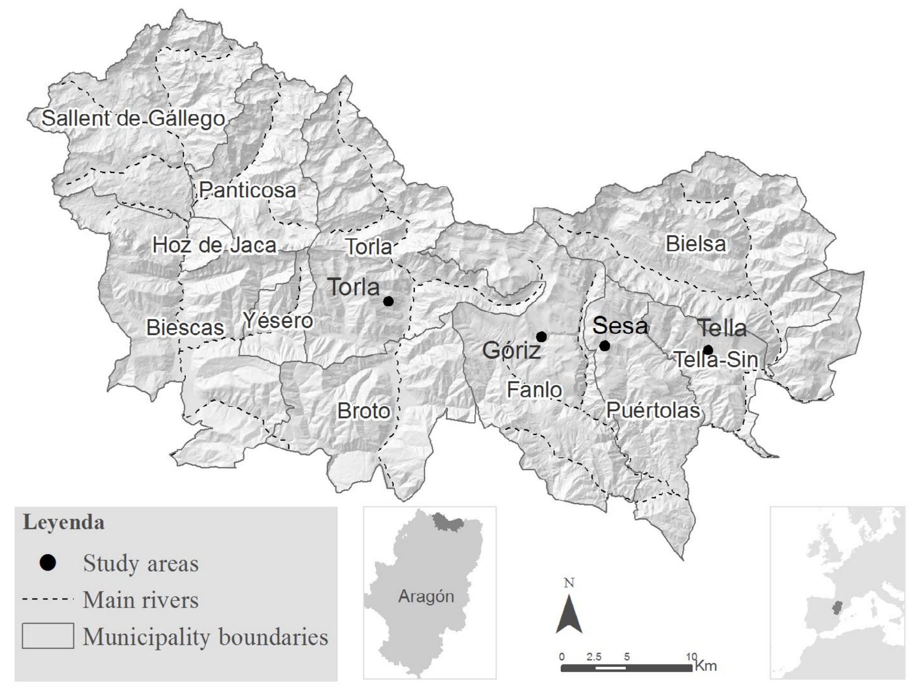

Figure 1. Study area and location of field sites.

In 2008 and 2010 autumn, *E. horridum* patches of 7.7 and 11.8 ha were burnt in Torla and Tella, respectively (Burnt treatment). Clear-cut treatment was established by clipping the aerial biomass of *E. horridum*: 100 m^2 were clipped in Torla in 2008 autumn and 1.25 ha in Tella in April 2012 (Fig. 2). Clipped material was left in the soil and it was homogeneously distributed to simulate the homogeneity of the *E. horridum* cover. We selected areas dominated by *E. horridum* located near the study sites (around 200-400 m away) as a control treatment (C-Erizón), that we sampled the first year of treatment establishment. We used data from pastures located in Góriz and Sesa sampled in 2004 and 2005, as controls of well-preserved *Bromion erecti* grassland community that is not invaded by *E. horridum* (C-Grass). Those grasslands are very resilient to environmental pressure as it is demonstrated after two decades of herbivore exclusion, which did not trigger large changes in community structure and diversity losses (Pardo *et al*., 2015). After the application of the treatments, sites were grazed yearly by sheep and cattle from early June to late September. Grazing pressure ranged between 0.7-0.8 livestock units (LU) /ha (1 sheep = 0.125 LU and 1 cow = 0.80 LU) during the summer grazing period (June to September). We surveyed the vegetation composition in control treatments once because plant communities were stable during the study period. However, soil properties were surveyed both the first and fourth year after the treatment in the control C-Erizón.

Figure 2. Brush-cutting of Echinospartum horridum *in Tella mountain.*

2.2. Data collection and analysis

At all sites vegetation was monitored at the peak of the vegetation growing season. We used the Point-Intercept Method (Goodall, 1952) to record the presence of individual plants (at 10-cm intervals) along sixty 210-m transects; 6 per Burnt treatment and year (33 in total, 18 in Torla during 6 years and 15 in Tella during 5 years), 3 transects per Clear-cut treatment and year (15 in total in Tella during 5 years period), 6 transects per control (12 in total, 6 per C-Erizón and 6 per C-Grass). The transects were marked with permanent labels every 50 m for the repeated measures. We identified a total of 234 different plant species, comprising 28 woody species, 18 legumes (excluding *E. horridum*), 155 non-legume forbs and 33 grass species. The relative vegetation cover was calculated for each functional group as the number of count of individual plants included in each functional group divided by the total number of individual plants present along each 210-m transect.

The reproductive capacity of *E. horridum* was evaluated by recording the number of seedlings that germinated annually and their subsequent yearly survival from 1 m^2 permanent plots (20 per treatment and year). Data were collected in mid-May of each year. Germination was collected during 5 years after treatment and survival was only recorded the second and third years after treatment because of the difficulty to differentiate between individual seedlings for longer periods.

Species diversity was estimated for each transect using the Evenness index, which was calculated as the Shannon Index divided by the natural logarithm of the species number.

Shannon Index, *H'* (Shannon, 1948), $H' = \sum_{i=1}^{N} p_i \ln \frac{1}{p_i}$

where p_i is the probability of the frequency of the *i*-th species. In our study, p_i was the relative cover of species *i* on a 210-m transect.

To evaluate the role of biotic interactions structuring the community, we measured the spatial pattern between pairs of species in the plant community. Although inferring biotic interactions from spatial patterns is not exempt of criticisms (Wiegand *et al.*, 2012; Chacón-Labella *et al.*, 2017), local spatial association is a common method to estimate biotic interactions in plant communities (Valiente-Banuet and Verdú, 2008; Cavieres and Badano, 2009). We calculated the number of positive and negative spatial associations within the matrices of co-occurring species on each transect. Specifically, we compared the observed number of co-occurrences considering the upper and lower limits of the 95% confidence intervals of the Poisson distribution (Saiz and Alados, 2012). Two species were said to co-occur if they were present at the same sampling point on a given transect. Recurrent or rare local co-occurrences were assumed to reflect plant interactions (i.e., facilitation or competition), instead of merely plants that share habitat requirements (Saiz and Alados, 2012; Soliveres and Maestre, 2014). We calculated the number of positive, K^+, and negative, K^-, associations between pairs of species on each transect as the number of pairs of species that presented significantly more or less co-occurrences than expected by the confidence interval. We assumed that two species that co-occurred more often than expected benefited from the association, and interference was inferred if two species segregated more than expected (Tilman and Kareiva, 1997; Tirado and Pugnaire, 2005). We calculated the dominant spatial pattern as the ratio of positive to negative associations $(K^+ - K^-)/(K^+ + K^-)$, which is a symmetrical estimate around zero that is used widely in ecology (Armas *et al.*, 2004). This ratio ranges from -1 (dominance of spatial segregation) to 1 (dominance of spatial aggregation). Mechanisms and consequences of the overall balance of interactions are easier to identify if the competition and facilitation components are evaluated individually (Callaway and Walker, 1997; Michalet *et al.*, 2014). To control the influence of species richness on association frequency, we divided the number of positive (K^+) and negative (K^-) spatial associations by the number of species (S) in the transect, referred as the density of positive (D^+) and negative (D^-) associations, respectively. We also estimated network connectivity (NC) as the number of significant spatial associations (K) divided by the number of all potential spatial associations ($NC = 2K/S(S-1)$).

Four soil samples were collected from the upper 15 cm of soil along each of the three 210-m transects associated to each combination of treatment (Burnt, Clear-cut, C-Erizón) and location (Torla and Tella) on the first and fourth year after treatment (total of 72 soil samples). Sampling was undertaken in 2009 and 2012 in Torla, and in 2012 and 2015 in Tella. In addition, 12 soil samples were collected in Góriz and Sesa in 2017.

Soil samples were dried in the laboratory and passed through a 2-mm sieve. Soil pH, organic matter content (OM), carbon (%C), nitrogen (%N), and the C/N relationship were quantified at each sample. After soil samples were polished, total C and N were quantified using an elemental analyzer Variomax Elementar (DUMAS procedure). Organic carbon content was quantified using dichromate (Heanes, 1984). Organic matter content was calculated multiplying % organic Carbon by the Van Bemmelen Factor 1.724 (Heanes, 1984), which assumes that OM is 58% organic C.

2.3. Statistical analyses

To analyze management treatment effect after 5 years (Burnt, Clear-cut) in comparison with control (C-Erizón) and with a well-preserved subalpine grassland community (C-Grass) we conducted a Linear Model (LM). The dependent variables were: vegetation spatial associations (network Connectivity (NC), density of negative associations (D^-), density of positive association (D^+), ratio of positive and negative spatial associations ($(K^+ - K^-)/(K^+ + K^-)$), Bare soil and *E. horridum* cover, and Evenness. Percentage values were subjected to angular transformation to achieve the normality of the data.

To evaluate the *E. horridum* reproductive capacity after treatment, we performed Generalized Linear Mixed Model (GLMM) with Poisson distribution errors. The number of germinated seeds per square meter was the dependent variable, treatment (C-Erizón, Clear-cut and Burnt) was the fixed factor, plots nested within locations were included as a random effect factor and year as repeated measure. C-Grass treatment was not included as *E. horridum* is not present in C-Grass.

The survival capacity of emerged seedlings one year after germination was evaluated by GLMM with a binomial distribution (survive/dead), treatment (Clear-cut and Burnt) was the fixed factor, proportion of seedlings that survived one year after treatment was the response variable, plots nested within locations were included as random effect factor, and year as repeated measure. C-Erizón was not included as treatment effect factor because the germinated seeds were almost neglected, and consequently the subsequent survival was not calculated.

To test the change of vegetation structure with time after the treatment (Burnt and Clear-cut) we used a Lineal Mixed Model (LMM) for each vegetation variable individually. Plots were included as a random factor. The controls C-Erizón and C-Grass were not included as treatment effects because these vegetation communities were stable during the study period. The dependent variables were vegetation spatial associations (network Connectivity (NC), density of negative associations (D^-), density of positive association (D^+), and ratio of positive to negative associations ($(K^+ - K^-)/(K^+ + K^-)$), and vegetation composition (Bare soil and *E. horridum* cover and Evenness). Percentage values were subjected to angular transformation to achieve normality.

To identify significant differences in the soil properties for each treatment, we also used a LMM with treatments (C-Erizón, Clear-cut and Burnt) as fixed factor and soil nutrients (nitrogen (%N), carbon (%C), Carbon/Nitrogen ratio (C/N), organic matter (MO), and pH) in first and fourth year after treatment as response variables. Plots were nested with locations and included as a random effect factor. Data in percentages were arcsine transformed for normalization.

LMM and GLMM were performed using the *lme* function in the *nlme* library and *glmer* in the *lme4* of the R package respectively (Pinheiro *et al*., 2014). The analyses followed the protocol of Zuur *et al*. (2009). The optimal structure of the model was identified based on the lowest Akaike's Information Criterion (AIC). Residuals were tested for normality and homogeneity of variance following model validation protocol of Zuur *et al* (2009). Post-hoc pairwise comparisons between treatments were performed with Tukey HSD test for mixed models with *multcomp* package (Hothorn *et al*. 2008). All the statistical analyses were performed using R 3.2.2 (R Core Team, 2014).

3. Results

3.1. *Effects of Burnt and Clear-cut the 5th year after the treatment on plant community structure in comparison with grassland community (C-Grass) and* E. horridum *community (C-Erizón)*

Bare soil varied significantly with treatment effects (Table 1). Tukey test showed that after 5 years from the treatment, bare soil cover was significantly higher in Burnt and Clear-cut treatments than in both controls. Conversely, *E. horridum* cover was significantly higher in C-Erizón in comparison with C-Grass, Burnt and Clear-cut treatments. Burnt treatment had higher *E. horridum* cover (more than double) than Clear-cut treatment. *E. horridum* was absent in C-Grass while C-Erizón had 69.51% of woody species cover; most of them were *E. horridum* (61.4%). C-Grass had a high cover of herbaceous species, being 45.5% non-legume forbs, 40.6% grasses and 12.3% legumes. On the 5th year after the Burnt and Clear-cut treatments, the relative cover of grasses and non-legume forbs increased. The abundance of woody species also increased, particularly *E. horridum* abundance was 34.8% and 15.1% five years after Burnt and Clear-cut treatments respectively. Comparisons between treatments revealed statistically significant differences in vegetation composition ($F_{3,17}$= 126.51, $P < 0.001$, for woody, $F_{3,17}$= 22.18, $P < 0.001$ grass, $F_{3,17}$= 53.98, $P < 0.001$ legumes, and $F_{3,17}$= 14.85, $P < 0.001$ non-legume forbs species). The abundance of legumes, grasses and non-legume forbs was significantly higher in C-Grass than in Burnt and C-Erizón. Clear-cut treatment presented vegetation covers closer to C-Grass than to the other two conditions, although Burnt treatment favored legumes rather than Clear-cut (Fig. 3).

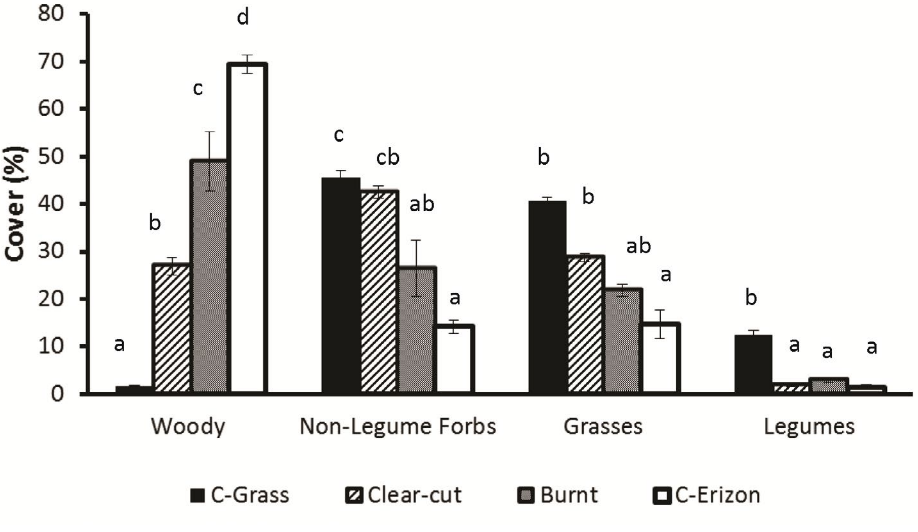

Figure 3. Bar graph representation of vegetation cover (woody, non-legume forbs, grasses, legumes) changes 5 years after the Burnt and Clear-cut treatments in comparison with controls (C-Grass and C-Erizón). Bars with different letters show significant differences between treatments (P < 0.05) as per Tukey test pairwise comparison.

Species diversity (Evenness index) was significantly lower in C-Erizón in comparison with the other treatments (Table 1). Species richness was the largest in C-Grass. Clear-cut and Burnt treatments did not differ in species diversity or species richness on the 5th year after the treatment.

Table 1. Vegetation cover (Bare soil and E. horridum*), plant community structure (Evenness, Richness) and plant-plant association network (Network Connectivity (NC), Density of negative association (D^-), Density of positive association (D^+), ratio of positive to negative association (Ratio)) 5 year after the treatment (Burnt, Clear-cut) and controls (C-Erizón, C-Grass). Differences between treatments were evaluated with linear model (one way ANOVA) and pairwise comparisons with Tukey test * $P < 0.5$, ** $P < 0.01$, *** $P < 0.001$.*

Variable response	**C-Grass mean±se**	**Burnt mean±se**	**Clear-cut mean±se**	**C-Erizón mean±se**	**F3,17**
Baresoil	7.08±1.30 ^{b}	17.37±4.11 ^{a}	18.27±2.76 ^{a}	2.09±0.52 ^{b}	12.85***
E.horridum	0±0 ^{a}	49.05±8.80 ^{c}	18.21±2.25^b	86.17±1.79 ^{d}	111.88***
Evenness	0.69±0.01 ^{a}	0.63±0.03 ^{a}	0.68±0.01 ^{a}	0.43±0.03 ^{b}	18.36***
Richness	64.17±2.02 ^{a}	58.0±4.13 ^{ab}	44.67±2.33 ^{b}	43.5±3.14 ^{b}	9.63***
NC	2.52±0.24 ^{a}	1.39±0.21 ^{b}	1.10±0.10 ^{b}	1.34±0.15 ^{b}	9.40***
Ratio	-0.03±0.06^a	0.46±0.06 ^{b}	-0.06±0.02 ^{a}	0.62±0.04 ^{b}	34.78***
D^-	2.07±0.15 ^{a}	0.62±0.11 ^{b}	1.00±0.04 ^{b}	0.71±0.16 ^{b}	23.12***
D^+	1.96±0.14 ^{ab}	1.87±0.37 ^{ab}	0.88±0.07 ^{b}	2.84±0.49 ^{a}	3.77*

The plant spatial associations in the community were also significantly influenced by treatment effects (Table 1). Network Connectivity (NC) was significantly higher in C-Grass in comparison with Burnt, Clear-cut and C-Erizón treatments. The ratio of positive to negative associations was significantly larger under C-Erizón and Burnt treatment in comparison with C-Grass or Clear-cut. The density of negative plant associations was significantly larger under C-Grass than under Burnt, C-Erizón and Clear-cut. The density of positive plant association was largest under C-Erizón and the lowest under Clear-cut.

3.2. Change in plant community structure with time from Burnt and Clear-cut treatments

Change in plant community structure with time from treatment was analyzed only for Burnt and Clear-cut treatments, as the control C-Erizón and C-Grass were only surveyed one year. Bare soil declined significantly over the time in Burnt ($F_{1,26} = 40.08$, $P < 0.001$, slope = -0.055 ± 0.01) and Clear-cut ($F_{1,8} = 52.17$, $P < 0.001$, slope = -0.065 ± 0.009), with random slope model as the optimal structure of the random component (Fig. 4). Conversely the cover percent of *E. horridum* increased significantly with time after Burnt ($F_{1,26} = 234.21$, $P < 0.001$, slope = 0.059 ± 0.01) and Clear-cut ($F_{1,8} = 214.58$, $P < 0.001$, slope = 0.044 ± 0.003) (Fig. 4). The optimal model was a random intercept model. Evenness showed different results for Burnt and Clear-cut treatment. It declined significantly during the 5-year experiment in the Burnt treatment ($F_{1,26} = 38.84$, P <

0.001, slope = -0.02 ± 0.003), but no significant changes were observed after Clear-cut ($F_{1,8}$ = 0.04, ns).

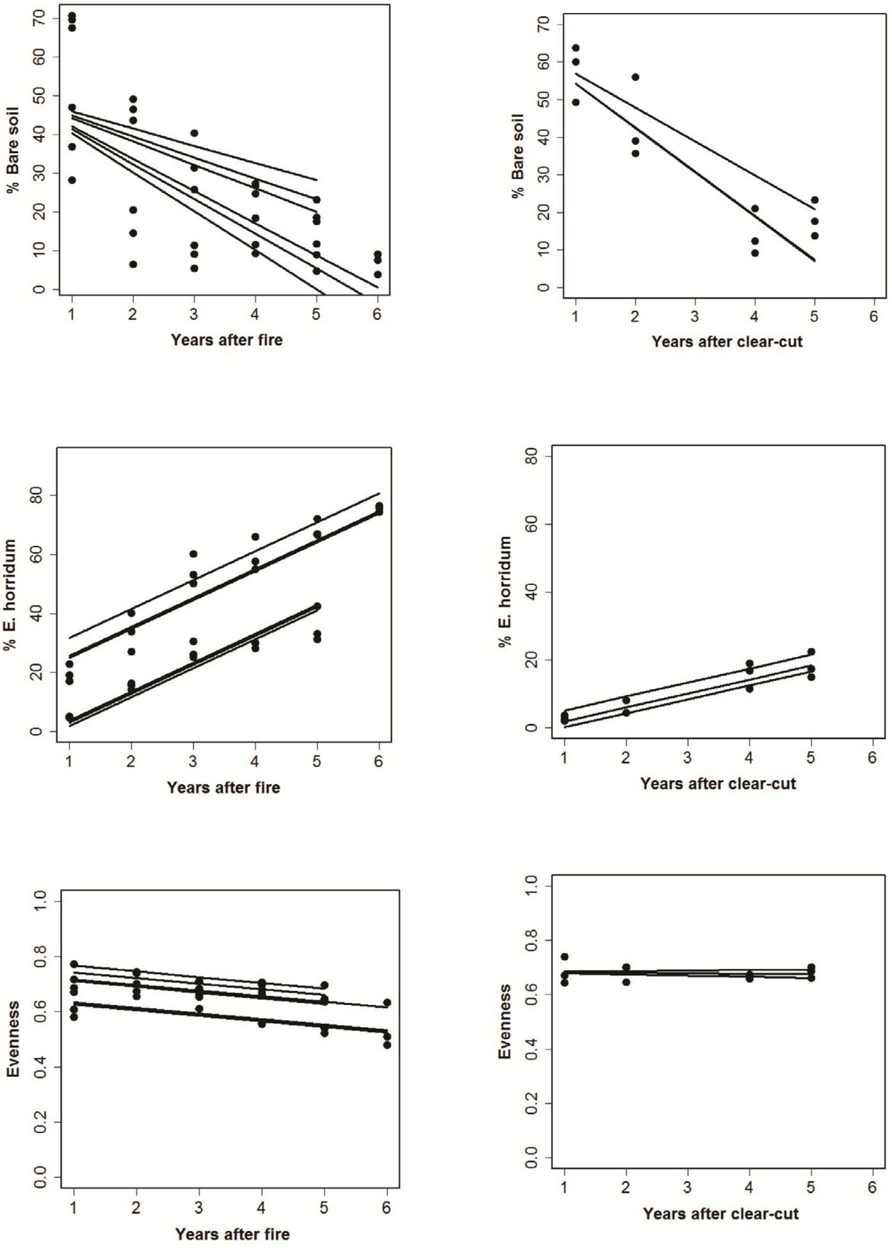

Figure 4. Change in Baresoil, E. horridum *cover and Evenness index with time from the Burnt and Clear-cut treatments. The linear mixed model (LMM) included sample site as a random factor.*

Network spatial structure changed with time after Burnt and Clear-cut treatments (Fig. 5). Network Connectivity increased significantly 5 years after Burnt ($F_{1,26}$ = 18.57, $P < 0.001$, slope = 0.13 ± 0.03). A similar trend was observed after Clear-cut, although the difference was not significant ($F_{1,8}$ = 1.36, ns). The density of negative (D^-) associations increased significantly with time after Clear-cut ($F_{1,8}$ = 3.60, P = 0.09, slope = 0.17 ± 0.09), but it did not after Burnt ($F_{1,26}$ = 1.53, ns). Conversely, the ratio of positive to negative association declined significantly with the number of years after Clear-cut ($F_{1,8}$ = 73.48, $P < 0.001$, slope = -0.24 ± 0.03), although not effect was observed after Burnt ($F_{1,26}$ = 0.40, ns). Similarly the density of positive associations (D^+) declined significantly with years from Clear-cut ($F_{1,8}$ = 7.10, $P < 0.05$, slope = -0.52 ± 0.19), but no effect was noticed after Burnt ($F_{1,26}$ = 0.003, ns). As the ratio of positive to negative association presented a significant interaction between location and year after Burnt, separated analyses per site were performed, revealing a significant decline in Tella ($F_{1,13}$ = 124.9, $P < 0.0001$, slope =-0.12± 0.01), but not in Torla ($F_{1,16}$ = 2.01, ns, slope = 0.06 ± 0.04).

3.3. *Effects of management treatment on* E. horridum *sexual reproduction*

Management treatment had a significant effect on *E. horridum* germination, as revealed by the significant difference between models with and without treatment effects (χ^2 = 28.46, df = 2, $P < 0.001$). *E. horridum* germination increased drastically after Burnt (104.34 ± 10.98, n = 80) and Clear-cut (54.12 ± 7.19, n = 60) treatments in comparison with control (C-Erizón) (2.27 ± 0.27, n = 70) (Table 2). Tukey´s *post hoc* HSD test showed significant differences in C-Erizón vs. Clear-cut (z = 18.79, $P < 0.001$), C-Erizón vs. Burnt (z = 23.24, $P < 0.001$) and Clear-cut vs. Burnt (z = 5.23, $P < 0.001$).

The number of germinated seeds declined progressively year after year from the treatment (Table 2). Seedling survival was analyzed only for Burnt and Clear-cut treatments, as the number of seeds germinating in C-Erizón, was negligible. The results of the GLMM showed not significant differences between Burnt and Clear-cut treatments (z = 1.34, P = 0.18, Tukey´s *post hoc* HSD test), but a significant effect of year of treatment (Table 2).

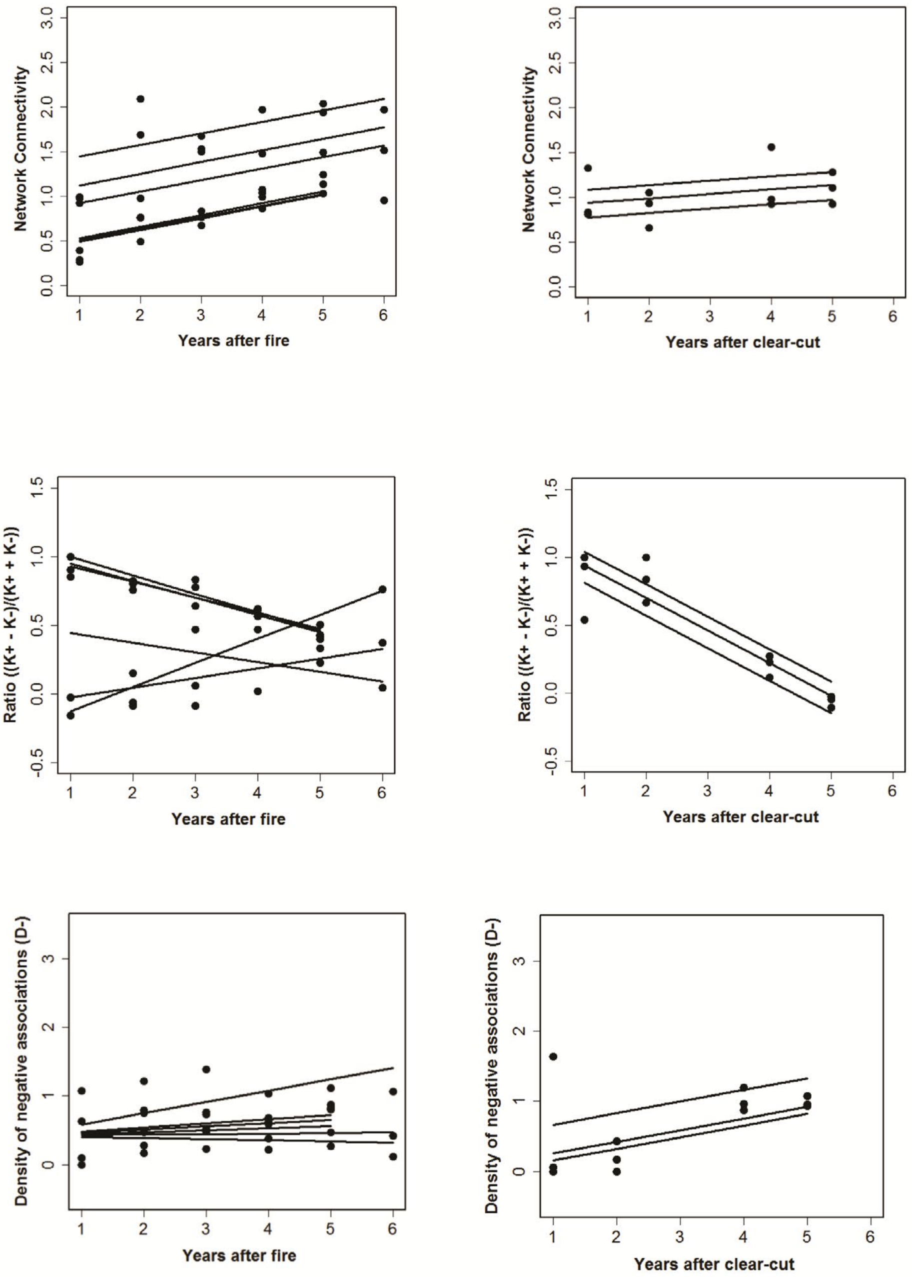

Figure 5. Change in Network Connectivity, ratio of positive to negative associations (K^+ - K^-)/(K^+ + K^-), and density of negative association (D^-) with time from the Burnt and Clear-cut treatments. The linear mixed model (LMM) included sample site as a random factor.

Table 2. Results of GLMM analyses for treatment effect (Burnt, Clear-cut and the control C-Erizón) on the number of germinated seeds per m^2 and yearly survival. The number of years after the treatment was included as repeated factor and plots were nested into location as random effect factor. Only Clear-cut and Burnt treatments were included on the yearly survival effects, as the number of germinated seeds on C-Erizón was negligible. Intercept includes the treatment effect C-Erizón and Year1 for the germination analyses, and Clear-cut and Year2 for the survival analyses.

Germination

Variable	**Estimate**	**z-Value**	**P<**
Intercept	0.339	2.09	0.04
Clear-cut	3.786	18.79	0.001
Burnt	4.672	23.24	0.001
Year2	-0.131	-5.89	0.001
Year3	-0.387	-16.14	0.001
Year4	-1.744	-27.34	0.001
Year5	-1.376	-25.39	0.001

Seedling survival

Variable	**Estimate**	**z-Value**	**P**
Intercept	-0.799	-2.31	0.02
Burnt	0.655	1.34	0. 18
Year3	0.544	10.47	<0.001

3.4. Effects of management treatments (Burnt, Clear-cut and C-Erizón) on soil nutrients after one and four years from the treatment, and comparison with grassland community (C-Grass)

Soil fertility was affected by treatments differently at the first and fourth year after Burnt and Clear-cut treatments in comparison with the control C-Erizón (Table 3). One year after treatment soil OM showed no significant differences between treatments, although C was significantly lower after Clear-cut, and C-Erizón had the highest C and N contents. Four years after the treatment, soil OM, C and N were lower under Burnt than under Clear-cut and C-Erizón treatments (Table 3). No significant differences were observed between Clear-cut and C-Erizón four years after the treatment (Table 3).

*Table 3. Results of the GLMM analyses for treatment effects (Burnt, Clear-cut and Control) on soil nutrients (organic matter (OM), carbon (%C), nitrogen (%N)) and pH one and four years after the treatment. Plots nested within location were included as random effect factor. The pairwise comparison between treatments was evaluated with Tukey test. Mean±se values were back transformed. • < 0.1, * P < 0.5, ** P < 0.01, *** P < 0.001.*

One year after treatment

Variable response	**Burnt mean±se**	**Clear-cut mean±se**	**C-Erizón mean±se**	**F2,32**
OM	10.30±1.09^{a}	9.85±1.37^{a}	10.99±0.86^{a}	1.41
C	7.70±1.03^{ab}	6.78±0.76^{b}	8.64±0.97^{a}	4.34
N	0.64±0.08^{ab}	0.59±0.06^{b}	0.73±0.08^{a}	3.93
C/N	9.56±0.26^{a}	9.61±0.43^{a}	9.09±0.38^{a}	0.28
pH	7.03±0.14^{a}	5.78±0.13^{a}	6.38±0.27^{a}	1.51

Four years after treatment

Variable response	**Burnt mean±se**	**Clear-cut mean±se**	**C-Erizón mean±se**	**F2,30**
OM	7.86±0.83^{a}	12.32±1.45^{b}	13.39±2.08^{b}	11.45•
C	5.63±0.72^{a}	10.80±1.65^{b}	9.09±1.13^{b}	6.03
N	0.52±0.06^{a}	0.79±0.10^{b}	0.75±0.09^{b}	9.61•
C/N	8.94±0.25^{a}	9.44±0.39^{a}	10.00±0.36^{a}	0.72
pH	6.40±0.16^{a}	5.64±0.11^{a}	6.15±0.21^{a}	2.12

C-Grass soil fertility values did not show significant differences from those observed on C-Erizón and Clear-cut (11.08 ± 0.71% of OM, 8.15 ± 0.66% of C). However, C-Grass showed a high percentage of N (0.84 ± 0.24) in comparison with Burnt treatment (z = -3.065, P < 0.05). Consequently, the C/N ratio was significantly lower in C-Grass (7.84 ± 0.51) ($F_{3, 42}$ = 5.74, P < 0.01), while it was similar among the other treatments after the first and fourth year (Table 3). Tukey test z score for C/N ratio showed significant differences between C-Grass and C-Erizón (z=-3.91, P < 0.01), and between C-Grass and Clear-cut (z = -3.08, P < 0.05), but no significant difference with Burnt treatment (z = 2.22, ns).

Soil pH values were not significantly influenced by treatment effect on the first or fourth year after the treatment (Table 3). pH values in C-Grass (5.41 ± 0.13) were the lowest. pH values after Clear-cut were lower than those measured in Burnt and C-Erizón.

4. Discussion

Our experiment demonstrated that Clear-cut treatment of *E. horridum* community was more effective controlling *E. horridum* colonization than Burnt treatment and contributed to a higher extent to recovering the original grassland vegetation, because

E. horridum seedling performed worse (lower germination rates) and plant species types were more similar to the original grassland (legumes, non-legumes, and grasses). However, 5 years after applying the Clear-cut, managed pastures still did not reach the conditions of control grasslands (C-Grass). Overall, vegetation recovery after treatment effects was fast after Burnt and Clear-cut, reducing the bare soil cover from 50% to 20% after 5 years. *E. horridum* re-encroachment efficiency depended on the removal mechanism, reaching 50% cover after Burnt, but only 18% after Clear-cut.

Mechanical removal is much more effective than fire because these two types of removal differently affect the seed establishment rates of *E. horridum* on bare soil (Nuche *et al*., 2018). Fire perturbation increased *E. horridum* seedling establishment more than clearing as also reported previously (Nuche *et al*., 2018). Shrubs have been found to increase seedling emergency after burning (De Luis *et al*., 2005; Rivas *et al*., 2006). Clear-cut showed less germination success than Burnt, but similar first-year survival rate. The number of germinated seeds declined with time from the treatment in both Clear-cut and Burnt. These results are in concordance with the pyrophytic nature of *E. horridum*, already reported in the literature (Komac *et al*., 2013).

Grazing promotes plants with higher nitrogen to carbon ratios, consequently increasing forage quality (Aldezabal *et al*., 2015). Here we observed an improvement of pasture quality after Clear-cut, with an abundance of grasses and forbs similar to the original grassland (C-Grass). Other studies have also observed an increase of grasses (Krahulec *et al*., 2001) and legumes (Mayer *et al*., 2009) abundance with grazing in subalpine zone, as they benefit from grazing by the relief from higher competitors. Furthermore, the selective foraging of palatable species by livestock may favor higher dispersion of palatable species with grazing, increasing the qualitative properties of grazed grasslands (Odriozola *et al*., 2014). As grazing activity was maintained in our treated study sites, we observed a higher proportion of legumes, non-legume forbs and grasses after Burnt and Clear-cut in comparison with the previous C-Erizón community, which was inaccessible for livestock. However, they did not reach abundances observed in C-Grass. On the other hand, the abundance of woody species and particularly *E. horridum*, was more similar between Burnt and C-Erizón due to the enhancement of *E. horridum* germination after fire events.

Overall, species richness and diversity increased after Burnt and Clear-cut in comparison with C-Erizón, but they were significantly lower than those observed in C-Grass. Burnt and Clear-cut treatments increased diversity relative to C-Erizón, where species richness decreased as typically occurs on shrub dominated communities due to competitive exclusion by shrubs (Price and Morgan, 2008). *E horridum* removal opened empty spaces that favored the recharge of soil with seeds that arrived by dispersal, resulting in a large soil seed bank after burning and in less extension after the clearing treatment (Nuche *et al*., 2018), as also occurs with other woody species (Fernandes *et al*., 2013). Plant diversity increases with grazing in ecosystems with long term history of grazing (Milchunas and Lauenroth, 1993), whereas cessation of grazing reduces plant diversity, particularly in mountain grasslands (Krahulec *et al*., 2001; DeGabriel *et al*., 2011; Speed *et al*., 2013). In Central Pyrenees subalpine grasslands also showed higher species diversity under grazing activity, although it is reduced in south oriented slopes where *E. horridum* preferentially colonizes (Komac *et al*., 2011b). Grazing modifies plant competition directly by reducing dominance of some plant species through consumption (Anderson and Briske, 1995) or indirectly by its effect on soil properties (Medina-Roldán *et al*., 2012a). In this study, the control grasslands (C-Grass) had the highest diversity and species richness although the differences were only clearly significant with C-Erizón, probably because the replacement of one species by other may mask changes in species diversity. Indeed previous studies reported that, soil seed bank was quite poor in *E. horridum*, even after its removal (Nuche *et al*., 2018), and did not reach the level of former grassland vegetation (Bekker *et al*., 1997; Bossuyt and Honnay, 2008).

Biotic interactions such as interspecific competition and facilitation are known to play an important role in plant communities (Callaway and Walker, 1997; Callaway *et al*., 2002). In subalpine communities, competition dominates while facilitation is more important as environmental conditions become more extreme (Callaway *et al*., 2002). In our study, plant associations increased with time after Burnt and Clear-cut treatments. The density of negative associations (a proxy of plant competition) increased over the time, resulting in a decline of spatial aggregation (a proxy of plant facilitation). Spatial aggregation only increased in one of the sites (Torla), probably because the faster expansion rate of *E. horridum* in Torla (68% cover after 5 years) than in Tella (35%) forced plants to co-occur in the gaps left by patches of *E. horridum* clumps, as also occur in C-Erizón. Control grasslands (C-Grass) showed the strongest spatial structure (higher connectivity) mostly characterized by spatial segregation (high D^-) and a low ratio of positive to negative association as theory predicts for competitive grasslands (Callaway and Walker, 1997; Callaway *et al*., 2002). The spatial structure of the plant community became more complex with time from the treatment, with higher connectivity and spatial association density. This was mainly due to the increase of spatial segregation between plants, although aggregation was relevant in the shrub encroached community because of the *E. horridum* presence. Nevertheless, community spatial structure after 5 years from Burnt and Clear-cut management was still far from the well preserved grassland community (C-Grass).

Prescribed fires and clearing are generally applied to improve soil quality and increase pasture productivity (Collins *et al*., 1998; Lasanta *et al*., 2009; Santín and Doerr, 2016). However, the way that management influences soil fertility depends on context situation. In this study we observed that soil fertility was differently affected by treatments at the first and fourth year after Burnt and Clear-cut in comparison with the control C-Erizón. Other studies also found higher soil nutrient contents in grasslands soils than under shrub encroached processes (Nadal-Romero *et al*., 2018). On year one after treatment, differences between Burnt and Clear-cut were low. However, Burnt significantly reduced soil fertility after the fourth year. Several studies also reported a decrease in soil fertility after prescribed fire events (Martínez-Mena *et al*., 2001; San Emeterio *et al*., 2016; Nuche *et al*., 2018), although other reported neutral or even positive effects on soil nutrients (Fernandes *et al*., 2013). The effect of fire on soil properties is closely related to the temperature reached during the burning process (Fernandes *et al*., 2013; Santín and Doerr, 2016), which mainly affects a shallow layer of soil. For example, a prescribed burnt performed on *E. horridum* community in one of our study areas (Tella), presented the highest temperature (397°C) at a depth of 1 cm and declined drastically to 121°C at a depth of 2 cm during the first few minutes after fire (Armas-Herrera *et al.*, 2016). Temperatures above 200ºC affect chemical soil properties (Santín and Doerr, 2016) and can lead to an important destruction of organic matter in the upper centimeters of the soil after burning (Armas-Herrera *et al.*, 2016). Nevertheless, they are diluted with soil depth as reported by the low variation in soil chemical properties after prescribed fires when analyzed for the top 10 cm of soil (Alexis *et al.*, 2007; San Emeterio *et al.*, 2016). Soil samples were collected from the upper 15 cm of the soil in our study and no relevant changes were observed on the first year after burning, although soil fertility declined four years after this treatment, probably due to associated erosion processes. The loss of protective vegetation and the enhancement of water repellency after fire result in increased surface runoff and erosion (Shakesby and Doerr, 2006a; Moody *et al.*, 2013). The erosion rate after a prescribed-fire also depends on other factors, such as slope, rain intensity or vegetation cover. It can vary from non-significant (Zavala *et al.*, 2009) to significant increases (Vega *et al.*, 2005; Fernández *et al.*, 2008, 2012) but it is usually lower than after wildfires events (Soto and Diaz-Fierros, 1998). In our case, the protective effect of the plant debris compensated the loss of vegetation cover after the Clear-cut operation (Fernández *et al.*, 2008, 2012), helping to maintain soil nutrients in Clear-cut areas close to those found in the C-Erizón treatment. Although the enhancement of soil fertility by burning of pastures is one of the main motivations for carrying out prescribed fires (Nigh and Diemont, 2013; Pereira *et al.*, 2015; Santín and Doerr, 2016), post-fire runoff and erosion (Shakesby and Doerr, 2006b; Pereira *et al.*, 2015) may result in loss of soil nutrients in the mid/long term, as it is showed in our study. Increases in soil erosion are greater after prescribed burning than after mechanical removal (Fernández *et al.*, 2008).

Soil pH increased after burning, as it was observed in other studies (Santín and Doerr, 2016), returning to values close to C-Erizón as time progressed from the treatment date. Overall, pH was the lowest in C-Grass. Furthermore, the pH value was lower in Clear-cut than in Burnt and C-Erizón.

Grazing induces changes on soil nutrients cycling due to the higher soil microbial activity and N mineralization, which produce higher quality plant litter (Medina-Roldán *et al.*, 2012b; Niu *et al.*, 2016), resulting in low C/N ratio (Fox *et al.*, 2015). We observed lower values of this ratio in C-Grass than in Clear-cut and C-Erizón, which revealed the higher protein contents of pastures grazed for long time. Grazing in highly productive grasslands, as it is the case of this study, favors species with high nitrogen content (Milchunas and Lauenroth, 1993; Semmartin *et al.*, 2004) which results in lower soil C/N ratio in comparison with ungrazed pastures (Speed *et al.*, 2014).

5. Conclusions

Our results reveal that although Burnt and Clear-cut treatments may control *E. horridum* expansion and improve pasture quality in terms of species diversity and species composition, they are not enough to return vegetation to the original well preserved grassland. Clearing is a better strategy than burning to recover grasslands colonized by *E. horridum*, because it is associated to smaller soil degradation and slower recovery of the pyrophyte shrub *E. horridum.* Nevertheless, intensive grazing after fire or mechanical clearing is recommended (Pittarello *et al*., 2016) because it accelerates nutrient cycling in temperate and productive grasslands (Frank and Evans, 1997; McNaughton *et al*., 1997; Bardgett *et al*., 1998; Semmartin *et al*., 2004), being the most effective pastoral practice to reverse shrub-encroachment and to increase plant diversity, herbage mass and forage quality.

Given the difficulty to recover shrub encroached grasslands it is recommended to prevent the loss of subalpine grasslands by active management practices addressed to maintain high grazing pressure, particularly in the shrubs advancing border. It is also counseled to prevent the isolation of grassland patches by the establishment of corridors connecting them and favoring the livestock access to those more remote areas. Finally, the use of enclosures to keep animals in less preferred grasslands for some days is also suggested.

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