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Fire increases the reproduction of the dominant grass *Brachypodium retusum* and Mediterranean steppe diversity in a combined burning and grazing experiment.

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Abstract

Questions

What are the effects of fire and grazing on vegetative growth and sexual reproduction of *Brachypodium retusum*, the dominant species of Mediterranean Thero-Brachypodietea grasslands (“steppes”) and on species composition of the associated plant community?

Location

“La Crau”, South-Eastern France.

Methods

We set up a split-plot experiment testing the effects of fire season (winter, summer) and grazing on plant cover, inflorescence number, seed set and germination of *B. retusum* in traditionally grazed grasslands. We further analyzed plant species composition and diversity in vegetation relevés. The same fire treatments were tested in a second experiment in long-term grazing exclosures.

Results

B. retusum showed a rapid post fire recovery, but other species of the associated plant community, in particular annuals, recovered as fast or even faster. Fire increased *B. retusum* inflorescence production and seed set per inflorescence and this effect was stronger in the summer fire treatment. At community level, fire significantly increased species richness, evenness and Bray-Curtis dissimilarity in the second post-fire season and again, the summer fire effect was stronger. Grazing exclusion for two seasons had only a small effect on *B. retusum* and the associated plant community. The effect of both fire treatments on *B. retusum*

was similar in long-term exclosures. In these exclosures, fire resulted in a community shift towards the species composition of traditionally grazed steppes.

Conclusions

The concomitant positive effects of experimental burning on *B. retusum* reproduction and on plant diversity of Mediterranean steppe vegetation suggest that the system is adapted to fire as an important driver of community composition. Annual species surviving as seeds are as successful in post-fire recovery as perennial resprouters. Prescribed burning may be an alternative strategy to restore community structure in abandoned (ungrazed) steppes showing a decline in typical grassland species after several years of grazing abandonment.

Keywords: exclosures; Mediterranean grassland; plant community; plant-environment interactions; population dynamics; prescribed burning; Thero-Brachypodieta.

Introduction

Mediterranean dry grasslands are semi-natural habitats that depend on human land use such as grazing and related fire management to maintain plant populations and communities (Naveh 1975; Bond & Van Wilgen 1996). Both increased land use intensity, in particular transformation to arable use, and land abandonment followed by shrub encroachment are threatening these highly diverse ecosystems (San Miguel, 2008). As in other European grassland ecosystems, diversity is linked to traditional extensive land use (Poschlod & WallisDeVries 2002; Pywell et al. 2007; Gazol et al. 2012). Sheep grazing is a key land use factor driving plant species composition and diversity across a variety of grassland types (reviewed by Cingolani et al. 2005). Wildfires and fire management by shepherds in the Mediterranean region were also important drivers until the industrial revolution but their role

in maintaining the ecosystem is nowadays less clear because fire suppression and abandonment of traditional pastoral fires have largely reduced their impact in the last decades (Naveh 1975; Parr & Andersen 2006).

Many plant species and communities are adapted to fire and depend on specific fire regime (Bond & Van Wilgen 1996). Changes in such disturbance regime often lead to shifts in plant community composition (Bond & Keeley 2005). In Mediterranean “Matorral” (shrublands), an increase in fire frequency favors seeder shrubs such as *Rosmarinus officinalis* and resprouter grasses such as *Brachypodium retusum* (Vilà-Cabrera et al. 2008). Accordingly, fire suppression may change community structure and diversity of such ecosystems (Bond et al. 2005). At species level, plants with different adaptive strategies to survive fires have been selected over centuries (Buhk et al. 2007). Resprouting from protected tissues and/or from undamaged below-ground organs are common strategies along with increased seed production, fire-resistant seeds, fire-stimulated germination or flowering (Clarke et al. 2013; Lamont & He 2017; Pyke 2017). For example, some fynbos and chaparral geophyte species only start flowering after fire and disperse seeds on bare soil to benefit from reduced competition and higher nutrient availability (Keeley 1993; Tyler & Borchert 2003).

Similarly to fire, grazing favors resprouting either from belowground organs or from the stem base (Briske & Noy-Meir 1998). This may be combined with other avoidance strategies such as small growth, early germination and flowering, and a short flowering period (Landsberg et al. 1999; Díaz et al. 2001). In grasslands, seedling recruitment is often quite low because grazing and dense grassland swards may hamper seed production, germination and seedling recruitment (Drobnik et al. 2011). However, Mediterranean steppe vegetation is a quite open grassland type and the grazing period is short allowing the survival of many annual species

(Briske & Noy-Meir 1998). Similar to fire, grazing increases mineralization of organic matter and nutrient availability during the seedling recruitment period (Bond & Keeley 2005). Although several studies have shown that grazing is needed to maintain the unique species composition of Mediterranean steppe communities (Briske & Noy-Meir 1998; Buisson & Dutoit 2006; San Miguel, 2008), the consequences of short-term and long-term grazing abandonment are not precisely known (Saatkamp et al. 2018). There is also a lack of studies analyzing the interaction of fire and grazing in Mediterranean grasslands. Annual fire may increase the productivity of ungrazed sites but not of recently grazed sites (Buis et al. 2009). The fire-by-grazing interaction was also found to depend on the annuals–perennials ratio of plant communities since annual species are usually less competitive in grazed habitats but may be favored by fire (Noy-Meir 1995).

In our study, we analyzed fire and grazing effects in a Mediterranean steppe (Thero-Brachypodietea, San Miguel 2008) dominated by the resprouter grass *Brachypodium retusum*. This steppe community is under decline and protected by the EU habitats directive (San Miguel 2008). *B. retusum* is still widespread in the Mediterranean region but also suffers from the loss of this habitat. In ecological restoration, *B. retusum* shows poor re-establishment (Coiffait-Gombault et al. 2012; Vidaller et al. 2018) and it is obvious that restoration remains incomplete if the dominant species of pristine steppes is lacking. Thus, a better knowledge on the ecology of the species and effects of major management factors is needed to better conserve these plant communities. Fire and grazing are two key environmental/management factors that have largely decreased (fire protection, land abandonment) potentially explaining the decline of Mediterranean steppes (San Miguel 2008).

Previous studies have demonstrated that *B. retusum* benefits from fire (Caturla et al. 2000; De Luis et al. 2004; Cassagne et al. 2011). Although wildfires most frequently occur in undergrazed or abandoned areas, prescribed burning has also been frequently applied to improve forage quality in traditionally grazed areas (Stouff 1986; San Miguel 2008). The dense below-ground rhizome network of *B. retusum* allows a fast post-fire regrowth (Caturla et al. 2000; De Luis et al. 2004). Fire may increase reproductive stalk number (Caturla et al. 2000) but it is unknown whether fire also promotes seed set and viability. We further do not know whether fire season influences population and community dynamics of Mediterranean steppes and their dominant species. Wildfires mainly occur during the dry and hot summer period whereas shepherds burned grasslands at the end of winter (pastoral fires) to remove standing litter and favor resprouting (Stouff 1986). Both fire types may also promote annual species by providing favorable conditions for autumn and spring germination.

Similarly, grazing was found to have a positive effect on the growth of *B. retusum* (Coiffait-Gombault et al. 2012) and on the diversity of its associated plant community (Saatkamp et al. 2018). However, grazing may reduce sexual reproduction due to vegetative biomass and/or inflorescence removal (Vidaller et al. 2018). We were particularly interested in combined grazing and fire effects on the dominant species *Brachypodium retusum* and on its associated plant community. We hypothesize that both fire and grazing favor *B. retusum* relative to other species of the plant community. We further hypothesize that both perennial resprouters and annual species benefit from fire and grazing, thereby increasing biodiversity and changing plant species composition. Our last hypothesis is that fire effects are stronger in ungrazed situations and that prescribed burning may be an efficient strategy to restore steppe communities in undergrazed or abandoned grasslands. We set up two experiments to specifically address the following research questions:

- (1) What are the effects of fire and grazing on the vegetative growth and sexual reproduction of *B. retusum* compared with co-occurring species cover of the Mediterranean steppe?**
- (2) How do fire and grazing affect plant species composition and diversity?**
- (3) Do fire effects depend on season and can fire help to maintain diversity of grazed or abandoned grasslands?**

Methods

Study area

The study was set up in the “Crau” Mediterranean grassland (“steppe”, EUNIS habitat E1.311, Natura 2000 habitat type 6220) in South-Eastern France. The study region is characterized by hot/dry summers and mild/humid winters with an annual precipitation of 517 mm (1980-2010) and a mean temperature of 15.3 °C (Meteo-France, meteorological station of Saint-Martin-de-Crau, Appendix S1). Summer drought is common but the summer of 2016 was even drier than average (55 mm instead of 100 mm on average). The soils of the study area are decalcified Red Mediterranean Soils (Haplic cambisol) with a mean pH of 6.8. The vegetation has been shaped by a long history of grazing back to the Neolithic (Henry et al. 2010) and by former winter fires (Stouff 1986; Chalvet 2016). The steppe is still annually grazed by itinerant sheep during spring. Due to risks for inhabitants and land users, winter fires have not been used as a management strategy since the end of the 19th century (Chalvet 2016). However, wildfires still occur during summer, in particular close to roads and field tracks. No fire was observed at the study site since 1973 (Prométhée fire database, 2018).

The grassland is species-rich, dominated by annual plants and the perennial grass *Brachypodium retusum* (Buisson & Dutoit 2006, Appendix S2). In long-term grazing enclosures (since 2001), 40% of initially occurring grassland species disappeared and have been replaced by high-growing herbaceous ruderal species (Saatkamp et al. 2018).

The study species, *Brachypodium retusum* (Pers.) P. Beauv., (ramose false brome, Poaceae), is a perennial grass species. Its rhizomes form a dense network close to the soil surface allowing resprouting after destruction of aboveground organs by fire or grazing (Caturla et al 2000). The species shows tillering at the stem base but also lateral branching at upper stem parts. Clonal growth is common but slow. *B. retusum* usually flowers from April to July but grazed or cut plants may also flower later in the season. At grazed sites, the species is highly dominant. Long-term grazing enclosure results in an increase of *B. retusum* height and the development of others competitive grass perennial species such as *Dactylis glomerata* (Saatkamp et al., 2018).

Design

Two experiments testing the effect of late-winter fires (= winter fires) simulating pastoral fires, summer wildfires (= summer fires) and sheep grazing were set up in March 2016 and run for two seasons. The winter fire treatment was applied once in March 2016 and the summer fire treatment once in July 2016. In the first experiment, fire treatments were applied to the traditionally grazed steppe (Appendix S3, A). In the second experiment, fire treatments were applied to long-term grazing enclosures (abandoned grassland, Appendix S3, B).

Effect of fire and grazing in a traditionally managed steppe area (experiment 1)

The experiment was set up at two different sites comprising three blocks each (Négreiron 43°32'18.28"N / 4°49'0.75"E, Collongue 43°31'37.55"N / 4°49'55.82"E) to reflect heterogeneity in grazing but the site effect was finally pooled into block for statistical analysis in order to increase parsimony.

Blocks were split into two parts (half-blocks) of which one was fenced to prevent grazing.

The three fire treatments (summer fire, winter fire, no fire) were applied to three plots of 4 m² within each of the twelve half-blocks (split-plot design) in order to test combined effects of fire and grazing (36 plots in total). The distance between plots within half-blocks was 1 m, between half-blocks within blocks 50 m and between blocks at least 200 m. The position of fire treatments was randomized within half-blocks and that of grazing treatment was randomized within blocks.

A thermal weeder was used to burn plots to simulate winter fire and summer wildfire. Thermal weeding was achieved using a portable device with a gas cylinder and a ramp comprising four nozzles for flame weeding (Appendix S4). Due to fast fire spread during summer, we removed the device once the vegetation was burning. We stopped the fire manually when flames arrived at the plot border. To prevent grazing, the control half-blocks were fenced with stretched, non-electrified nets (1 m high). The other half-blocks allowed free sheep grazing during the grazing period from April to June. The mean grazing intensity was of 646 sheep*ha⁻¹*season⁻¹ at Négreiron site and 328 sheep* ha⁻¹*season⁻¹ at Collongue site.

In July 2016, the aboveground vegetation was harvested in two plots of 50*50 cm in each grazed and ungrazed half-block to measure biomass removal by sheep. Samples were dried at 80°C to a constant biomass and weighed afterwards. Grazing reduced aboveground biomass from $70 \pm 11 \text{ g/m}^2$ in ungrazed plots to $50 \pm 9 \text{ g/m}^2$ at the end of the grazing period.

Effect of fire in long-term grazing exclosures (experiment 2)

The same fire treatments were established in long-term grazing exclosures. The aboveground vegetation was harvested as described above. Standing biomass ($110 \text{ g/m}^2 \pm 16$) was twice as high as in traditionally grazed steppe area. The design included three plots per block comprising the three fire treatments and six replicate blocks (18 plots in total). Corresponding to the first experiment, three blocks were set up at the Négreiron site fenced in August 2001 (3 ha) and three blocks at the Collongue site fenced in June 1999 (2.9 ha). The distance between blocks and to exclosure fences was at least 50 m.

Data collection

B. retusum survey

The cover percentage of the species was estimated at six dates (May, July, October 2016 and February, May, July 2017) including two growing seasons. At the same time, total vegetation cover was estimated. Cover was measured as the vertical projection of all aboveground organs. Visual cover estimation is as reliable as the more objective pin-point or point-intercept method and allows an analysis of larger areas (Symstad 2008; Damgaard 2014). Cover values were always estimated within one day by the same person to avoid observer bias. *B. retusum* cover was divided by total vegetation cover to obtain weighted cover. The cover of May 2016 and 2017 was finally used for analyses representing peak aboveground biomass in unburned plots before aboveground organs partially die due to summer drought.

The regeneration of *B. retusum* was measured by comparing May 2017 and October 2016 cover. In order to evaluate sexual reproduction, the number of inflorescences was counted in each plot during flowering peak in July 2016 and 2017. At the same time, twenty inflorescences per plot were harvested to count seeds. If number of inflorescences per plot was lower than twenty all inflorescences were sampled. Seeds were prepared by crushing the inflorescences in a plastic tube with glass beads using a vortex, then spreading the separated spikelets on an overhead projector in order to check whether spikelets are filled. Empty seeds or spikelets were removed from seed counts. Seeds were stored at room temperature and germinated in peat plugs (4 x 4 cm). Four seeds of each experimental plot (block x treatment combination) were sown to one plug. The plug trays were placed in a growth chamber under optimum germination conditions (temperature 15/20 °C, 12/12h, night/day, Vidaller et al. (2018)) and watered regularly. Coleoptile emergence was used as a proxy of germination and was recorded every 2-3 days for seven weeks.

Vegetation survey

Species composition of the associated plant community was analyzed in May 2016 and May 2017 during the peak of flowering. The cover of all vascular plant species was estimated using a modified Braun-Blanquet scale (Braun-Blanquet 1932: + = one individual per plot, 1 < 5% cover, 2: 5 - 25 %, 3: 26 - 50 %, 4: 51 - 75 %, 5:> 75%). Contrary to the *B. retusum* survey, the sum of individual species cover may be higher than 100%.

Data analysis

In the combined fire and grazing experiment, a split-plot ANOVA was performed to analyze fire treatment and grazing effects on individual response variables (individual species cover, *B. retusum* inflorescence, seed number and germination rate, species richness, diversity

indices). Grazing (whole-plot factor) was tested against the block x grazing interaction. Fire (split-plot factor), the fire x grazing interaction and block were tested against the model residuals. In the long-term enclosure experiment, a reduced model was applied only including the fire treatment and block. When necessary $\log_{10}(x+1)$ and square root transformations were used to comply with assumptions of linear models (normality, homoscedasticity). A Tukey HSD posthoc test was calculated to analyze differences between treatment levels if treatment main effects or interactions were significant.

In order to analyze plant community data, Braun-Blanquet scores were transformed into percentage cover: + = 0.5%; 1 = 2.5%; 2 = 15.0%; 3 = 37.5%; 4 = 62.5%; 5 = 87.5%. Species richness (S), evenness (J') and Bray-Curtis index (BC) were calculated using vegan v2.4-2 package. J' evenness was calculated as $H'/\ln(S)$, with H' being the Shannon diversity index (Pielou 1969). Species composition was compared using NMDS (Non-Metric Multidimensional Scaling, metaMDS function) based on the similarity index of Bray-Curtis (Borcard et al. 2011) in order illustrate changes in plant species composition as well as the species most correlated with each treatment. NMDS analyses were run using 30 random starting configurations in 1 to 15 dimensions. The run with the lowest stress value was finally applied. A permutation multivariate analysis of variance (PERMANOVA, Anderson 2001) with 9999 permutations was used to test whether the community composition was significantly different between the fire and grazing treatments. A pairwise posthoc test with Bonferroni adjustment was calculated to analyze differences between levels of the fire treatment. All statistical analyses were run in R (R, version 3.3.1, R Development Core Team (2013)) including multivariate analyses using the vegan package.

Results

B. retusum survey

In the combined fire and grazing experiment, fire significantly reduced *B. retusum* cover in the following two years (Tab. 1, Appendix S5). Several months after fire treatments (October 2016), even cover relative to neighboring plants (weighted cover) was lower (Tab.1). Accordingly, inflorescence and seed production were significantly reduced but a higher germination rate was found in seeds produced in winter fire plots compared with control plots (Tab.1). In the second post-fire year (2017), the fire main effect on weighted cover of *B. retusum* was not significant any more (Fig. 1A, Tab.1). *B. retusum* showed a rapid regeneration of its vegetative cover in the burned plots (Fig. 1C, Tab.1) compared with control plots in which its cover decreased from 2016 to 2017. At the end of the survey period in July 2017, inflorescence number was higher in burned plots but differences were only significant between summer fire treatment and control (Fig. 2A, Tab.1). We also found a significantly higher seed number per inflorescence in summer and winter fire plots (Fig. 2C, Tab.1) whereas germination rate was no longer different between seeds from the different treatments.

The effect of grazing was not significant for any of these variables (Tab. 1). Only a significant fire x grazing interaction occurred in 2017 for *B. retusum* cover. Grazing reduced absolute and weighted cover in unburned controls.

In the long-term exclosures, fire effects were similar to those in the combined grazing and fire experiment (Tab. 1). Cover (weighted and non-weighted), inflorescence number and seed number per inflorescence decreased in the beginning of the first year, but recovered rapidly in the second post-fire year (Tab. 1, Fig. 1B, 1D). Although absolute *B. retusum* cover was still

lower in 2017, relative (weighted) cover was not different any more to the control whereas inflorescence number was even higher in the summer fire treatment compared with the unburned control (marginally significant). Due to the low seed set in all treatments, differences in seed number per inflorescence were not significant.

Table 1: ANOVA F-values and significance level for effects of fire and grazing on *Brachypodium retusum* in the two experiments: cover and weighted cover adjusted for total vegetation cover (both May), post-fire regeneration (cover difference between October 2016 and May 2017), inflorescence number, seed number per inflorescence (both July) and germination rate. F×G= fire x grazing interaction. . $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS not significant. Factor effect: ↓:decrease; ↑: increase.

		<i>df</i>	Cover (%)	Weighted cover (%)	Regeneration (%)	Inflorescences (number.4m ⁻²)	Seeds (number.inflor ⁻¹)	Germination (%)
A. Combined fire and grazing experiment								
2016	Fire	1.10	469.29 *** ↓	365.43 *** ↓		18.99 *** ↓	42.44 *** ↓	4.06 * ↑
	Grazing	1.10	0.39 NS	1.43 NS		0.18 NS	0.56 NS	0.01 NS
	F×G	1.10	0.13 NS	0.13 NS		0.09 NS	1.59 NS	0.03 NS
2017	Fire	2.20	12.35 *** ↓	2.21 NS	143.04 *** ↑	11.48 *** ↑	5.86 ** ↑	1.25 NS
	Grazing	1.10	1.62 NS	0.58 NS	1.12 NS	0.01 NS	0.24 NS	0.35 NS
	F×G	2.20	3.64 *	3.62 *	0.65 NS	0.90 S	0.18 NS	0.31 NS
B. Fire experiment in long-term exclosures								
2016	Fire	1.10	311.00 *** ↓	115.60 *** ↓		1.10 NS	1.08 NS	0.87 NS
2017	Fire	2.20	0.66 NS	1.85 NS	72.94 *** ↑	3.76 . ↑	2.27 NS	-

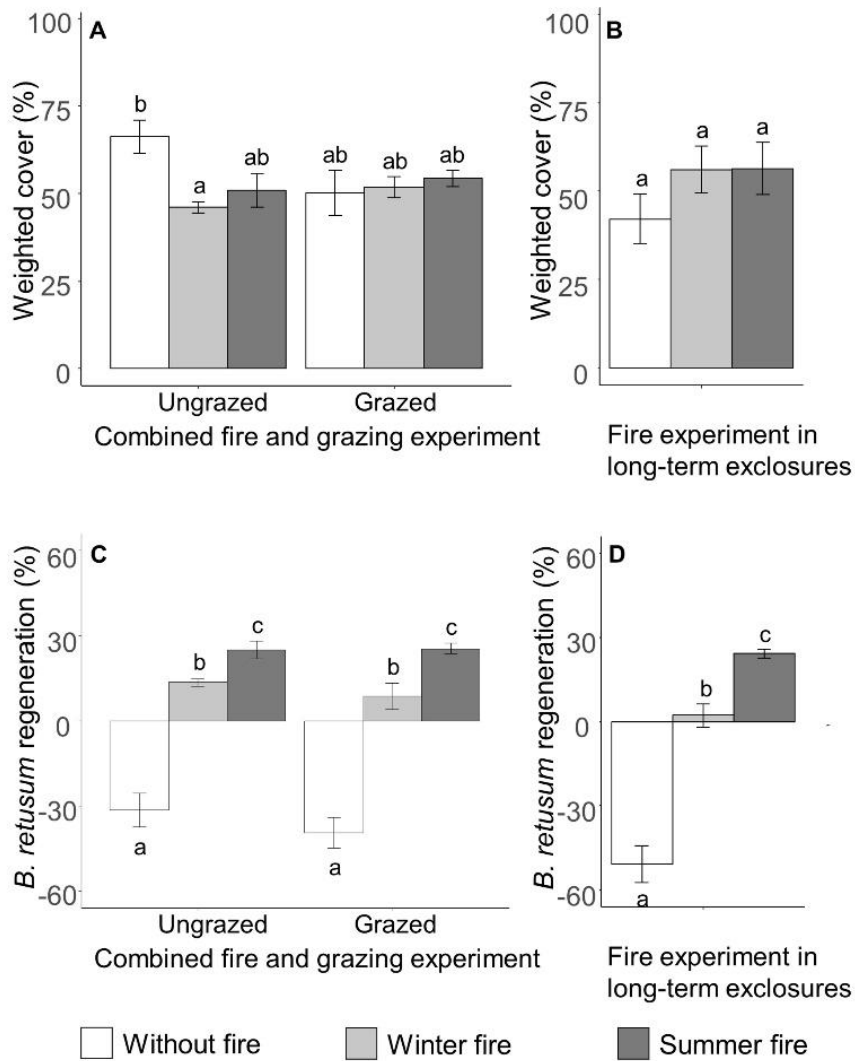


Figure 1: Effects of fire and grazing on vegetative growth of *B. retusum* in the combined fire and grazing experiment (left) and the fire experiment in long-term exclosures (right). A, B: weighted cover one year after fire treatments (May 2017, mean \pm SE); C, D: Post-fire regeneration of cover (mean difference between October 2016 and May 2017, \pm SE).

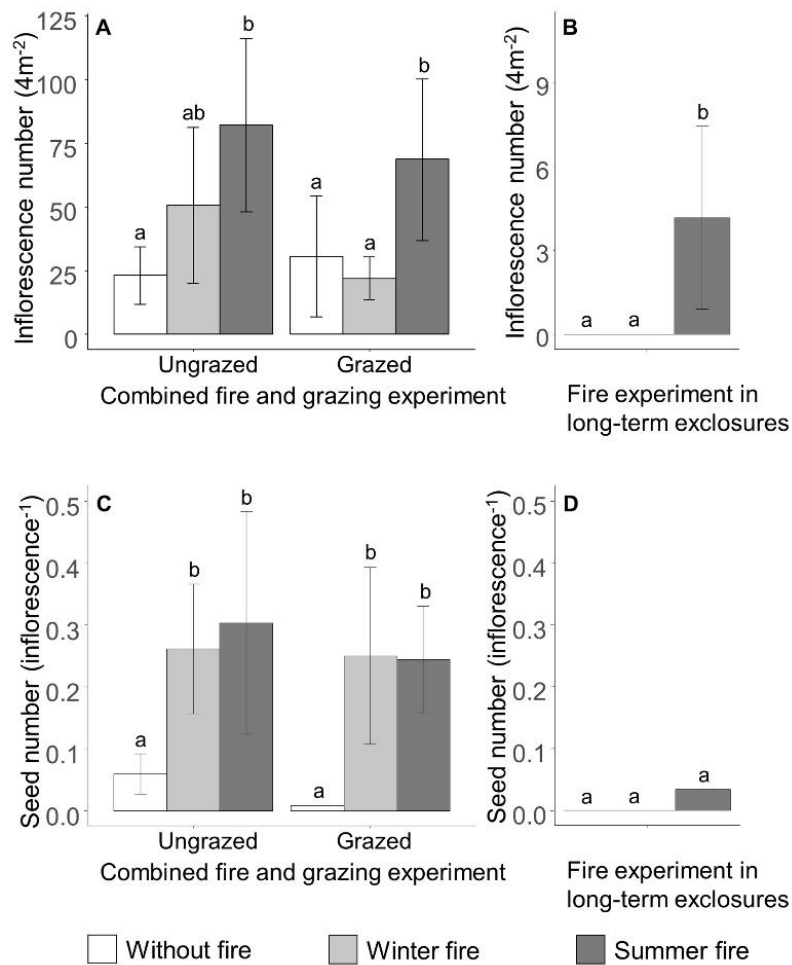


Figure 2: Effects of fire and grazing on the reproduction of *B. retusum* (mean \pm SE) in the combined fire and grazing experiment (left) and the fire experiment in long-term exclosures (right) in the second post-fire year (July 2017). A, B: Inflorescence number; C, D: Seed number per inflorescence.

Plant community

In the combined fire and grazing experiment, fire significantly reduced species richness three months after treatments in 2016 but one year later, in 2017, species richness was significantly higher in burned plots than in unburned controls (Tab. 2, Fig. 4). The second year differences in species richness were significant between summer fire and control plots whereas winter fire species richness was not different from the other treatments. In both years, evenness and Bray

Curtis dissimilarity were significantly higher in the fire treatments. Regardless of the year, grazing effect and the fire x grazing interaction were not significant.

In the long-term exclosures, species richness was not significantly affected three months after fire treatment (May 2016) but in the second year, a significant increase was measured between summer fire and control. As in the first experiment, evenness (marginally) and Bray-Curtis dissimilarity were significantly higher in burned plots compared to the controls. However, the fire effect on Bray-Curtis dissimilarity was not significant any more in the second post-fire year.

Table 2: ANOVA *F*-values, significance levels for effects of fire and grazing on species richness (4m²), evenness and Bray-Curtis dissimilarity in the two experiments. F×G= fire x grazing interaction. . *P* < 0.1, * *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001, NS not significant. Factor effect: ↓: decrease; ↑: increase.

		<i>df</i>	Species-Richness	Evenness	Bray-Curtis
A. Combined fire and grazing experiment					
2016	Fire	1.10	4.97 * ↓	12.26 ** ↑	24.14 *** ↑
	Grazing	1.10	0.45 NS	0.01 NS	0.45 NS
	F×G	1.10	0.01 NS	3.12 NS	0.16 NS
2017	Fire	2.20	4.18 * ↑	14.00 *** ↑	3.32 * ↑
	Grazing	2.20	0.03 NS	0.00 NS	0.04 NS
	F×G	2.20	0.42 NS	0.31 NS	0.40 NS
B. Fire experiment in long-term exclosures					
2016	Fire	1.10	3.05 NS	4.82 . ↑	32.06 ** ↑
2017	Fire	2.10	5.03 * ↑	3.95 * ↑	1.45 NS

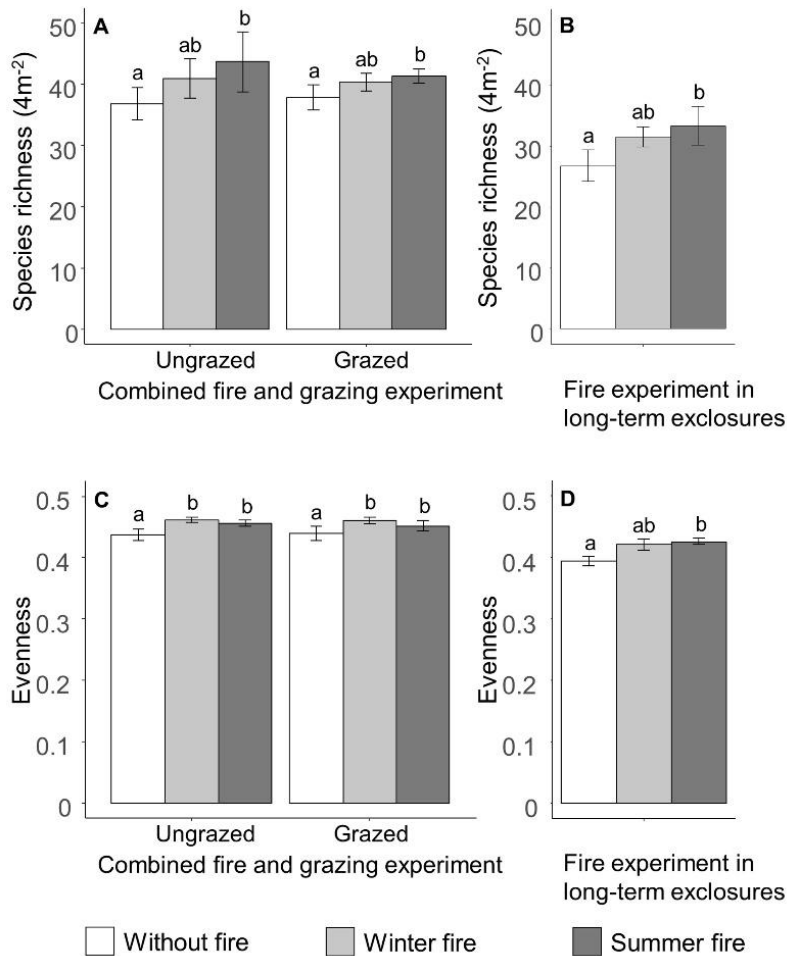


Figure 3: Effects of fire and grazing on the plant community (mean \pm SE) one year after fire treatments (May 2017) in the combined fire and grazing experiment (left) and the fire experiment in long-term exclosures (right). A, B species richness; C, D: evenness.

In 2017, one year after fire treatments, NMDS ordination showed a clear separation between the plant community of the combined fire and grazing experiment in the steppe area and the fire experiment in long-term exclosures (Fig. 4). Along axis 1 of the NMDS, *B. retusum* and ruderal species such as *Sonchus oleraceus*, *Avena sterilis* and *Avena barbata* characterize the vegetation of the long-term exclosures whereas short annual and stress-tolerant species such as *Polycarpon tetraphyllum*, *Evax pygmaea*, *Euphorbia falcata*, *Galium murale* are more abundant in the traditionally managed steppe. In the long-term exclosure, fire changed the plant community more than in the steppe (Fig. 4). The burned long-term exclosures were closer to the traditionally managed steppe than the unburned controls. The PERMANOVA testing differences in species composition between treatments showed a significant effect of

fire in the combined fire and grazing experiment ($F_{2,35}=2.865^*$) and in long-term exclosures (marginally significant, $F_{2,17}=1.78^{(*)}$). In the combined fire and grazing experiment, the effect of summer fire was stronger than that of winter fire whereas no such differences occurred in the long-term exclosures (Appendix S6). The effect of grazing and the grazing x fire interaction were not significant (grazing: $F_{1,35}=1.512^{NS}$, fire x grazing: $F_{2,35}=0.212^{NS}$).

In both experiments, the cover of annual species such as *Medicago monspeliaca*, *Euphorbia falcata*, and *Bromus rubens* as well as the perennial grass *Poa bulbosa* particularly benefitted from fire treatments (Appendix S7). In particular, summer fire had a strong positive effect on the cover of *M. monspeliaca* and *B. rubens* whereas *E. falcata* and *P. bulbosa* also benefitted from winter fire. The grazing effect was not significant for these species.

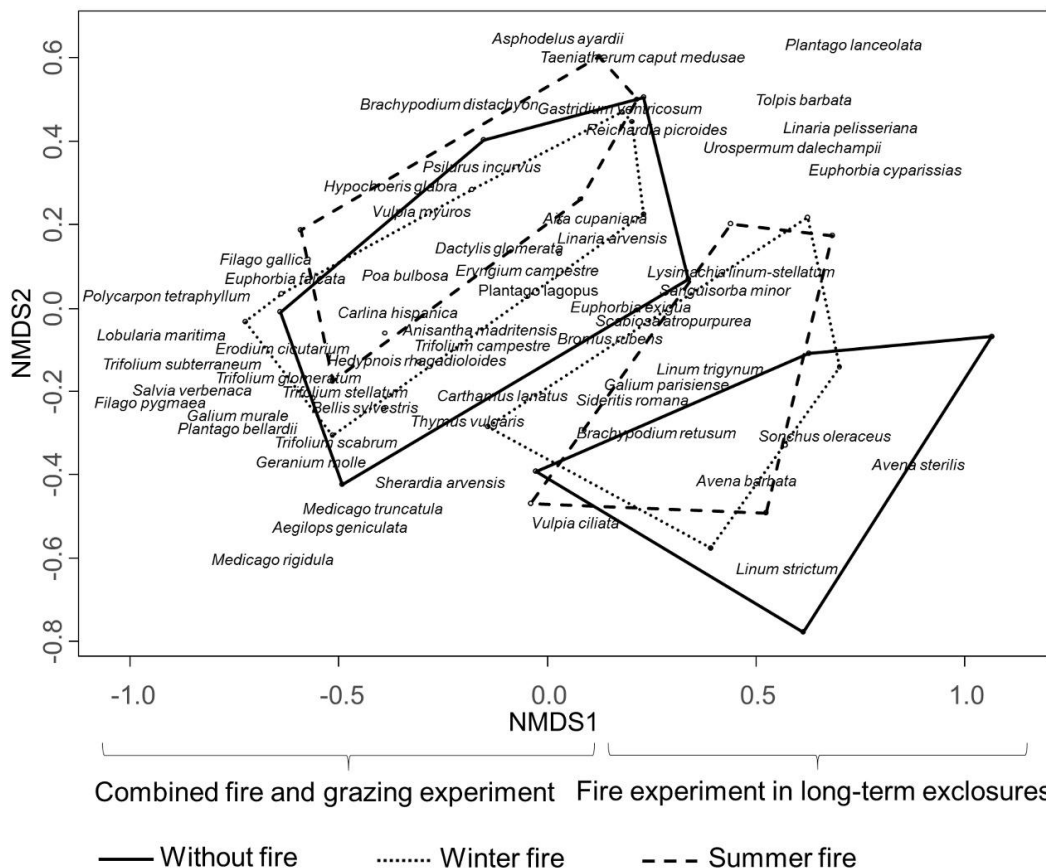


Figure 4: Effect of fire on plant species composition in the combined fire and grazing experiment set up in traditionally managed steppe and in the fire experiment set up in long-

term exclosures using NMDS on May 2017 data. Polygons indicate the position of the outmost plots in each treatment (NMDS stress: 0.147, nine dimensions).

Discussion

Across the tested populations of the dominant plant species *Brachypodium retusum* and the associated plant community, the fire effect was much stronger than the grazing effect. Grazing reduced aboveground biomass by 40% but did not significantly influence the majority of measured *B. retusum* traits and community parameters. Fire had a similar effect in the combined fire and grazing experiment at traditionally managed sites and in the long-term exclosures allowing a fast recovery of typical steppe species such as *B. retusum*.

Effects of fire and grazing on *B. retusum*

B. retusum can survive fire by resprouting from rhizomes favored by axillary buds (Clarke et al. 2013). Adapted plant species such as rhizomatous resprouters may even benefit, since fire increases resource availability (Neary et al. 1999), stimulates re-growth from below-ground buds (Fidelis et al. 2014) and opens the canopy reducing competition for light, water and nutrients (Everson & Everson 1987). In our study, *B. retusum* cover increased rapidly after fire whereas controls showed a decrease in cover due to the summer drought in 2016. In particular, reduced competition for water resulting from biomass removal was likely the reason for the better post-fire regeneration (Everson & Everson 1987). However, weighted cover of *Brachypodium retusum* relative to total vegetation cover was in the first season significantly lower in fire treatments than in the control indicating that post-fire regeneration was slower than in other species of the plant community. Thus, our results do not confirm studies in Eastern Spain showing a faster recovery of *B. retusum* compared to accompanying

species resulting in a rapid increase of weighted *B. retusum* cover (Caturla et al. 2000, De Luis et al. 2004).

Regeneration was faster in the summer than in the winter fire treatment suggesting that *B. retusum* is better adapted to natural summer fire. The period of fire management by shepherd may not have been long enough for an evolutionary response whereas summer fire disturbance is much older allowing adaptive processes. The stronger summer fire effect on *B. retusum* regeneration may also be the result of a higher standing biomass and a lower water content (dry leaves and stems) corresponding to higher fire temperatures and biomass loss compared with winter fire (Hobbs 1991; Trabaud 1979). Nevertheless, the traditional winter fire management is already well-known to improve pasture quality and vigor by allowing the regeneration of *B. retusum* aboveground biomass (Stouff 1986).

In the long-term exclosures, fire effects on *B. retusum* cover were similar to those of the combined grazing and fire experiment in the traditionally managed steppe. However, the species reached cover values of the unburned control already in the second post-fire year indicating a faster recovery. Long-term exclosure from grazing results in a strong biomass increase mainly due to the growth of perennial grass species (Bond & Parr 2010). Abandonment of grazing also increases litter biomass, C:N ratios and decreases soil nutrient content (Peco et al. 2012; Saatkamp et al. 2018). Thus, fire temperatures are higher and therefore fire has a stronger effect on plant species than in grazed systems with lower living and dead biomass (Hobbs et al. 1991). The high recovery of *B. retusum* in our exclosures suggests that wildfire or prescribed burning may help to maintain the typical species composition and community structure in long-term absence of grazing.

In addition to vegetative resprouting, fire increased allocation of resources to reproductive organs in the second post-fire year favoring seed production and quality. The production of inflorescences was significantly higher in both fire treatments, but in particular after summer fire. Fire-stimulated flowering is already known for several species in the Mediterranean regions of Australasia and South Africa with peak flowering occurring five to eighteen months after fire (Lamont & Downes 2011, Pyke 2017). Flowering may be triggered by fire-specific cues such as chemical compounds of smoke and ash or scorching of below-ground storage organs (Keeley 1993; Tyler & Borchert 2003) but also by a fire-induced increase in light and temperature (Fidelis & Blanco 2014). As with resprouting, inflorescence production may be favored by a higher resource availability due to reduced competition and higher nutrient or water availability (Coates & Duncan 2009).

Fire also increased the seed set measured as seed production per inflorescence in the second post-fire year whereas high fire damage to photosynthetically active tissues (leaves, stems) reduced seed set in the first year. A higher post-fire seed set in the following years was also measured for two Australian perennials (Lamont & Runciman 1993). The effect on ex-situ germination was less strong being only positive in the same year of the fire treatments. In the second season, when the increase in inflorescence production and seed set occurred, differences in germination were not significant any more. Germination is an important trait under selection for adaptation to fire (Keeley et al. 2012). Many species from a wide range of taxa show a rapid and increased germination after fire (Naveh 1975; González-Rabanal et al. 1994). However, *B. retusum* seeds were produced after fire excluding a direct exposure to fire cues. Our germination experiment was set up in a growth chamber not taking into account modified conditions in burned plots (nutrient availability, destruction of organic matter,

presence of ashes, etc.). Moreover, in some species of fire-prone ecosystems, there is no evidence that fire triggers germination (Le Stradic et al. 2015).

The grazing main effect on vegetative growth and on reproduction was neither significant in the first nor in the second season. Although statistical power to test grazing as the whole-plot factor of the split-plot design was lower than for fire as split-plot factor the small differences between grazing treatment means confirm that grazing impact is much less strong than fire impact. *B. retusum* tolerates the short-term absence of grazing even though grazing is an important factor in maintaining population cover (Coiffait-Gombault et al. 2012). However, a significant fire x grazing interaction was measured during the second season with plant cover being lower only in unburned plots. The result confirmed our hypothesis that fire impact is stronger in ungrazed situations. Higher fire temperatures due to higher litter biomass already cited for abandoned grasslands (Peco et al. 2012, Hobbs 1991) may have increased the impact of fire in ungrazed control plots. However, this significant interaction was also visible in winter fire plots that were burned before grazing. This effect could be explained by the behavior of sheep avoiding recently burned *B. retusum* plants, thus increasing the positive effect of fire by reducing post-fire biomass consumption.

Effects of fire and grazing on the plant community

In the combined fire and grazing experiment, fire reduced species richness three months after treatments but in the second year, the fire effect was already strongly positive. Fire also increased evenness by removing biomass of the dominant *B. retusum* and community dissimilarity. Infrequent and/or irregular fire disturbance may result in species loss and community composition changes (Laurance 2003). However, in fire-prone ecosystems, such disturbance maintains species richness and community structure (Bond et al. 2005, Fidelis et

al. 2012). Accordingly, fire suppression may considerably reduce plant diversity of fire-prone systems (Sparks et al. 1998, Leach & Givnish 1996).

Again, the effect of summer fire was stronger than that of winter fire. Fire season was found to affect plant communities. Fire during the growing season may, for example, increase plant diversity, in particular the number of annuals and cool-season perennials whereas no such effect was observed for dormant season (fall, spring) fire (Biondini et al. 1989; Howe 1994). The growing season of *B. retusum* and most other species of the community starts in late winter and lasts until July corresponding to the two fire dates. The stronger summer fire effect may be the result of a higher standing biomass and a lower water content (dry leaves and stems) corresponding to higher fire temperatures and biomass loss (Hobbs 1991; Trabaud 1979).

The fire effect on long-term exclosures was similar to that on traditionally managed steppe plots. Fire generally increased diversity in the second season. Contrary to the traditionally managed steppe, there was no decrease in species richness confirming the particularly beneficial effect of fire in abandoned grassland for conserving species-rich dry grasslands (Bond & Parr 2010). Plant species composition of burned long-term exclosures was closer to the traditionally managed steppe than that of the unburned control.

In both experiments and systems, differences in species composition were mainly explained by an increase in native annual seeder species whereas fire reduced the cover of resprouter grasses in the first post-fire year. Similar to the results on the dominant species *B. retusum*, fire-induced community changes do not correspond to those of earlier studies in Spanish *B. retusum* grasslands (Caturla et al. 2000, De Luis et al. 2004). The La Crau steppe is a more

open and less nutrient-rich grassland type than the Spanish field sites allowing the development of a higher diversity of annual species (Buisson & Dutoit 2006). Apart from resprouting, seedling recruitment is therefore a second successful strategy of post-fire regeneration as it is already known for other dry and nutrient-poor grasslands (Valone & Kelt 1999). Although the short study period does not allow conclusions on the duration of facilitative effects, we were able to demonstrate that fire helps annual species to develop. Further research is needed to identify the optimum frequency of fire disturbance to maintain such positive effects on plant diversity.

Grazing was expected to have positive but less strong effects on plant diversity of the steppe community. Such positive effects are mediated by sward opening, biomass reduction and soil surface disturbance (Coiffait-Gombault et al. 2012; Saatkamp et al. 2018). In our study, the effects of grazing and the interaction between fire and grazing were not significant. Again, the small differences between treatment means confirmed that grazing has a much smaller effect than fire in spite of lower statistical power for testing whole-plot effects. The hypothesis that fire effects are stronger in ungrazed situation was not supported at community level. As already demonstrated for the dominant species *B. retusum*, the plant community tolerated the short-term absence of grazing without species loss or differences in diversity indices. These findings confirmed results of a previous study in the same system showing only small changes in the first five years after grazing abandonment (Saatkamp et al. 2018).

Conclusions

We showed a concomitant positive effect of fire on the reproduction of the dominant grass *B. retusum* and the species diversity of its associated plant community. Contrary to our expectations, fire did not favor perennial resprouters such as *B. retusum* over annuals

confirming that both strategies resprouting from below-ground organs and seedling recruitment are successful in short term post-fire vegetation recovery. Short-term grazing exclusion had only small effects on *B. retusum* and associated plant community. However, the long-term exclosures abandoned 17 years before our experiments showed large differences to the traditionally managed steppe such as a lower *B. retusum* reproduction and a lower plant diversity. In such abandoned or undergrazed systems, fire has a particularly positive effect on *B. retusum* performance and plant diversity and may thus compensate for long-term grazing absence to conserve this unique Mediterranean grassland ecosystem.

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Supporting Information

Appendix S1: Climate diagram of Saint-Martin de Crau.

Appendix S2: Full list of the 138 species found in the study zone.

Appendix S3: Design of the combined fire and grazing experiment and the fire experiment in long-term exclosures.

Appendix S4: Thermal weeder device.

Appendix S5: Effects of fire and grazing treatments on plant species most benefitting from fire (mean \pm SE) in the combined fire and grazing experiment (A) and the fire experiment in long-term exclosures (B) one year after fire treatments (May 2017).

Appendix S6: Results of Permutational Multivariate Analysis of Variance (PERMANOVA) contrast pairwise tests between different levels of fire treatment.

Appendix S7: Effects of fire and grazing treatments on plant species most benefitting from fire in the combined fire and grazing experiment and the fire experiment in long-term exclosures.