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RESEARCH ARTICLE

Pyric herbivory in a temperate European wood-pasture system

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Abstract

1. The term *pyric herbivory* was first introduced in 2009, describing how fire shapes herbivory as burned areas attract herbivores and, simultaneously, herbivory shapes fuel load and fire behaviour. Pyric herbivory results in a mosaic of patches with varying levels of herbivory and grazing intensity fire intensity and frequency. The importance of pyric herbivory for ecosystem heterogeneity and biodiversity has been described for North American, Australian and African systems, but the concept remains largely untested in a European context.
2. We introduced fire and herbivory in a full-factorial experiment in a temperate European wood-pasture system to test whether pyric herbivory operates in ways comparable to grassy systems elsewhere in the world. Using camera traps, we observed the behaviour of cattle in burned subplots (49 m^2) compared with unburned subplots. We measured grass height and the proportion of the subplot that burned as variables affecting cattle preference and to assess how grazing affects fire behaviour. We also examined the effect on plant species and life-form composition after six seasons of treatment.
3. Cattle spent more time grazing in burned than in unburned subplots in the most productive paddock, where a larger proportion of the subplot burned. The proportion of a subplot that burned was positively related to pre-fire grass height. Moreover, both grass height and the proportion of subplot burned declined in the burned subplots during the 6-year study period and fire and cattle grazing altered the relative cover of graminoids and shrubs (*Rubus* spp.), with more graminoids in grazed and/or burned subplots and more shrubs in ungrazed subplots at the end of the study.

Mats Niklasson and Marcin Churski contributed as senior authors.

4. *Synthesis and applications*. In our temperate European wood pasture, fire and (cattle) grazing interacted in ways comparable to pyric herbivory in grassy ecosystems elsewhere in the world, especially in the most productive paddock. Fire attracted grazing, with cattle grazing longer on subplots that burned more fully. Grazing also affected fire, where over the course of our experiment cattle grazing reduced grass height and the proportion of a subplot that burned. We suggest that pyric herbivory is an interesting management method to further explore in the European context to address the loss of biodiversity in open ecosystems, particularly in more productive sites.

KEYWORDS
cattle, fire–herbivory interaction, foraging behaviour, grazing preference, patch burn, pyric herbivory, shifting mosaic, temperate ecosystem

1 | INTRODUCTION

In terrestrial ecosystems, fire and herbivory by large mammalian herbivores (hereafter 'herbivores') are two strong drivers of vegetation structure and diversity (Archibald & Hempson, 2016; Bond, 2005; Keeley et al., 2011; Kuijper et al., 2010; Veldman et al., 2015). These two processes can have strong effects when acting separately, but may be even stronger when combined (Fuhlendorf & Engle, 2004). In 2009, Fuhlendorf et al. first introduced the term 'pyric herbivory', which is defined as 'herbivory driven by fire'. The term was used to define the spatiotemporal interaction of fire and herbivory, where herbivores are attracted to newly burned vegetation and, by influencing fuel loads, also affect future fire characteristics (Fuhlendorf et al., 2009). Since then, the term has been used frequently, mostly in studies from North America (e.g. see Allred et al., 2011; Lautenbach et al., 2021; Leverkus et al., 2018; Starns et al., 2020), Australia (Reid et al., 2023) and Africa (Archibald, 2008; Archibald & Hempson, 2016; Donaldson et al., 2018; Eby et al., 2014; Krook et al., 2007). These studies suggest that pyric herbivory creates heterogeneity on much broader scales than when fire and herbivory act as two separate forces (see also Fuhlendorf et al., 2009).

The process of pyric herbivory is driven by the preference of herbivores to graze in recently burned areas (Allred et al., 2011; Archibald et al., 2005; Archibald & Bond, 2004; Donaldson et al., 2018; McGranahan et al., 2014). Recently burned areas attract herbivores because grass that re-sprouts after a fire has an increased nutritional value, leaf-to-stem ratio, live-to-dead-tissue ratio and digestibility of dry matter relative to before the area was burned (Allen et al., 1976; Blair, 1997; Eby et al., 2014; McGinty et al., 1983; Reid et al., 2023; Sittler et al., 2019; Thapa et al., 2022). The attraction of herbivores is often strong in the growing season following a fire event and can remain several years after the fire (Ranglack & Du Toit, 2015). Several studies on different species of herbivores show that they prefer burned areas for foraging. For example, Leverkus et al. (2018) found that feral horses *Equus ferus* were attracted to recently burned open patches in a study in British Columbia, Canada. American bison *Bison bison* prefer to graze in recently burned areas in prairies in the USA (Ranglack & Du Toit, 2015; Raynor et al., 2015; Winter et al., 2015), and both cattle and American bison can spend up to 70% of their time in recently burned patches (Fuhlendorf & Engle, 2004; West et al., 2016). However, the influence of fire on herbivory differs between herbivores of different size, digestive physiology and feeding type (Nieman et al., 2022; Reid et al., 2023). In Africa, studies on herbivore behaviour have found that larger herbivores tend to be less attracted to recently burned areas than smaller herbivores (Eby et al., 2014) and ruminants are more attracted than non-ruminants (Nieman et al., 2021). Nieman et al. (2021) also found that grazers were more likely to prefer recently burned patches than browsers.

The strength of the attraction of herbivores to newly burned patches also depends on vegetation productivity (Augustine & Derner, 2014), which in general is correlated with vegetation height in the absence of herbivores (Savadogo et al., 2007; Stewart et al., 2001). Higher vegetation generally implies higher plant biomass, and thus more fuel for fires (Augustine & Derner, 2014; Fernandes, 2001). Higher plant biomass creates conditions for larger and more intense fires, and larger burned areas attract herbivores more strongly than smaller burned areas (Archibald & Bond, 2004; Augustine & Derner, 2014).

Moreover, herbivores do not only respond to fire but also shape subsequent fire patterns. Increased grazing pressure in newly burned areas reduces fuel accumulation and, thereby, also reduces the likelihood of new fires (Donaldson et al., 2018; Fuhlendorf et al., 2009; Kirkpatrick et al., 2011; Starns et al., 2019; Young et al., 2022). Cattle can reduce the amount of grass by up to 80% in newly burned patches compared with unburned patches (Vermeire et al., 2004). Patches that are not grazed instead accumulate aboveground biomass, which increases with time since fire, thus increasing the likelihood of fires (Fuhlendorf & Engle, 2004).

As a result, spatial patterns of herbivory are shaped by fire and also affect future spatial patterns of fire, while these future fire patterns also shape future herbivory patterns (i.e. pyric herbivory; Fuhlendorf et al., 2009; McGranahan et al., 2012). These highly dynamic herbivore–fire interactions create a shifting mosaic of patches with varying levels of herbivory and fire intensity and frequency (Fuhlendorf & Engle, 2004). As such, pyric herbivory can increase ecosystem heterogeneity (Fuhlendorf & Engle, 2004; McGranahan et al., 2012; Winter et al., 2012). This resulting heterogeneity ultimately increases biodiversity by varying effects on vascular plant species and life-form composition (Collins, 1992; Fuhlendorf & Smeins, 1999; Kirkpatrick et al., 2016; McGlinn & Palmer, 2019). Previous work has shown an increase in graminoids and a decrease in woody species under herbivory and fire (Fuhlendorf & Engle, 2004; Herrera et al., 2021; Pekin et al., 2012; Van Uytvanck & Hoffmann, 2009).

Pyric herbivory has since long been integrated into studies on the ecology and management of grassy ecosystems in many continents, but much less so in Europe and especially in the more temperate parts (Allred et al., 2011), where it has rarely been applied or even examined, despite recent studies showing that herbivory (Bakker et al., 2016; Kuijper et al., 2010; Svenning, 2002; Vera, 2000) and fire (Bond & Keeley, 2005; Feurdean et al., 2018; Niklasson et al., 2010; Svenning, 2002; Zin et al., 2022) have had a great impact on the European vegetation since the early Holocene. Compared with tropical grasslands and savannas, large wild grazing herbivores have been absent from European temperate grasslands since the extinction of Europe's wild cow, the Aurochs *Bos primigenius*, in 1627 and wild horse, the Tarpan *Equus ferus gmelini*, in 1909. Despite their extinction, both fire and herbivory were an important part of the European landscape in the form of grazing livestock (i.e., the domesticated successors of aurochs and tarpan) and prescribed fires until relatively recently (Atlestam, 1942; Högbom, 1934). However, since the late 1900s, livestock are increasingly kept in stables for large parts of the year (Bakker et al., 2016; Ziobro et al., 2016). Similarly, fire exclusion has been a widespread practice in European systems during the last decades and traditional management methods are now abandoned (Bradshaw et al., 2003; Estes et al., 2011).In this paper, we therefore investigate whether the application of fire and herbivory, that is, pyric herbivory, intemperate Europe could work in ways comparable as has been described for grassy ecosystems elsewhere.

In this pioneering experimental study, we tested whether and how cattle grazing and low-intensity fires interact under temperate European conditions and how such pyric herbivory affects vegetation composition and structure in a wood-pasture system in South-western Sweden. To our knowledge, this is the first time the interaction between fire and grazing is experimentally studied in a temperate Northern European ecosystem. We specifically tested the following hypotheses based on what we know from studies on pyric herbivory elsewhere in the world. We hypothesised that: (1) cattle would prefer newly burned patches and (2) show a stronger preference for subplots with larger proportion burned; (3) proportion burned would be related to pre-fire grass height; (4) preferred grazing of newly burned areas would affect the amount of fuel (grass height) for future fires; and finally (5) fire and grazing would alter the plant species and life-form composition and, specifically, increase the cover of hemicryptophytes (graminoids and forbs) and decrease the cover of phanerophytes (shrubs) and chamaeophytes (dwarf shrubs). To test these hypotheses, we conducted an experiment with 24 study plots, where we applied annual low-intensity grass fires and seasonal grazing by cattle. Using camera traps, we recorded the presence and foraging behaviour of cattle. We additionally measured the proportion of a subplot burned and pre-fire grass height. Finally, we inventoried the plant species and life-form composition after six seasons of repeated treatments.

2 | MATERIALS AND METHODS

2.1 | Study area and experimental design

Our experiment was carried out in the Ecopark of Nordens Ark (ENA; Figure 1) on the Swedish west coast (58°27′ N 11°25′ E). The area is located within the temperate climate zone and has mild winters and cool summers (annual mean temperature 8–9°C; standard period 1991–2020, www.smhi.se/kunskapsbanken/klimat/normaler/normalperioden-1991-2020-1.166930, 2023-09-18, Wastenson et al., 2004). ENA has a total area of 400 ha, and until the early 1900s, the area was used as a wood pasture for cattle and sheep, followed by a period of commercial forestry (Ernby, 2010). In 2011 and 2012, about 100 ha of the conifer plantation were harvested and converted back into wood pastures, and since then, the area has been grazed mainly by cattle and to a minor extent by sheep, goats and horses. The region has a history of prescribed annual fires up to the early 1900s before commercial forestry started (Atlestam, 1942) and also natural fires ignited by lightning (Granström, 1993; Högbom, 1934).

In 2015, we established 24 study plots, with six plots in each of four paddocks in ENA (Figure 1). The paddocks differed in terms of initial vegetation biomass, indicated by a difference in the initial grass height before application of the treatments started in 2015. Paddock 1, which had the highest initial grass height (see Figure S1), has the lowest elevation and is located next to a cliff under a plateau, which provides additional rainwater to the grasslands below. Paddocks 2–4 are located on ground that is flatter and generally drier than paddock 1 and had a lower initial grass height (Figure S1). Each of the study plots measured 14 × 14 m and was divided into four subplots of 7 × 7 m. Two of these subplots were fenced with a 2-m high mesh wired fence, protecting them from herbivory. One of the two unfenced subplots was chosen for burning, together with the adjacent fenced subplot. This design resulted in four treatment combinations: no fire and no herbivory (*control*), fire but no herbivory (*fire*), herbivory but no fire (*herbivory*), and both fire and herbivory (*fire + herbivory*) with 24 replicates of each (Figure 1).

The prescribed fire was conducted in April annually until 2020. With a drip torch, we applied a 7-m drip line at surface level on the leeward side of each subplot. If not self-spreading, we ignited five more drip lines across the subplot, 1 m apart.

During the study period, the paddocks were grazed by cattle of the Swedish breeds Rödkulla and Fjällnära and of the English breed Hereford. Groups of cattle, mixed and single breed, with cows and

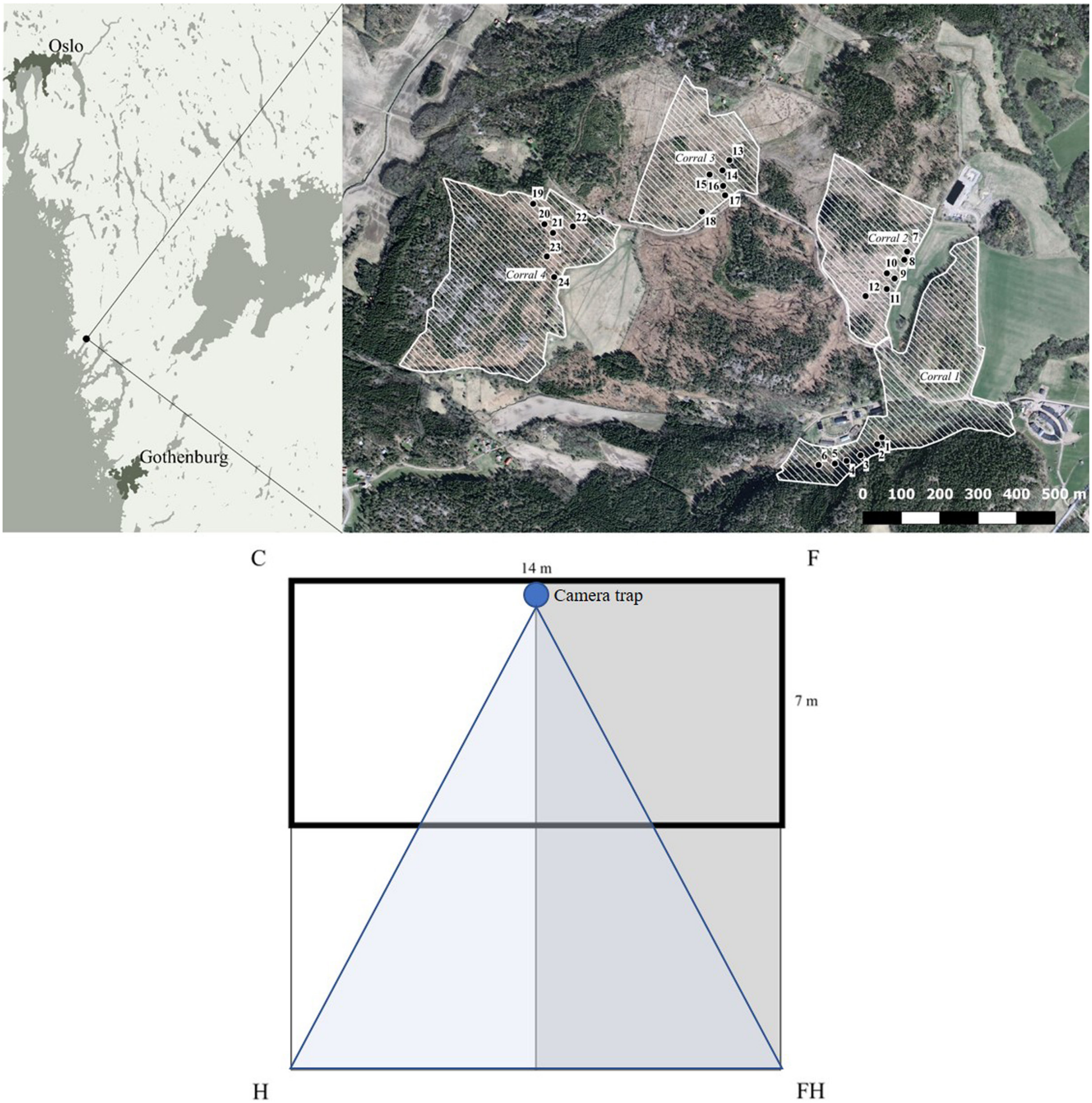

FIGURE 1 Location of study area (ENA) on the Swedish west coast (upper left), position of study plots in the four paddocks in ENA (upper right) and study plot design (lower middle). All 24 study plots were divided into four subplots; FH = *fire + herbivory*, H = *herbivory*, F = *fire* and C = *control*. The thicker line indicates the fenced subplots and the grey colour indicates the subplots exposed to fire. Blue triangle indicates the view of the camera trap, covering ca 75% of the *herbivory* and *fire + herbivory* subplots (figure modified from Amsten et al., 2021).

calves separated from juveniles (1–2 years), were randomly placed in and moved among the four paddocks. The cattle density was documented during the first grazing season and varied among the paddocks from 1 to 2.5 cows/ha (calves were counted as 0.5 individual; Table S1). The grazing period began in May–June and ended in September–October. This grazing regime (grazing period and cattle density) continued until the fall of 2020. Access to drinking water differed among paddocks, with paddock 1 having a natural stream with fresh water at 30–50 m from each plot and paddock 2–4 had water tanks at 50–400 m from the plots.

In each of the 24 plots, we placed a camera trap (Ltl Acorn 5210A). The camera view covered approximately 75% of the grazed parts of the plots (*fire + herbivory* and *herbivory*; Figure 1; Figure S2). Triggered by body heat and movement, the cameras recorded a 1-min video every time they were triggered (for further camera settings, see Table S2). The camera traps were used during the first grazing season of the study (May–October 2015) for seven periods of 2–4 weeks each.

For a more detailed description of the study site and experimental design, see Amsten et al. (2021).

2.2 | Data collection

Visitation and foraging behaviour of the cattle were recorded using videos from the camera traps. Unfortunately, no videos were recorded for one of the plots (no. 23) due to technical failure, so this plot was excluded from the behaviour analysis, leaving 23 replicated plots. All empty videos without animals were removed, and only videos containing animals were further analysed. Due to the low number of videos containing wild ungulates (<10 videos with roe deer and moose, compared with >4000 with cattle), they were not included in the analysis. A photo template was used for each plot with subplot demarcations to determine the position of the cattle (e.g. see Figure S3). The videos were analysed for both visitation (defined as the head located within the subplot boundaries) and grazing (defined as the head positioned close to the ground within the subplot boundaries; e.g. see Figure S2). The total time in seconds spent by cattle on each activity (visitation and grazing) in each subplot (*fire + herbivory* and *herbivory*) per 1-min video was recorded. This process was repeated for each individual animal in those cases where there was more than one individual in a video and was regarded as separate observations. In total, 4091 visitation observations were included in the analysis, of which 2117 also included a grazing event. The observations were averaged to time in seconds per 1-min video and subplot (hereafter 'visiting/grazing time').

As an indicator of fire intensity (Savadogo et al., 2007), we estimated the proportion of the *fire* and *fire + herbivory* subplots that burned (hereafter 'proportion burned'). This was done by visual evaluation right after each burning took place until 2020.

As an indicator of fuel load for fire (Savadogo et al., 2007), we measured the pre-fire grass height in each of the *fire* and *fire + herbivory* subplots before the burning took place, including only graminoids (hereafter 'grass height'). This was done using a folding ruler to measure the height (cm) of the majority (80%) of the grass swards in nine evenly distributed points. This method is further described in Stewart et al. (2001) as the 'direct measurement method'. Grass height values were averaged per subplot and measured until 2020.

Plant species composition was surveyed in September 2020, at the end of the flowering season, after six seasons of fire and herbivory treatment. In two randomly chosen points in each subplot, we put out a 45 × 60 cm quadrant and noted all herbaceous species and their coverage in percentage of the quadrant rate. To evaluate differences in vegetation structure among treatments further, we classified the species found according to the following plant life forms: hemicryptophytes, phanerophytes (large shrubs and trees) and chamaephytes (dwarf shrubs, such as *Vaccinium* spp.). Hemicryptophytes were further subdivided into graminoids, forbs and ferns. Plant life forms were determined based on the TRY database (Kattge et al., 2020). We decided to test for an effect of fire and grazing on these life forms, since studies on pyric herbivory elsewhere in the world show that fire and grazing can strongly alter the relative cover of these life forms, especially in terms of the relative cover of grasses and shrubs (Fuhlendorf & Engle, 2004; Herrera et al., 2021; Pekin et al., 2012; Van Uytvanck & Hoffmann, 2009). In the below text, we refer to the different plant life forms as graminoids, forbs, ferns, shrubs and dwarf shrubs instead of the above categories. Since in our plots *Rubus idaeus* and *Rubus fruticosus* were the only shrub species, we use *Rubus* spp. as the name for that life form.

No ethics or field approval was required for this study.

2.3 | Data analysis

For all statistical analyses, we used the R 4.1.2. program (R Foundation for Statistical Computing, Vienna). For all linear mixed-effects models (LMM), we used the 'lmer' function in the 'lmerTest' package (Kuznetsova et al., 2018). For generalised mixed-effects models (GLMM), we used the 'glmmTMB' function in the 'glmmTMB' package (Brooks et al., 2023) with a beta distribution. For the Permutational Multivariate Analysis of Variance (perMANOVA), we used the 'adonis2' function in the 'vegan' package (Oksanen et al., 2022), which was based on the Bray–Curtis dissimilarity and ran with 9999 permutations. For multiple comparisons, we performed Tukey's post hoc tests using the 'emmeans' function in the 'emmeans' package (Lenth et al., 2018). Paddock was used as random variable, except when paddock was used as explanatory variable; then, plot ID was used as random variable (for further details, see Table S3).

We checked whether there was a difference in initial grass height between the four treatment combinations before the start of our experiment, using an LMM with (logged) grass height per subplot in all four treatments as response variable, and found no significant difference with grass heights varying between 10.0 ± 1.5 cm (*control*) and 12.1 ± 2.4 cm (*herbivory*; $\chi^2 = 0.832$; df = 3; $p = 0.842$).

To test whether the initial grass heights differed between the four paddocks, we used an LMM with (logged) grass height per subplot in all four treatments as response variable. As mentioned above, this analysis confirmed that there was a difference in the initial grass heights in 2015 between the paddocks (Figure S1).

The effect of fire on cattle behaviour was analysed with an LMM. As response variable, we used the visiting time and grazing time. Treatment (*fire + herbivory* and *herbivory*) and paddock were used as explanatory variables. We also tested the relationship between the proportion burned in *fire + herbivory* and the proportion of the total visiting or grazing time in a plot, that was spent in *fire + herbivory* (hereafter 'proportion visiting/grazing') in a GLMM with a beta distribution.

To test the relationship between grass height and proportion burned, we also conducted a GLMM with a beta distribution. We used the proportion burned in all burned subplots (*fire + herbivory* and *fire*) from 6 years of repeated burnings (2015–2020) and the corresponding mean grass heights. To remove zeros and ones in the data set, we used the transformation suggested by Cribari-Neto and Zeileis (2021):

$$x = \frac{y \times (n - 1) + 0.5}{n},$$

where n is the sample size.

The effect of increased grazing on future fuel load was analysed with an LMM. As response variable, we used the (logged) grass height from the grazed subplots (*fire + herbivory* and *herbivory*) from the whole study period (2015–2020). Treatment (*fire + herbivory* and *herbivory*), paddock and year and also their interactions were used as explanatory variables. The effect on the proportion burned was analysed with a GLMM with a beta distribution. We used proportion burned in *fire + herbivory* as response variable and paddock, year and their interaction as explanatory variables.

To assess whether there were any differences in plant species composition among the four treatment combinations in fall 2020, after six seasons of repeated treatment, we conducted a perMANOVA on the species community data (cover) with treatment (*fire + herbivory*, *herbivory*, *fire* and *control*) and paddock as explanatory variables. For pairwise comparisons of the treatments, we performed a perMANOVA for each pair of treatment in each paddock separately. We compensated for multiple tests, by using the Holm method (Holm, 1979).

Differences in plant life-form composition among the treatments were analysed with a GLMM with a beta distribution. We used the summed cover of all species in each life form as response variable and treatment (*fire + herbivory*, *herbivory*, *fire* and *control*) and life form (graminoids, forbs, ferns, *Rubus* spp. and dwarf shrubs) as explanatory variables. Again, to remove zeros and ones, we used the transformation suggested by Cribari-Neto and Zeileis (2021).

3 | RESULTS

During the first season of the experiment, when we monitored the behaviour of the cattle, there was no overall difference in cattle visitation time between the *fire + herbivory* and *herbivory* treatments, with 15.8 (±1.0) and 15.2 (±1.4) seconds, respectively, and no interaction with paddock (Table S4). We also found no significant relationship between the proportion burned and the proportion visiting ($\chi^2 = 0.014$; df = 1; $p = 0.907$). However, the time spent grazing was significantly affected by treatment and there was an interaction between treatment and paddock (Table S4). Cattle spent more time grazing in the burned (*fire + herbivory*) than in the unburned (*herbivory*) treatments, but only in Paddock 1, with 18.5 (±1.3) and 11.4 (±2.5) seconds for burned and unburned, respectively (Figure 2; Table S5). In the other paddocks, there was no difference in time grazing between the treatments (Figure 2; Table S5). We found a significant positive relationship between proportion burned and proportion grazed, with a higher proportion of the time spent grazing burned subplots with a higher proportion burned (Figure 3).

There was a significant positive relationship between proportion burned and grass height (Figure 4; Figure S4), with higher grass leading to a higher proportion burned.

We found a significant effect of year and paddock on grass height (Table S6). We also found a significant interaction between treatment and paddock and year and paddock (Table S6). Over 6 years (2015–2020), there was a reduction in grass height in both the *fire + herbivory* and *herbivory* treatment in Paddock 1, but not in the other paddocks (Figure 5; Table S7). However, at the end of the experiment (2020), grass height was lower in the *fire + herbivory* than in the *herbivory* treatment (Figure 5).

Similarly, we found a significant effect of year and paddock on proportion burned in *fire + herbivory*, and an interaction between year and paddock (Table S9). In Paddock 1, proportion burned

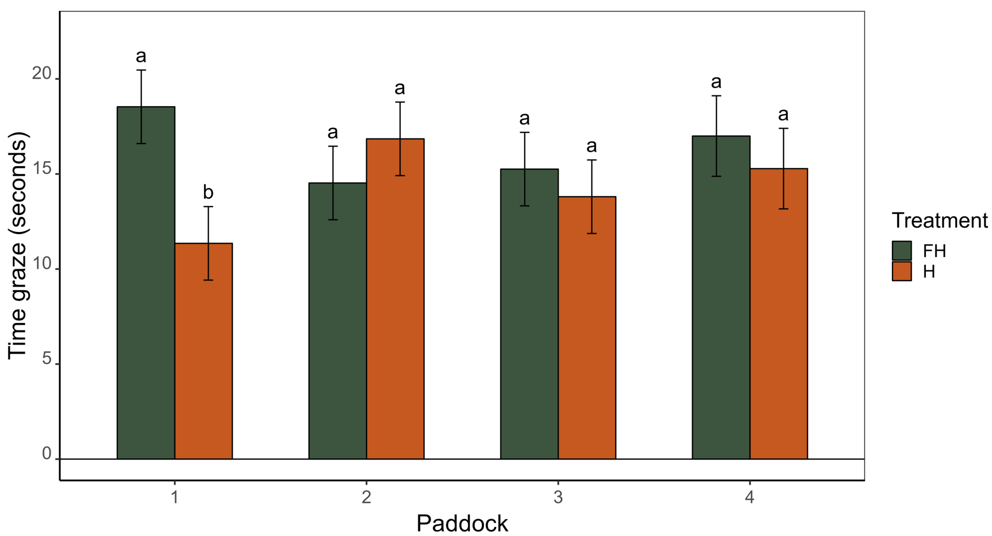

FIGURE 2 Mean time in seconds spent on grazing per 1-min video for each treatment and paddock (based on 2117 videos; error bars represent ±1 SE). Significance within each paddock is indicated with letters ($p < 0.05$; test statistics in Table S5). Treatment abbreviations: FH = *fire + herbivory* and H = *herbivory*.

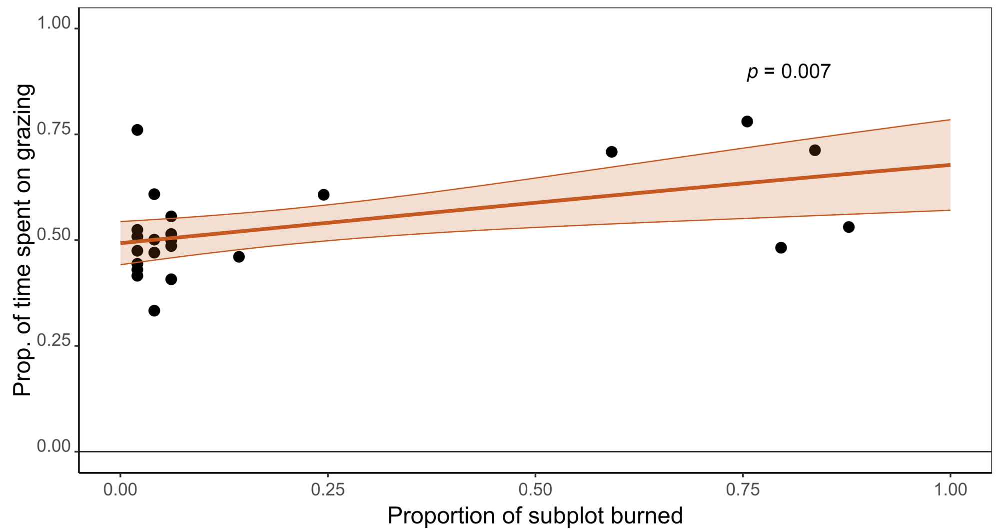

FIGURE 3 Relationship between proportion of subplot burned and the proportion of the time spent on grazing in the *fire + herbivory* subplot per video (based on 2117 videos). A predicted regression line is added with a confidence interval of 2 × SE. *p*-value of the regression is indicated in the figure ($\chi^2 = 7.198$; df = 1).

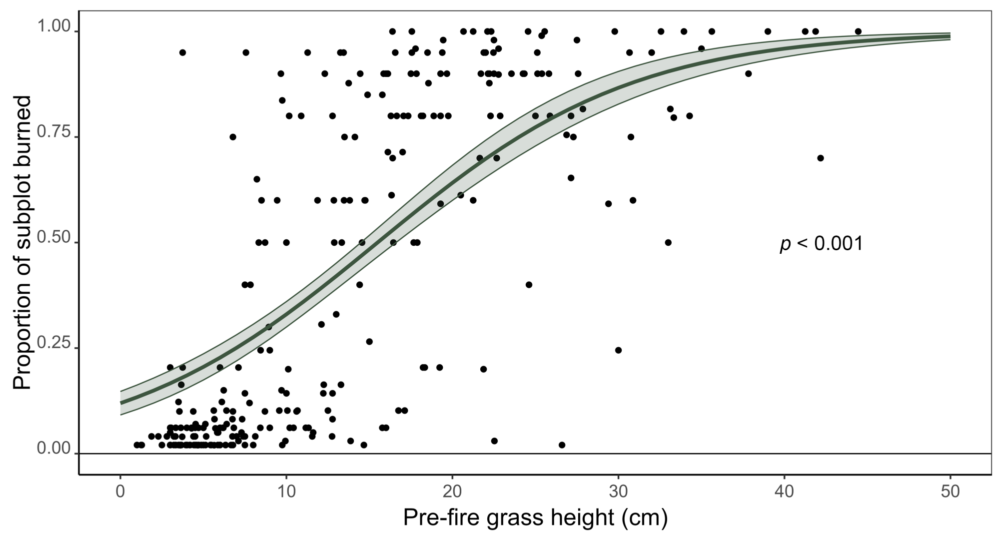

FIGURE 4 Relationship between pre-fire grass height in the *fire + herbivory* and *fire* subplots and proportion of subplot burned (data from 2015 to 2020). A predicted regression line is added with a confidence interval of 2 × SE. *p*-value of the regression is indicated in the figure ($\chi^2 = 230.620$; df = 1).

decreased strongly over the years from around 70% to only 10% of a plot burned (Figure 6; Table S10). During the first 4 years, proportion burned was also much higher in Paddock 1 than in the other paddocks. By 2020, there was no difference in proportion burned among the paddocks (Table S11). In the other paddocks, there was no clear trend over the years in proportion burned and proportion burned was low from the start.

The inventory of plant species composition resulted in 42 species, and 12 of them were found in all treatments (Figure S5). The highest number of species was found in *fire + herbivory* (32) and the lowest in *control* (23; for a full species list, see Table S12). Treatment, paddock and the interaction between these two factors all had a significant effect on the plant species composition (Table S13). The pairwise comparison showed a difference in plant species composition between the grazed (*fire + herbivory* and *herbivory*) and the ungrazed subplots (*fire* and *control*) in Paddock 1, 2 and 4 (Table S14). In Paddock 3, there was only a difference between *herbivory* and the *control* (Table S14).

Grazing and fire also altered the cover of different life forms (Table S15). *Fire* subplots had higher graminoid cover than the *control* subplots but lower than the *fire + herbivory* and *herbivory* subplots (Figure 7; Table S16). The cover of *Rubus* spp. was significantly higher in the two ungrazed treatments (*fire* and *control*) than in the grazed (*fire + herbivory* and *herbivory*) (Figure 7; Table S16).

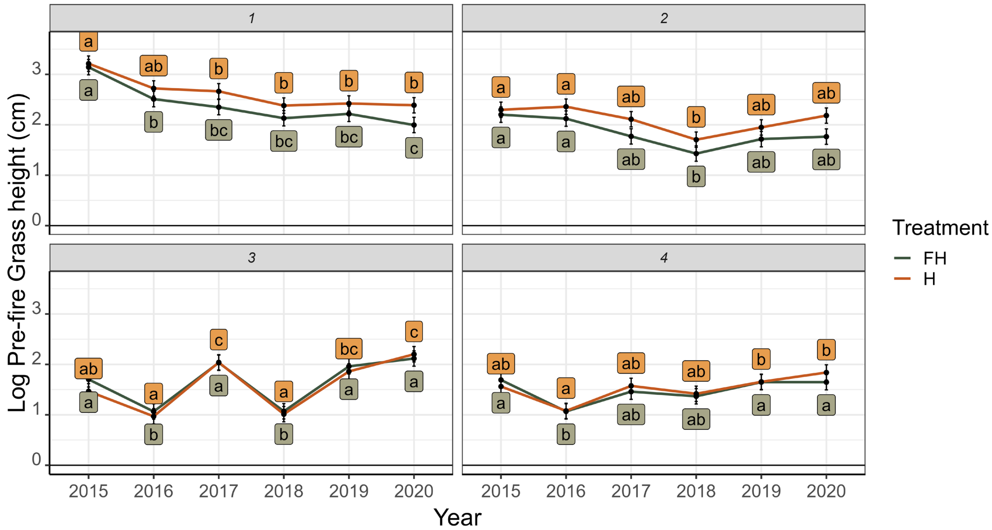

FIGURE 5 Logged pre-fire grass height (cm) measured in spring before the annual prescribed fires were conducted for each treatment and paddock (1–4) over 6 years (error bars represent ±1 SE). 2015 measurement was conducted before any treatment was applied. Significance between years within each treatment and paddock is indicated with letters ($p < 0.05$; test statistics in Tables S7 and S8). Treatment abbreviations: FH = *fire + herbivory* and H = *herbivory*.

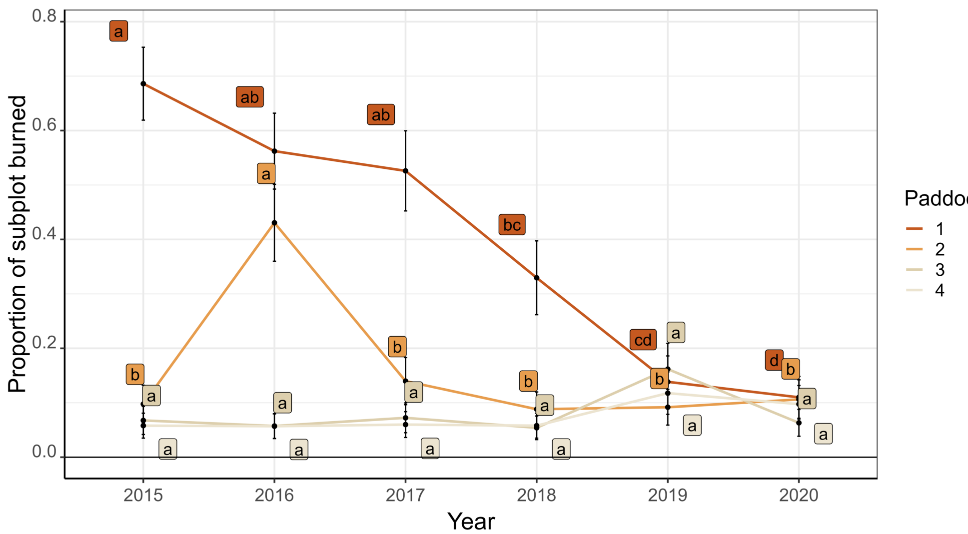

FIGURE 6 Proportion of subplot burned in *fire + herbivory* for each paddock over 6 years (2015–2020; error bars represent ±1 SE). 2015 fire was conducted before the herbivory treatment started. Significance between years within each paddock is indicated with letters ($p < 0.05$; test statistics in Tables S10 and S11).

4 | DISCUSSION

4.1 | Pyric herbivory in a temperate European ecosystem

The combination of fire and herbivory, that is, pyric herbivory, has received much attention in North America, Africa and Australia (Bond, 2005; Bowman et al., 2011; Kirkpatrick et al., 2011; Reid et al., 2023). Despite some studies on pyric herbivory in the southern, Mediterranean, parts of Europe (e.g., see San Emeterio et al., 2023), we are not aware of similar studies in the northern temperate parts of Europe. In this pioneering study, we showed that the process of pyric herbivory under temperate European conditions behaves in ways comparable to systems elsewhere in the world, both in terms of burned areas attracting further herbivory and this herbivory influencing future fire behaviour.

We saw the strongest signs of pyric herbivory in Paddock 1. In this paddock, cattle spent more time grazing in the burned than in the unburned treatment (Figure 2). Overall, we found that cattle spent more time grazing in subplots where a higher proportion of the subplot burned (Figure 3). This is in line with the findings by Archibald and Bond (2004), who found that larger burns attracted herbivores more strongly than smaller burns. We did not see an increase in overall cattle visitation to burned plots, probably because

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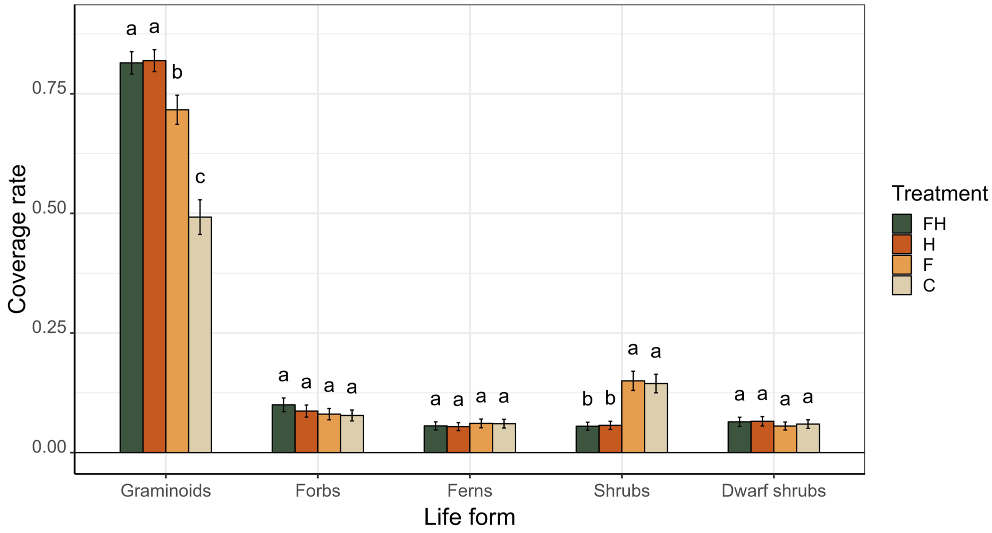

FIGURE 7 Coverage rate of five different plant life forms in each treatment in September 2020, after six seasons of treatment (error bars represent ±1 SE). Significance within each life form is indicated with letters ($p < 0.05$; test statistics can be found in Tables S15 and S16). Treatment abbreviations: FH = *fire + herbivory*, H = *herbivory*, F = *fire* and C = *control*.

our burned patches were much smaller than most other areas where this has been studied (49 m^2 compared with, e.g., >8000 ha in Archibald & Bond, 2004).

In Paddock 1, over 6 years (2015–2020), grass height decreased and it decreased more strongly in the *fire + herbivory* than in the *herbivory* treatment (Figure 5). The combination of fire and grazing in this paddock thus decreased grass biomass more than grazing alone, confirming findings from other studies (Donaldson et al., 2018; Fuhlendorf et al., 2009; Starns et al., 2019; Young et al., 2022). In the other paddocks, we did not find this temporal change in grass height. In Paddock 1, the proportion of a plot burned declined dramatically in the *fire + herbivory* treatment (Figure 6), from almost 70% at the start of the experiment to less than 20% at the end. This pattern matches the decrease in grass height in the *fire + herbivory* treatment of Paddock 1. There was no consistent change in proportion burned in the other paddocks (Figure 6).

One of the more striking findings of our study is the large difference in responses among the four paddocks, with Paddock 1 showing the strongest interaction between fire and cattle grazing. There may be multiple reasons for this difference among the paddocks. A likely driver is the difference in grass productivity among the paddocks, which was highest in Paddock 1 from the start (Figure S1). This increased productivity in Paddock 1 is likely due to the increased water availability through rainwater fed from the cliff bordering the plots in Paddock 1. This higher grass productivity led to higher initial fuel load in Paddock 1 at the start of the experiment, leading to a much higher proportion of subplot area burned during the first fire in 2015 (Figure 6). This then led to a larger attraction of cattle grazing. Augustine and Derner (2014) described a similar role of plant productivity in determining the preference of herbivores for burned patches, with higher productivity leading to higher fuel loads and more intense fires, which in turn attracted more herbivores. In this respect, it is relevant to stress that we found indications of a possible threshold at approximately 10 cm in grass height above which it is more likely that a subplot burns (Figure 4). Below 10 cm grass height, the proportion of a subplot burned was minimal, whereas the area burned increased markedly above 10 cm. Donaldson et al. (2018) showed a similar threshold effect with grass shorter than 10 cm limiting fire in an African savanna. Notably, the initial average grass height in Paddock 1, where on average 70% of a subplot burned, was clearly above the threshold (24.7 ± 1.8 (SE) cm), while the grass height in Paddock 2–4, where less than 20% of a plot burned, was below the threshold with 4.9–9.3 cm (Figure 6; Figure S1).

In addition to the variation in grass productivity, cattle density and distance to drinking water also varied among the paddocks. As seen in Table S1, Paddock 1 had the lowest number of 'cattle days' (defined as the number of individual cattle multiplied by the number of days of grazing). The distance to drinking water also varied, with Paddock 1 having a natural stream flowing through the paddock, while the other paddocks had a water tank. This meant that, on average, treatment plots were closer to water in Paddock 1. Proximity to a water source may affect the strength of pyric herbivory, with a further distance to water decreasing the attraction to burned areas (Augustine & Derner, 2014). Due to the pilot nature of our experiment and the lack of replication with respect to these factors, we were unable to formally test for the effects of cattle density and distance to water in our study. Still, we suggest that these factors should be included in future research on pyric herbivory in a temperate European context.

4.2 | Pyric herbivory as a management tool to improve heterogeneity in vegetation

Patch-burn grazing has been suggested as a way to incorporate pyric herbivory in grazing management regimes (Fuhlendorf &

Engle, 2001, 2004), as a form of rotational grazing without fencing. Patch-burn management can increase heterogeneity in vegetation structure (Leis et al., 2013; McGranahan & Kirkman, 2013; Starns et al., 2020) and also the variability in functional groups in plants (McGranahan et al., 2012). Until now, the common idea of conservation management practices has been to allow an intermediate level of grazing, which is often applied to entire areas creating uniform and homogenised ecosystems (Briske et al., 2003; Fuhlendorf & Engle, 2001). However, these traditional management methods ignore the spatiotemporal changes and patterns resulting from pyric herbivory, that is, the creation of a shifting mosaic landscape (Briske et al., 2003; Fuhlendorf & Engle, 2001). Fire and herbivory as strongly interacting processes can therefore be considered as potential tools in conservation management to create or increase heterogeneity in vegetation structure and composition in grasslands and other potentially flammable ecosystems (Bowman et al., 2021; Fuhlendorf et al., 2012; McGranahan & Kirkman, 2013; Wilcox et al., 2021).

We showed that cattle preferred to graze in the burned patches during the first year of the study. Since we only monitored the cattle behaviour during the first year, we were not able to test whether the effect of fire on grazing preference was maintained during the annual burns over the course of our experiment (Ranglack & Du Toit, 2015). However, we showed that both grass height and proportion burned continued to decrease 5 years after the initial fire similar to what Donaldson et al. (2018) showed in a study in a South African savanna with annual burnings. Similar to our findings, they showed that repeated burnings led to long-term attraction of herbivores, resulting in a reduction in grass height to levels that excluded fires. The continued attraction of cattle to the burned patches during the later years of our experiment, when only a small part of the subplots burned, can be explained by grazing-induced vegetation regrowth (Cromsigt & Olff, 2008). In our study, we burned and grazed the same patches of similar size (study plots) every year, similar to the study by Donaldson et al. (2018). We used annual burning to mimic the most recent fire regime in the area, which were human-induced annual fires to improve pastures for livestock (Atlestam, 1942). We acknowledge that natural, non-human-induced, fires will occur much less frequently than once a year. It remains unknown what fire frequency, but also fire size, would be optimal to restore biodiversity and ecosystem functioning in temperate European systems. We, therefore, strongly recommend future studies to specifically test the effect of varying fire sizes and intervals on fire behaviour, fire–herbivore interactions, and the effects of pyric herbivory on biodiversity and ecosystem functioning.

We found that fire and herbivory affected plant species composition and the relative cover of plant life forms (Figure 7). The species composition differed between the treatments, especially between the grazed and ungrazed subplots. In all paddocks, except Paddock 3, there was a difference in species composition between grazed and the ungrazed treatments (Table S14). Most striking was the strong negative impact of grazing on the two *Rubus* spp. *Rubus idaeus* was completely absent from the grazed treatments while it was present in 22 out of 48 quadrants in the fire subplots and 16 in the *control* subplots without fire and grazing. *Rubus fruticosus* also frequently occurred in the ungrazed treatments (in 15 of the fire and 22 of the *control* quadrants), while it only occurred in two of the *fire + herbivory* and five of the *herbivory* quadrants. This confirms previous studies that showed that *Rubus* spp. are readily eaten by herbivores and are quickly reduced in presence in grazed areas (e.g., see Horsley et al., 2003). Cattle grazing also altered the vegetation structure by promoting graminoids and restricting shrubs (in our case *Rubus* spp.) (Figure 7). Interestingly, fire did not reduce the shrub cover as has been seen in previous studies (e.g. see Pekin et al., 2012). This can probably be linked to the ability of *Rubus* to re-sprout after fires (Ainsworth & Mahr, 2004). Fire did not have a significant effect on species composition in our study after six seasons compared with the *control* without fire or herbivory (Table S14), although fire increased the amount of graminoids compared with the *control* (Figure 7; Table S16). Changes in plant life-form composition point not only to structural, but also functional changes in plant communities in response to pyric herbivory (Taylor et al., 2023).

5 | CONCLUSIONS

Our study provides some of the first insights into the potential use of pyric herbivory as a conservation management tool in temperate European grasslands. We show that fire can attract cattle grazing in a temperate wood pasture and that increased grazing on burned areas can reduce the fuel and thereby the extent of future fires. We also show that this effect may be stronger under more productive (wetter) conditions. Furthermore, we show that fire and herbivory may alter plant species composition and the relative cover of different plant life forms. These combined effects of fire and herbivory created heterogeneity in the plant species composition and structure in the landscape, similar to what has been shown in other parts of the world. Today, the need to restore and maintain open habitat biodiversity is greater than ever and, at the same time, we need to identify cost-efficient and sustainable management methods. Pyric herbivory-based management has been shown to maintain cattle stocking rates and provide high-quality forage throughout the whole season and still increase biodiversity (Limb et al., 2011) and could therefore be considered as an alternative to traditional conservation management methods also in Europe. This study is a first step in re-incorporating fire–herbivore interactions into contemporary nature management techniques in Northern Europe as a potential tool to increase both heterogeneity and diversity. We recommend further studies on the combined effects of different grazing and fire regimes and their effects on long-term temperate ecosystem structure and functioning.

AUTHOR CONTRIBUTIONS

Karin Amsten (K.A.), Joris P. G. M. Cromsigt (J.P.G.M.C.), Dries P.J. Kuijper (D.P.J.K.), Mats Niklasson (M.N.) and Marcin Churski (M.C.) planned and designed the experiment. K.A., Jenny Loberg (J.M.), Jens Jung (J.J.), My Strömgren (M.S.), M.N. and M.C. performed the

experiment and conducted fieldwork. K.A., J.L. and M.C. analysed the data. K.A., M.N. and M.C. drafted and revised the manuscript. J.P.G.M.C., D.P.J.K., J.L., J.J. and M.S. contributed to the revising of the manuscript. This study is a collaboration between scientists from many nationalities and research areas, such as ecology and ethology. Local historical documentation on land use and management was used in the process to ensure the local context.

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CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest when producing this manuscript.

DATA AVAILABILITY STATEMENT

Data used to obtain the results of this study are available at SND (Svensk nationell datatjänst), https://doi.org/10.5878/zwe7-5w02 (Amsten et al., 2024).

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REFERENCES

Ainsworth, N., & Mahr, F. (2004). Regrowth of blackberry two years after the 2003 wildfires in Victoria. *Fifteenth Australian Weeds Conference*, pp. 211–214.

Allen, L. J., Harbers, L. H., Schalles, R. R., Owensby, C. E., & Smith, E. F. (1976). Range burning and fertilizing related to nutritive value of bluestem grass. *Journal of Range Management*, *29*(4), 306–308. https://doi.org/10.2307/3897089

Allred, B. W., Fuhlendorf, S. D., Engle, D. M., & Elmore, R. D. (2011). Ungulate preference for burned patches reveals strength of fire-grazing interaction. *Ecology and Evolution*, *1*(2), 132–144. https://doi.org/10.1002/ece3.12

Amsten, K., Cromsigt, J. P. G. M., Kuijper, D. P. J., Loberg, J. M., Churski, M., & Niklasson, M. (2021). Fire- and herbivory-driven consumer control in a savanna-like temperate wood-pasture: An experimental approach. *Journal of Ecology*, *109*, 4103–4114. https://doi.org/10.1111/1365-2745.13783

Amsten, K., Cromsigt, J. P. G. M., Kuijper, D. P. J., Loberg, J. M., Jung, J., Strömgren, M., Churski, M., & Niklasson, M. (2024). Data from: Pyric herbivory in a temperate European wood-pasture system (Version 1) [Dataset]. *Sveriges Lantbruksuniversitet*, https://doi.org/10.5878/zwe7-5w02

Archibald, S. (2008). African grazing lawns: How fire, rainfall, and grazer numbers interact to affect grass community states. *Journal of Wildlife Management*, *72*(2), 492–501. https://doi.org/10.2193/2007-045

Archibald, S., & Bond, W. J. (2004). Grazer movements: Spatial and temporal responses to burning in a tall-grass African savanna. *International Journal of Wildland Fire*, *13*, 377–385. https://doi.org/10.1071/wf03070

Archibald, S., Bond, W. J., Stock, W. D., & Fairbanks, D. H. K. (2005). Shaping the landscape: Fire–grazer interactions in an African savanna. *Ecological Applications*, *15*(1), 96–109. https://doi.org/10.1890/03-5210

Archibald, S., & Hempson, G. P. (2016). Competing consumers: Contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 20150309. https://doi.org/10.1098/rstb.2015.0309

Atlestam, P. O. (1942). *Bohusläns ljunghedar. En geografisk studie*. University of Gothenburg. http://hdl.handle.net/2077/12678

Augustine, D. J., & Derner, J. D. (2014). Controls over the strength and timing of fire-grazer interactions in a semi-arid rangeland. *Journal of Applied Ecology*, *51*(1), 242–250. https://doi.org/10.1111/1365-2664.12186

Bakker, E. S., Gill, J. L., Johnson, C. N., Vera, F. W. M., Sandom, C. J., Asner, G. P., & Svenning, J.-C. (2016). Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(4), 847–855. https://doi.org/10.1073/pnas.1502545112

Blair, J. M. (1997). Fire, N availability, and plant response in grasslands: A test of the transient maxima hypothesis. *Ecology*, *78*(8), 2359–2368. https://doi.org/10.2307/2265898

Bond, W. J. (2005). Large parts of the world are brown or black: A different view on the "green world" hypothesis. *Journal of Vegetation Science*, *16*(3), 261–266. https://doi.org/10.1111/j.1654-1103.2005.tb02364.x

Bond, W. J., & Keeley, J. E. (2005). Fire as a global "herbivore": The ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, *20*(7), 387–394. https://doi.org/10.1016/j.tree.2005.04.025

Bowman, D. M. J. S., Balch, J., Artaxo, P., Bond, W. J., Cochrane, M. A., D'Antonio, C. M., DeFries, R., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., Kull, C. A., Mack, M., Moritz, M. A., Pyne, S., Roos, C. I., Scott, A. C., Sodhi, N. S., & Swetnam, T. W. (2011). The human dimension of fire regimes on earth. *Journal of Biogeography*, *38*(12), 2223–2236. https://doi.org/10.1111/j.1365-2699.2011.02595.x

Bowman, D. M. J. S., French, B. J., Williamson, G. J., & Prior, L. D. (2021). Fire, herbivores and the management of temperate Eucalyptus savanna in Tasmania: Introducing the Beaufront fire—Mammalian herbivore field experiment. *Ecological Management and Restoration*, *22*(S2), 140–151. https://doi.org/10.1111/emr.12453

Bradshaw, R. H. W., Hannon, G. E., & Lister, A. M. (2003). A long-term perspective on ungulate-vegetation interactions. *Forest Ecology and Management*, *181*(1–2), 267–280. https://doi.org/10.1016/S0378-1127(03)00138-5

Briske, D. D., Fuhlendorf, S. D., & Smeins, F. E. (2003). Vegetation dynamics on rangelands: A critique of the current paradigms. *Journal of Applied Ecology*, *40*(4), 601–614. https://doi.org/10.1046/J.1365-2664.2003.00837.X

Brooks, M., Bolker, B., Kristensen, K., Maechler, M., Magnusson, A., McGillycuddy, M., Skaug, H., Nielsen, A., Berg, C., van Bentham, K., Sadat, N., Lüdecke, D., Lenth, R., O'Brien, J., Geyer, C. J., Jagan, M., Wiernik, B., & Stouffer, D. B. (2023). *glmmTMB: Generalized linear mixed models using template model builder*. R package version 1.1.7. https://cran.r-project.org/web/packages/glmmTMB/glmmTMB.pdf

Collins, S. L. (1992). Fire frequency and community heterogeneity in tallgrass prairie vegetation. In *Ecosystem management* (pp. 99–105). Springer. https://doi.org/10.1007/978-1-4612-4018-1_11

Cribari-Neto, F., & Zeileis, A. (2021). *Beta regression in R*. http://cran.r-project.org/package=betareg

Cromsigt, J. P. G. M., & Olff, H. (2008). Dynamics of grazing lawn formation: An experimental test of the role of scale-dependent processes. *Oikos*, *117*(10), 1444–1452. https://doi.org/10.1111/j.0030-1299.2008.16651.x

Donaldson, J. E., Archibald, S., Govender, N., Pollard, D., Luhdo, Z., & Parr, C. L. (2018). Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns. *Journal of Applied Ecology*, *55*(1), 225–235. https://doi.org/10.1111/1365-2664.12956

Eby, S. L., Anderson, T. M., Mayemba, E. P., & Ritchie, M. E. (2014). The effect of fire on habitat selection of mammalian herbivores: The role of body size and vegetation characteristics. *Journal of Animal Ecology*, *83*(5), 1196–1205. https://doi.org/10.1111/1365-2656.12221

Ernby, E. (2010). *Margareta Hvitfeldts donation, vision och verklighet*. Bohusläns museums förlag.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., … Wardle, D. A. (2011). Trophic downgrading of planet earth. *Science*, *333*(6040), 301–306. https://doi.org/10.1126/science.1205106

Fernandes, P. A. M. (2001). Fire spread prediction in shrub fuels in Portugal. *Forest Ecology and Management*, *144*(1–3), 67–74. https://doi.org/10.1016/S0378-1127(00)00363-7

Feurdean, A., Ruprecht, E., Molnár, Z., Hutchinson, S. M., & Hickler, T. (2018). Biodiversity-rich European grasslands: Ancient, forgotten ecosystems. *Biological Conservation*, *228*, 224–232. https://doi.org/10.1016/j.biocon.2018.09.022

Fuhlendorf, S. D., & Engle, D. M. (2001). Restoring heterogeneity on rangelands: Ecosystem management based on evolutionary grazing patterns. *BioScience*, *51*(8), 625–632. https://doi.org/10.1641/0006-3568(2001)051[0625:RHOREM]2.0.CO;2

Fuhlendorf, S. D., & Engle, D. M. (2004). Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *Journal of Applied Ecology*, *41*(4), 604–614. https://doi.org/10.1111/j.0021-8901.2004.00937.x

Fuhlendorf, S. D., Engle, D. M., Elmore, R. D., Limb, R. F., & Bidwell, T. G. (2012). Conservation of pattern and process: Developing an alternative paradigm of rangeland management. *Rangeland Ecology & Management*, *65*(6), 579–589. https://doi.org/10.2111/REM-D-11-00109.1

Fuhlendorf, S. D., Engle, D. M., Kerby, J., & Hamilton, R. (2009). Pyric herbivory: Rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology*, *23*(3), 588–598. https://doi.org/10.1111/j.1523-1739.2008.01139.x

Fuhlendorf, S. D., & Smeins, F. E. (1999). Scaling effects of grazing in a semi-arid grassland. *Journal of Vegetation Science*, *10*(5), 731–738. https://doi.org/10.2307/3237088

Granström, A. (1993). Spatial and temporal variation in lightning ignitions in Sweden. *Journal of Vegetation Science*, *4*(6), 737–744. https://doi.org/10.2307/3235609

Herrera, A. H., Ballera, B. L. G. B., Toro-Manríquez, M. D. R., Lencinas, M. V., Pastur, G. J. M., & Ramírez, H. H. (2021). Changes in vegetation of flooded savannas subject to cattle grazing and fire in plains of Colombia. *Land*, *10*(2), 1–14. https://doi.org/10.3390/LAND10020108

Högbom, A. G. (1934). *Om skogseldar förr och nu och deras roll i skogarnas utvecklingshistoria*. Almqvist & Wiksells boktryckeri AB.

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, *6*(2), 65–70.

Horsley, S. B., Stout, S. L., & DeCalesta, D. S. (2003). White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications*, *13*(1), 98–118. https://doi.org/10.1890/1051-0761(2003)013[0098:WTDIOT]2.0.CO;2

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar, C. C., Aleixo, I., Ali, H., … Wirth, C. (2020). TRY plant trait database—Enhanced coverage and open access. *Global Change Biology*, *26*(1), 119–188. https://doi.org/10.1111/gcb.14904

Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J., & Bradstock, R. A. (2011). Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, *16*(8), 406–411. https://doi.org/10.1016/j.tplants.2011.04.002

Kirkpatrick, J. B., Marsden-Smedley, J. B., Di Folco, M. B., & Leonard, S. W. J. (2016). Influence of grazing and vegetation type on post-fire floristic and lifeform composition in Tasmania, Australia. *Plant Ecology*, *217*, 57–69. https://doi.org/10.1007/s11258-015-0559-4

Kirkpatrick, J. B., Marsden-Smedley, J. B., & Leonard, S. W. J. (2011). Influence of grazing and vegetation type on post-fire flammability. *Journal of Applied Ecology*, *48*(3), 642–649. https://doi.org/10.1111/j.1365-2664.2011.01962.x

Krook, K., Bond, W. J., & Hockey, P. A. R. (2007). The effect of grassland shifts on the avifauna of a south African savanna. *Ostrich*, *78*(2), 271–279. https://doi.org/10.2989/OSTRICH.2007.78.2.24.104

Kuijper, D. P. J., Cromsigt, J. P. G. M., Jedrzejewska, B., Miścicki, S., Churski, M., Jedrzejewski, W., & Kweczlich, I. (2010). Bottom-up versus top-down control of tree regeneration in the Białowieża Primeval Forest, Poland. *Journal of Ecology*, *98*(4), 888–899. https://doi.org/10.1111/j.1365-2745.2010.01656.x

Kuznetsova, A., Bruun Brockhoff, P., & Haubo Bojesen Christensen, R. (2018). *lmerTEST: Tests in linear mixed effects models*. R package version 3.0-1. https://github.com/runehaubo/lmerTestR

Lautenbach, J. D., Haukos, D. A., Lautenbach, J. M., & Hagen, C. A. (2021). Ecological disturbance through patch-burn grazing influences lesser prairie-chicken space use. *Journal of Wildlife Management*, *85*(8), 1699–1710. https://doi.org/10.1002/jwmg.22118

Leis, S., Morrison, L. W., & Debacker, M. D. (2013). Spatiotemporal variation in vegetation structure resulting from pyric-herbivory. *The Prairie Naturalist*, *45*, 13–20.

Lenth, R., Singmann, H., Love, J., Buerkner, P., & Herve, M. (2018). *Emmeans: Estimated marginal means, aka least-squares means*. R package version 1.2.4. https://github.com/rvlenth/emmeans

Leverkus, S. E. R., Fuhlendorf, S. D., Geertsema, M., Allred, B. W., Gregory, M., Bevington, A. R., Engle, D. M., & Scasta, J. D. (2018). Resource selection of free-ranging horses influenced by fire in northern Canada. *Human-Wildlife Interactions*, *12*(1), 85–101. https://doi.org/10.26077/j5px-af63

Limb, R. F., Fuhlendorf, S. D., Engle, D. M., Weir, J. R., Elmore, R. D., & Bidwell, T. G. (2011). Pyric-herbivory and cattle performance in grassland ecosystems. *Rangeland Ecology & Management*, *64*(6), 659–663. https://doi.org/10.2111/REM-D-10-00192.1

McGinty, A., Smeins, F. E., & Merrill, L. B. (1983). Influence of spring burning on cattle diets and performance on the Edwards plateau. *Journal of Range Management*, *36*(2), 175–178. https://doi.org/10.2307/3898157

McGlinn, D. J., & Palmer, M. W. (2019). Examining the assumptions of heterogeneity-based management for promoting plant diversity in a disturbance-prone ecosystem. *PeerJ*, *7*, e6738. https://doi.org/10.7717/peerj.6738

McGranahan, D. A., Engle, D. M., Fuhlendorf, S. D., Winter, S. J., Miller, J. R., & Debinski, D. M. (2012). Spatial heterogeneity across five rangelands managed with pyric-herbivory. *Journal of Applied Ecology*, *49*(4), 903–910. https://doi.org/10.1111/j.1365-2664.2012.02168.x

McGranahan, D. A., Henderson, C. B., Hill, J. S., Raicovich, G. M., Wilson, W. N., & Smith, C. K. (2014). Patch burning improves forage quality and creates grass-bank in old-field pasture: Results of a demonstration trial. *Southeastern Naturalist*, *13*(2), 200–207. https://doi.org/10.1656/058.013.0203

McGranahan, D. A., & Kirkman, K. P. (2013). Multifunctional rangeland in Southern Africa: Managing for production, conservation, and resilience with fire and grazing. *Land*, *2*(2), 176–193. https://doi.org/10.3390/land2020176

Nieman, W. A., van Wilgen, B. W., Radloff, F. G., & Leslie, A. J. (2021). A review of the responses of medium-to large-sized African mammals to fire. *African Journal of Range & Forage Science*, *38*, 1–15. https://doi.org/10.2989/10220119.2021.1918765

Nieman, W. A., Wilgen, B. W., Radloff, F. G. T., Tambling, C. J., & Leslie, A. J. (2022). The effects of fire frequency on vegetation structure and mammal assemblages in a savannah-woodland system. *African Journal of Ecology*, *60*(3), 1–16. https://doi.org/10.1111/aje.12971

Niklasson, M., Zin, E., Zielonka, T., Feijen, M., Korczyk, A. F., Churski, M., Samojlik, T., JeDrzejewska, B., Gutowski, J. M., & Brzeziecki, B. (2010). A 350-year tree-ring fire record from Białowieza Primeval Forest, Poland: Implications for central European lowland fire history. *Journal of Ecology*, *98*(6), 1319–1329. https://doi.org/10.1111/j.1365-2745.2010.01710.x

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., … Weedon, J. (2022). *vegan: Community ecology package*. R package version 2.5-6 ed. https://cran.r-project.org/web/packages/vegan/index.html

Pekin, B. K., Wittkuhn, R. S., Boer, M. M., Macfarlane, C., & Grierson, P. F. (2012). Response of plant species and life form diversity to variable fire histories and biomass in the jarrah forest of southwest Australia. *Austral Ecology*, *37*(3), 330–338. https://doi.org/10.1111/j.1442-9993.2011.02280.x

Ranglack, D. H., & Du Toit, J. T. (2015). Wild bison as ecological indicators of the effectiveness of management practices to increase forage quality on open rangeland. *Ecological Indicators*, *56*, 145–151. https://doi.org/10.1016/j.ecolind.2015.04.009

Raynor, E. J., Joern, A., & Briggs, J. M. (2015). Bison foraging responds to fire frequency in nutritionally heterogeneous grassland. *Ecology*, *96*(6), 1586–1597. https://doi.org/10.1890/14-2027.1

Reid, A. M., Murphy, B. P., Vigilante, T., & Bowman, D. M. J. S. (2023). Pyric herbivory and the nexus between forage, fire and native and introduced large grazing herbivores in Australian tropical savannas. *Ecosystems*, *26*, 610–626. https://doi.org/10.1007/s10021-022-00781-6

San Emeterio, L., Baquero, E., Antón, R., Jordana, R., Múgica, L., Sáez, J. L., Virto, I., & Canals, R. M. (2023). Pyric herbivory increases soil microbial diversity but has a site-dependent effect on soil mesofauna in the mid-term. *Agriculture, Ecosystems and Environment*, *356*, 108632. https://doi.org/10.1016/j.agee.2023.108632

Savadogo, P., Zida, D., Sawadogo, L., Tiveau, D., Tigabu, M., & Odén, P. C. (2007). Fuel and fire characteristics in savannawoodland of West Africa in relation to grazing and dominant grass type. *International Journal of Wildland Fire*, *16*, 531–539. https://doi.org/10.1071/WF07011

Sittler, K. L., Parker, K. L., & Gillingham, M. P. (2019). Vegetation and prescribed fire: Implications for stone's sheep and elk. *Journal of Wildlife Management*, *83*(2), 393–409. https://doi.org/10.1002/jwmg.21591

Starns, H. D., Fuhlendorf, S. D., Elmore, R. D., Twidwell, D., Thacker, E. T., Hovick, T. J., & Luttbeg, B. (2019). Recoupling fire and grazing reduces wildland fuel loads on rangelands. *Ecosphere*, *10*(1), 1–15. https://doi.org/10.1002/ecs2.2578

Starns, H. D., Fuhlendorf, S. D., Elmore, R. D., Twidwell, D., Thacker, E. T., Hovick, T. J., & Luttbeg, B. (2020). Effects of pyric herbivory on prairie-chicken (*Tympanuchus* spp) habitat. *PLoS ONE*, *15*(6), e0234983. https://doi.org/10.1371/JOURNAL.PONE.0234983

Stewart, K. E. J., Bourn, N. A. D., & Thomas, J. A. (2001). An evaluation of three quick methods commonly used to assess sward height in ecology. *Journal of Applied Ecology*, *38*(5), 1148–1154. https://doi.org/10.1046/j.1365-2664.2001.00658.x

Svenning, J.-C. (2002). A review of natural vegetation openness in northwestern Europe. *Biological Conservation*, *104*(2), 133–148. https://doi.org/10.1016/S0006-3207(01)00162-8

Taylor, A., Weigelt, P., Denelle, P., Cai, L., & Kreft, H. (2023). The contribution of plant life and growth forms to global gradients of vascular plant diversity. *The New Phytologist*, *240*, 1548–1560. https://doi.org/10.1111/nph.19011

Thapa, S. K., de Jong, J. F., Hof, A. R., Subedi, N., Joshi, L. R., & Prins, H. H. T. (2022). Fire and forage quality: Postfire regrowth quality and pyric herbivory in subtropical grasslands of Nepal. *Ecology and Evolution*, *12*(4), e8794. https://doi.org/10.1002/ece3.8794

Van Uytvanck, J., & Hoffmann, M. (2009). Impact of grazing management with large herbivores on forest ground flora and bramble understorey. *Acta Oecologica*, *35*(4), 523–532. https://doi.org/10.1016/j.actao.2009.04.001

Veldman, J. W., Buisson, E., Durigan, G., Fernandes, G. W., Le Stradic, S., Mahy, G., Negreiros, D., Overbeck, G. E., Veldman, R. G., Zaloumis, N. P., Putz, F. E., & Bond, W. J. (2015). Toward an old-growth concept for grasslands, savannas, and woodlands. *Frontiers in Ecology and the Environment*, *13*(3), 154–162. https://doi.org/10.1890/140270

Vera, F. W. M. (2000). *Grazing ecology and forest history*. CABI Publishing. https://doi.org/10.2307/1587257

Vermeire, L. T., Mitchell, R. B., Fuhlendorf, S. D., & Gillen, R. L. (2004). Patch burning effects on grazing distribution. *Journal of Range Management*, *57*, 248–252. https://doi.org/10.2111/1551-5028(2004)057[0248:pbeogd]2.0.co;2

Wastenson, L., Raab, B., Vedin, H., SMHI, & Lantmäteriverket. (2004). *Sveriges nationalatlas*. Kartförlaget.

West, A. L., Zou, C. B., Stebler, E., Fuhlendorf, S. D., & Allred, B. (2016). Pyric-herbivory and hydrological responses in tallgrass prairie. *Rangeland Ecology & Management*, *69*(1), 20–27. https://doi.org/10.1016/j.rama.2015.10.004

Wilcox, B. P., Fuhlendorf, S. D., Walker, J. W., Twidwell, D., Wu, X. B., Goodman, L. E., Treadwell, M., & Birt, A. (2021). Saving imperiled grassland biomes by recoupling fire and grazing: A case study from the Great Plains. *Frontiers in Ecology and the Environment*, *20*(3), 179–186. https://doi.org/10.1002/fee.2448

Winter, S. L., Allred, B. W., Hickman, K. R., & Fuhlendorf, S. D. (2015). Tallgrass prairie vegetation response to spring fires and bison grazing. *The Southwestern Naturalist*, *60*(1), 30–35. https://doi.org/10.1894/FMO-19.1

Winter, S. L., Fuhlendorf, S. D., Goad, C. L., Davis, C. A., Hickman, K. R., & Leslie, D. M. (2012). Restoration of the fire-grazing interaction in *Artemisia filifolia* shrubland. *Journal of Applied Ecology*, *49*(1), 242–250. https://doi.org/10.1111/j.1365-2664.2011.02067.x

Young, T. P., Kimuyu, D. N., LaMalfa, E. M., Werner, C. M., Jones, C., Masudi, P., Ang'ila, R., & Sensenig, R. L. (2022). Effects of large mammalian herbivory, previous fire, and year of burn on fire behavior in an African savanna. *Ecosphere*, *13*(3), e3980. https://doi.org/10.1002/ecs2.3980

Zin, E., Kuberski, Ł., Drobyshev, I., & Niklasson, M. (2022). First spatial reconstruction of past fires in temperate Europe suggests large variability of fire sizes and an important role of human-related ignitions. *Frontiers in Ecology and Evolution*, *10*, 768464. https://doi.org/10.3389/fevo.2022.768464

Ziobro, J., Koziarz, M., Havrylyuk, S., Korol, M., Ortyl, B., Wolański, P., & Bobiec, A. (2016). Spring grass burning: An alleged driver of successful oak regeneration in sub-carpathian marginal woods. A case study. *Prace Geograficzne*, *146*, 67–88. https://doi.org/10.4467/20833113PG.16.018.5548

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Grazing period and animal density in the four paddocks.

Table S2: Settings for the 24 camera traps.

Table S3: Details on all the analyses in the study.

Table S4: Analysis of deviance explaining the variation in (a) time cattle spent visiting and (b) time cattle spent grazing.

Table S5: Multiple pairwise comparisons test of time spent grazing between treatments.

Table S6: Analysis of deviance explaining the variation in grass height.

Table S7: Multiple pairwise comparisons test of logged pre-fire grass height between years.

Table S8: Multiple pairwise comparisons test of logged pre-fire grass height between treatments.

Table S9: Analysis of deviance explaining the variation in proportion burned in fire+herbivory.

Table S10: Multiple pairwise comparisons test of proportion burned in fire+herbivory between years for each paddock.

Table S11: Multiple pairwise comparisons test of proportion burned in fire+herbivory between paddocks for each year.

Table S12: Full list of determined wild herbaceous species found in fall 2020.

Table S13: Analysis of variance explaining the variation in plant species composition (cover).

Table S14: Pairwise comparison with Permutational Multivariate Analysis of Variance of plant species.

Table S15: Analysis of deviance explaining the variation in coverage of different life forms.

Table S16: Multiple pairwise comparisons test of life form coverage between treatments for each life form.

Figure S1: Logged initial mean fuel heights.

Figure S2: View of the camera trap and example of determination of video events.

Figure S3: Example of a photo template of a plot.

Figure S4: Examples of two different *fire+herbivory* subplots in spring 2015.

Figure S5: Venn chart over the number of unique species found in the four treatments.

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