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Maintaining an open landscape: Comparison of management methods for semi-natural grasslands: A Swedish multi-site study

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A R T I C L E I N F O

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A B S T R A C T

Traditional management of semi-natural grasslands by grazing or annual mowing is not always feasible and the current study set out to evaluate alternative management methods. At eleven locations in southern Sweden, block experiments were conducted evaluating seven treatments in 5 m*20 m plots: grazing, annual mowing, annual spring burning, mowing every third year, mechanical removal of woody plants, herbicide control of woody plants, and untreated control. After approximately 13 years, trends for woody plants and species richness, and the occurrence of management-dependent plant species, low-grown species, and pollinator-attracting plant species were analysed. Overall, the annual mowing and grazing treatments resulted in fewer woody plants, the highest species richness, and more management-dependent, low-grown, and pollinator-attracting species. The untreated control plots showed the opposite effect, whereas less intense management (annual burning, mowing every third year, and mechanical and chemical treatments of woody plants) showed mixed and often intermediate effects. Compared to grazing and mowing, less intense management methods do not constitute long-term management alternatives to preserve typical features of species-rich grasslands. However, they may be short-term alternatives at sites where the recruitment of woody species is absent or rare. However, to prevent the encroachment of woody species, less intensive management might be a better long-term alternative at more productive sites with slow or inhibited woody species recruitment.

1. Introduction

Semi-natural grasslands around the world are important habitats because they are often species-rich (Habel et al., 2013) and provide ecosystem services such as fodder production, pollination and climate mitigation (Bengtsson et al., 2019). Furthermore, semi-natural grasslands in Central and Northern Europe are recognised as legacies of grass-dominated environments that existed before and during the early Holocene (Svenning, 2002; Hejcman et al., 2013; Feurdean et al., 2018; Eriksson, 2020; Bråthen et al., 2021), which explains their high species richness and emphasises their importance in species conservation.

The tremendous changes in European agriculture in the decades after the 2nd World War led to marginal and low-productivity land being either abandoned or subjected to treatments aimed at improving productivity (Fuller, 1987; Cousins et al., 2015; Ridding et al., 2015). The abandonment of previously mown or grazed semi-natural grasslands can be expected to result in encroachment of woody species, decreased species richness, especially of management-dependent or low-grown plant species, and altered vegetation

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composition, as well as drastic changes in regional or national landscapes (Dupré and Diekmann, 2001; Pykälä, Öckinger et al., 2005, 2006; Hellesen and Levin, 2014; Rupprecht et al., 2022; Prangel et al., 2023). The steady transformation of grassland and arable land into forest in the 1950 s and 60 s (Statistics Sweden, 2019) suggested an ever-darkening landscape and a need for countermeasures (Flygare, 2004). Around 1970, independent field trials aimed at exploring how to preserve grasslands and "keep the landscape open" started in Sweden (1972, 11 trials, Steen, 1976), northern Germany (1972, 1 trial, Dierschke, 1985), southern Germany (1973; 14 trials, Schreiber et al., 2009) and Switzerland (1977–78, 2 trials, Köhler et al., 2005).

Fifty years later, much effort was still focused on maintaining the remaining low-productivity semi-natural grasslands to conserve their plant and animal species, cultural heritage and landscape openness (Poschlod et al., 2009; D'Aniello et al., 2011; Habel et al., 2013; Babai and Molnár, 2014). Threats to these values remain, with continued grassland abandonment as livestock farming is concentrated geographically, with livestock often kept indoors (Biró et al., 2018, Valkó et al., 2018), and because of the high costs of fencing and mowing (Schreiber et al., 2009; Török et al., 2011; Glimskär et al., 2023). Hence, the original aims of the field trials conducted 50 years ago remain highly relevant: how to effectively prevent woody encroachment and preserve semi-natural grasslands. Although the benefits of maintaining or reintroducing mowing or grazing in semi-natural grasslands are well established (e.g. Öckinger et al., 2006, Tälle et al., 2016, Waldén and Lindborg, 2016), the effects of less intensive management methods in terms of preventing woody encroachment or maintaining desirable vegetation attributes are not well established. However, there seem to be benefits from methods like prescribed burning or mowing at low frequencies for plant species conservation (Valkó et al., 2014 Tälle et al., 2018). Furthermore, it is now well established that although most grassland plants do well under intensive management (mowing or grazing that leaves little biomass of fodder by the end of the growth seasons), this does not apply to most insects (Littlewood et al., 2012; van Klink et al., 2015; Johansen et al., 2019; Fumy et al., 2023). Hence, the long-term effects of less intensive management remain relevant from a management perspective.

In the current study, we summarised data from trials that started in the 1970 s: a series of 11 Swedish replicated block trials, which ran for approximately 13 years and compared the effectiveness of several different management methods of varying intensities in preventing or slowing the encroachment of woody plants and maintaining features typical of traditionally managed semi-natural grasslands.

Here, we aim to compare seven management methods regarding the level at which the vegetation (i) is prevented from encroachment by woody plants, (ii) is rich in species, (iii) contains management-dependent species, (iii) contains low-grown plant species, (iv) sustains plant species attractive to pollinators and (v) maintains a composition similar to that under traditional management, that is, annual mowing.

2. Material and methods

2.1. Design of study

In the early 1970 s, grassland researcher Eliel Steen initiated a series of trials comparing management methods aimed at preventing the encroachment of woody plants. The hope was for the trials to run for at least 20 years (Steen, 1976), but when funding ceased after approximately 13 years, most trials were abandoned.

The study included 11 trials conducted at nine locations in southern Sweden (Fig. 1a). Two of the locations (Ekenäs, Tagel) had two experimental sites each. The mean annual temperature in the study region is approximately 6∘C, the mean annual precipitation is 500–1000 mm (Alexandersson et al., 1991) and the growing period is 180–220 days (Sjörs, 1999).

The sites were selected with the aid of local conservation authorities striving for diversity in soil type and land-use history, thereby reflecting the type of marginal grassland that was at risk of abandonment and overgrowth in the early 1970 s. Overall, the study sites represent different types of open lands that have been grazed for a long time (Steen, 1976). Before the trials began, most sites were grazed. However, one site (Dämkärr) had not been managed for three years, and one site (Gränö) had been mowed and irregularly fertilised for a decade. Furthermore, two of the sites (Gränö and Tagel arable) had a history as fertilised arable fields (up until approx. 10 and 20 years before the onset of the trials, respectively; Hansson, 1991). It is worth noting that these former, small arable fields were embedded in old-style, small-scale agricultural landscapes, where there used to be some degree of alternation between mowing and arable farming (Ekstam and Forshed, 1996). During the 20 years of grazing before the start of the trial, the Tagel arable was regularly fertilised (Hansson, 1991). Thus, at the onset, three of the trials (Dämkärr, Gränö and Tagel arable) might have been less floristically diverse and, consequently, less suited to manifest losses in biodiversity relevant for conservation. On the other hand, the encroachment of woody species is relevant to evaluate also on more fertile sites.

The sites differed in vegetation type and productivity; however, most of the sites were mesic meadows (Hansson, 1991). If using the Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora (Swedish Environmental Protection Agency, 2011), the sites would be classified as one or more of the following: semi-natural dry grasslands (6210), hay meadows in submontane zones (6510), Fennoscandian wooded pastures (9070), wet meadows (Molinion caeruleae) (6410).

The trial design was a block with two replicates (blocks). The blocks were most often parallel (Fig. 1b), with a randomised order of treatments within the block (in all but one trial). All woody plants at the sites were removed when the trials were set up. All treatment plots (5 × 20 m), except those grazed, were fenced. In one trial (Dämkärr), there were two grazed plots per block. The seven treatments were (Steen, 1976, Hansson, 1991):

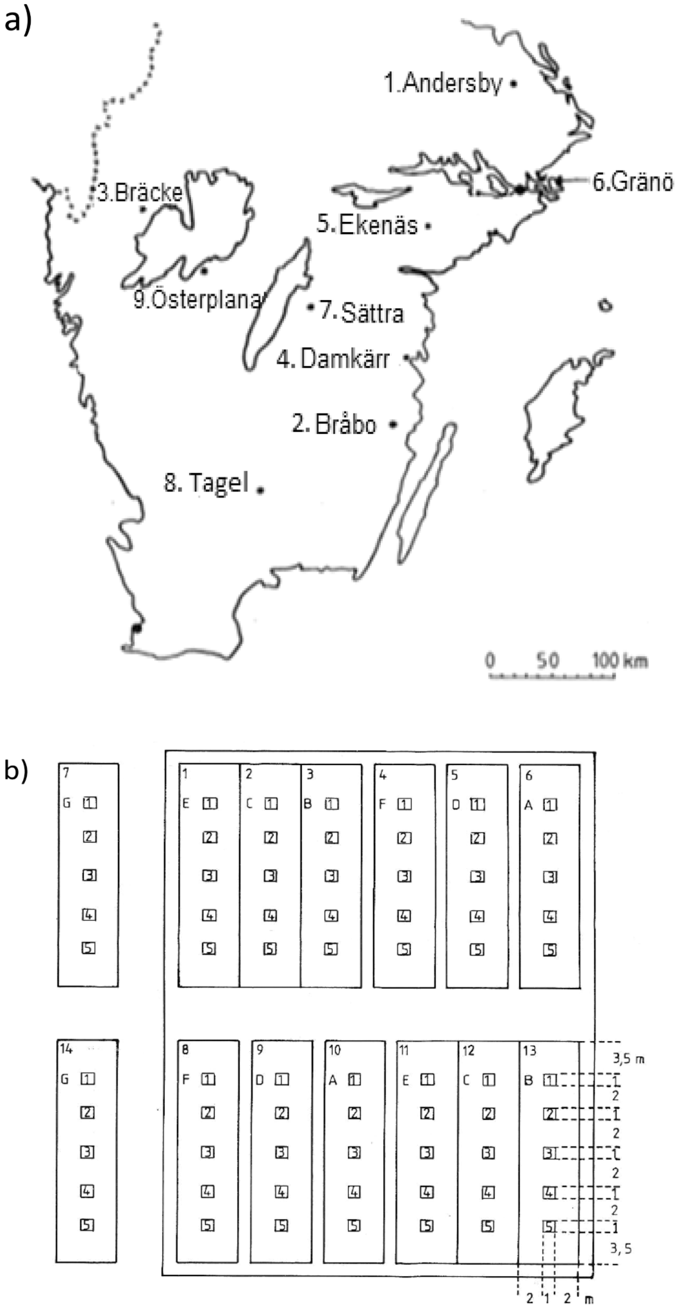

Fig. 1. a) Map of southern Sweden with the nine study sites; b) conceptual layout of a trial, with the five square-metre plots sampled in each of the 14 treatment plots (5 m*20 m). Treatment plots were organised in two blocks; all plots except those grazed were fenced.

A. Untreated control: no treatment.
B. Mowing once a year: Mowing was conducted in late July or early August, initially using a scythe but from 1982 using a sickle bar mower. The cut material was then removed by raking.
C. Mowing every third year: Mowing was conducted as described above but only every third year.
D. Herbicide treatment of woody plants. If woody plants were present, herbicides were applied to these plants (excluding *Rubus idaeus*) at the start of the trial, the following year, and thereafter “when needed”. This treatment was applied in conjunction with mowing, during which dead woody plants were removed. Initially, a combination of 2,4,5-T and 2,4-D was used. Since 1982, a combination of 2,4-D and MCPA has been used.
E. Mechanical removal of woody plants: Woody plants were cut by axe or pruning shears “when needed” (excluding *Rubus idaeus*).

Table 1
Description and years of inventory for the trial sites established in southern Sweden for the comparison of management methods in semi-natural grassland vegetation.

Site	Year of inventory					Vegetation type	Soil category	Management at start of trial	Grazing animal*	Grazing intensity*
	1973	1975	1980	1986	1987					
Andersby, Dannemora	x		x	x		Moist meadow	Humus-rich light clay	Grazing	Cattle	Low
Bråbo, Oskarshamn	x		x	x		Mesic meadow	Rock moraine	Grazing	Cattle	Normal
Bräcke, Åmål	x		x	x		Mesic meadow	Silt	Grazing	Cattle	Somewhat low
Dämkärr, Gamleby	x			x		Mesic meadow	Humus-rich silt	Abandoned	Cattle, sheep, horses	Low
Ekenäs, Flen										
Moist		x		x		Moist meadow	Highly humus-rich light clay	Grazing	Cattle	Normal
Mesic		x	x	x		Dry-mesic meadow	Humus-rich loamy	Grazing	Cattle	Normal
Gränö, Värmdö	x			x		Moist meadow	Slightly humus-rich silt	Mowing, fertilized	Cattle, sheep	No data
Sättra, Ödeshög	x		x	x		Mesic meadow	Slightly clayey sand	Grazing	Cattle	Low
Tagel, Alvesta										
Mesic	x		x	x		Mesic meadow	Rocky sand	Grazing	Sheep	High
Arable	x				x	Mesic meadow	-	Grazing, fertilized	Cattle	Somewhat low
Österplana, Götene	x		x	x		Dry meadow	Gravelly clay loam	Abandoned	Cattle	Somewhat low

* As assessed by Hansson (1991) during the final inventory.

F. Annual spring burning with mechanical removal of woody plants: Same as treatment E combined with burning in March or April (after snowmelt but before the onset of growth). Kerosene was used to start and promote fires, which consumed litter from the previous season, whereas fire breaks were created by watering. Because this treatment was weather-dependent, it failed on a few occasions, according to one trial manager. No records survive on the occurrence of such failures.
G. Grazing: According to the instruction, "normal" grazing intensity should be applied using cattle, or a combination of cattle and sheep. No consistent records were kept on stocking density or the type of animals used, but Hansson (1991) assessed the grazing intensity and grazing animals used at the end of the trials (Table 1). At that time, one site was grazed by sheep and was considered to have high grazing intensity, nine were grazed by cattle (three were considered to have satisfactory grazing intensity, three were "somewhat low" and three were low) while information is missing for one site.

Plots subjected to treatments A, D and F were surrounded by a 1 m safety buffer.

In the present study, we ranked the treatments in terms of their intensity, from annual mowing and grazing via spring burning to three low-intensity treatments (mowing every third year, herbicide application and mechanical removal) to the untreated control.

2.2. Previous follow-ups

The sites and 11 trials were described by Steen (1976), including data on the initial vegetation and soil chemistry in 1973 (nine trials) and 1975 (two trials). In eight trials, vegetation was assessed as the percentage of cover (or biomass) per species in the treatment plot (5 m × 20 m), whereas in the other three trials, cover according to the Hult-Sernander scale was assessed in 1-m^2 subplots (five or three per treatment plot). These differing inventory methods have made it difficult to incorporate early data into subsequent formal analyses (but see Milberg et al., 2014).

A follow-up of eight of the 11 trials was conducted in 1980, after six or seven years (1 and 7 trials, respectively; Fogelfors, 1982). Hansson (1991) visited all trials in 1986 (10 trials) and 1987 (one trial) after 12, 13 and 14 years (two, eight and one sites, respectively). During the latter two inventories, the cover of plant species was recorded in five fixed square metre plots (except for Bräcke, where three square metre plots were surveyed) per treatment and block (Fig. 1b). Hansson (1991) presented data on plant species, chemical soil analyses and maps of dominant vegetation types and noteworthy species.

After Hansson's inventory in, 1986–87, financial support ceased, and most of the trials were abandoned. However, management of some of the treatments continued at three sites, which enabled long-term follow-up of vegetation development: 1990 (Österplana; Milberg and Hansson (1994, 1991) (Sättra; Milberg, 1995), 2000 (Sättra; Wahlman and Milberg, 2002), 2005 (Österplana; Roffey, 2006), 2011 (Sättra; Milberg et al., 2014) and 2012 (Bråbo; Tälle, 2013). The current status (2022) of these three trials is as follows: (i) the trial at Sättra is still running with six of the seven original treatments; (ii) the full trial at Österplana ran until 1991, but since then, only the grazing and control plots have been maintained; and (iii) the trial at Bråbo was abandoned after 2012.

So far, the full results have only been presented in Swedish (in a detailed departmental report with limited circulation; Hansson, 1991). Some of the data for the selected methods have been analysed more recently: spring burning (Milberg et al., 2014, 2018); mowing vs. grazing (Tälle et al., 2015); and mowing of different intensities (Milberg et al., 2017). In addition, data from one of the trials (Ekenäs mesic) were analysed and presented by Hansson and Fogelfors (2000).

2.3. Vegetation database

All known vegetation data from the 11 trials were compiled into a database [https://www.doi.org/10.5281/zenodo.6570242]. The main part of these data and metadata are from three Swedish reports (Steen, 1976; Fogelfors, 1982; Hansson, 1991), but additional data from later surveys have also been included (Milberg and Hansson, 1994; Milberg, 1995; Wahlman and Milberg, 2002; Roffey, 2006; Tälle, 2013; Milberg et al., 2014). Compiling this database involved aligning the nomenclature (Karlsson, 1998) and correcting typing and printing errors.

2.4. Statistical analyses

In the present study, we used data from the last comprehensive inventory from 1986 to 87, approx. 13 years after the trials began, to analyse the development of vegetation using different management methods. In several of the analyses, we used data from "annual mowing" as the control. This was preferred over "grazing" as the latter is sensitive to grazing intensity.

2.4.1. Plant species characteristics

For analyses on the effects of management methods on the encroachment of woody plants, management-dependent species, low-grown species and species attractive to pollinators, the attributes of plant species were classified or assigned a value.

Tree and shrub species with woody stems were classified as woody plant species, except for the semi-woody species *R. idaeus* and *Rubus* subg. *Rubus*. We used the classifications of Tyler et al. (2021) to classify species based on their response to management (hereafter, *management dependence*) using an eight-degree scale, where 1 indicates that a species does not endure any grazing/mowing and 8 indicates that a species requires continuous or repeated grazing/mowing. Species were assigned a height value from information available in the LEDA trait database ("Life history traits of the northwest European flora: a DAtabase"; Kleyer et al., 2008). For species with more than one record in LEDA, we used the average height across all records. Species not included in Tyler et al. (2021) or the LEDA trait database (Kleyer et al., 2008) remained unclassified, as did plants identified only at the genus level in the inventory. Finally,

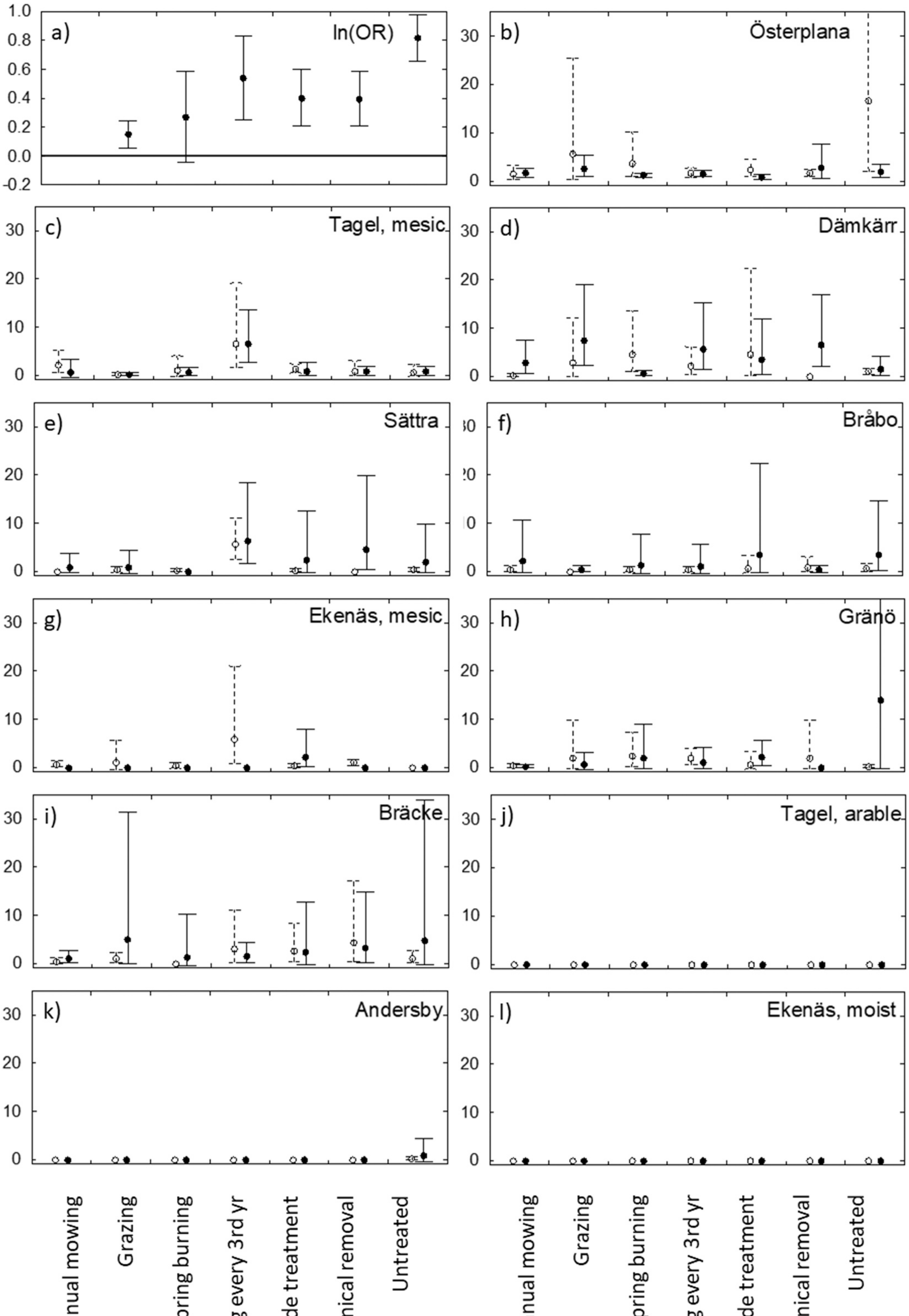

Fig. 2. Woody species in management trials after 12, 13 or 14 years. a) Meta-analyses of odds of finding woody species in each treatment. A negative value means higher odds of finding woody species with annual mowing. Three sites with no or few woody species were excluded from the

analysis. b-l) Site-wise results showing average percentage cover of woody species in square-metre plots, per block (two blocks were used). Average and $CI_{95\%}$ were calculated on logit-transformed data, here back-transformed to facilitate interpretation. Trials are organised from the least (Österplana) to the most (Ekenäs moist) productive site.

some plant species were classified as "pollinator-attracting plants", based on several sources (mainly Ehlers et al., 2021 and Tyler et al., 2021). These species typically attract pollinators owing to their ability to produce pollen and/or nectar.

2.4.2. Statistics

For woody plant species, the average percentage cover of woody plant species was calculated across all subplots per block, treatment and site. Averages were calculated using logit-transformed data and used for display purposes only. In addition, the average number of pollinator-attracting and non-attracting species across all subplots per treatment plot and site were calculated. The logarithm of the odds ratio [ln(OR)] of the occurrence of woody or pollinator-attracting species per site and treatment plot, using annual mowing as the control, was calculated using the following equation:

$$\ln(OR) = \ln[(a * d)/(b * c)]$$

where a is the frequency of woody or pollinator-attracting species with annual mowing (control), b is the frequency of non-woody or non-attracting species with annual mowing, c is the frequency of woody or pollinator-attracting species with treatment and d is the frequency of non-woody or non-attracting species with treatment. These values were used to calculate the mean and variance of ln(OR) across the two blocks per site and treatment.

Species richness was calculated as the mean number of species per m^2, across all subplots for the individual sites and treatment plots. Additionally, the total number of species per treatment plot and the mean across the two plots per treatment and site were calculated. Information on the management dependence or plant height of individual species and the frequency of occurrence of individual species was used to calculate the weighted mean of all species for each site and treatment. The mean species richness, weighted mean management dependence and plant height per treatment and site were used to calculate separate response ratios (RR) for each treatment and site, contrasting each treatment with the annual mowing (control). To avoid bias in RR due to small sample sizes, Lajeunesse (2015) method was used for calculating ln (RR) and the variance in ln (RR).

$$\ln(RR) = \ln(X_T/X_C + 1/2[SD_T^2/N_T X_T^2 - SD_C^2/N_C X_C^2]$$

$$\mathrm{var}(RR) = [SD_T^2/N_T X_T^2 + SD_C^2/N_C X_C^2] + 1/2[SD_T^4/N_T^2 X_T^4 + SD_C^4/N_C^2 X_C^4]$$

where, X is the mean, T is the treatment group, C is the control group (annual mowing), SD is the standard deviation and N is the sample size.

The calculated values for ln(OR) and ln(RR) were used to perform random-effects meta-analyses, with each site and treatment contributing a single value, and with separate meta-analyses performed for each treatment. For the meta-analysis of woody species, three sites with few or no woody species were excluded. Meta-analyses were performed in R (R Core Team, 2017), using the Metafor package (Viechtbauer, 2010).

The species composition at each site and treatment was analysed in a partial RDA, using the two blocks as categorical covariables (performed in CANOCO 5.12; Ter Braak and Šmilauer, 2018).

3. Results

3.1. Woody species

Overall, the odds of finding woody species was lowest with grazing and highest when vegetation was left unmanaged (the odds was 2.2 times higher than when mowing), while low-intensity management, i.e. mowing every third year, and mechanical and chemical treatment of woody species (that occurred "when needed") resulted in intermediate odds of finding woody species (Fig. 2a; i.e the odds was 1.5 times higher than mowing). The three most productive sites had no or very limited occurrences of woody species (Figs. 2j-2l).

3.2. Plant species number

Overall, the number of species per m^2 was higher with annual mowing than with the other treatments, except for grazing, where species richness was similar for both treatments (Fig. 3a). In the untreated plots, approximately 30% of the species per square meter were lost, and approximately 20% were lost in the treatments of intermediate intensity. In individual sites, species richness was generally the highest with either mowing or grazing and the lowest in unmanaged plots (Fig. 3b-l).

3.3. Management dependence, plant height and pollinator-attracting plants

The average management dependence index of species (AMD) was the highest, and the average plant height index (APH) of species was the lowest with annual mowing, except for grazing, where the effects were similar (Fig. 4a-b). AMD in the untreated control was

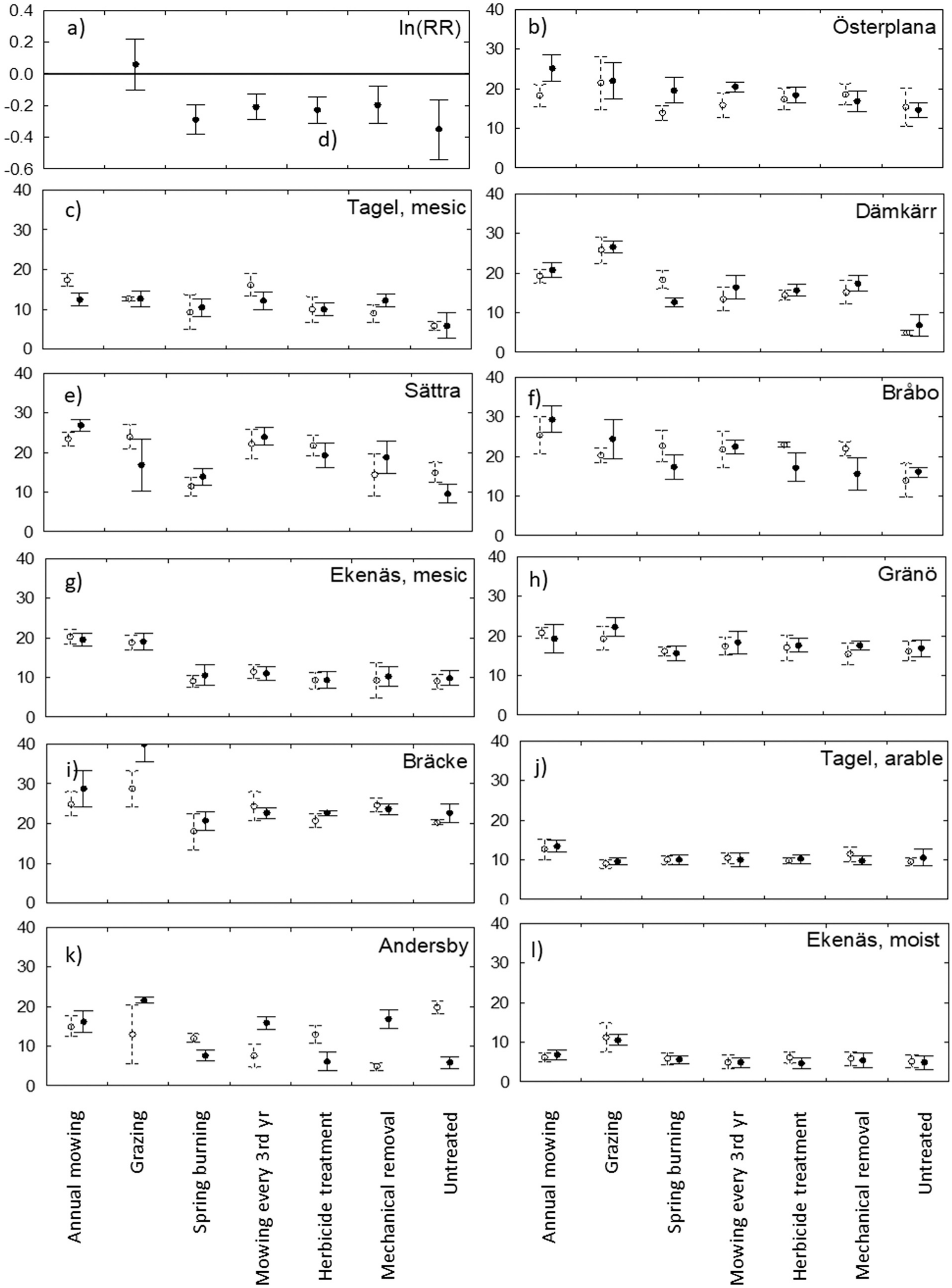

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Fig. 3. The number of species per block (a) or per m^2 (b-l) in management trials after 12, 13 or 14 years. a) Meta-analyses conducted of response ratios (ln(RR)) contrasting the treatments with annual mowing. A negative value means the number of species was higher with annual mowing. b-l) Site-wise results showing the average number of species in square-metre plots, per block (two blocks were used), with $CI_{95\%}$. Trials are organised from the least (Österplana) to the most (Ekenäs moist) productive site.

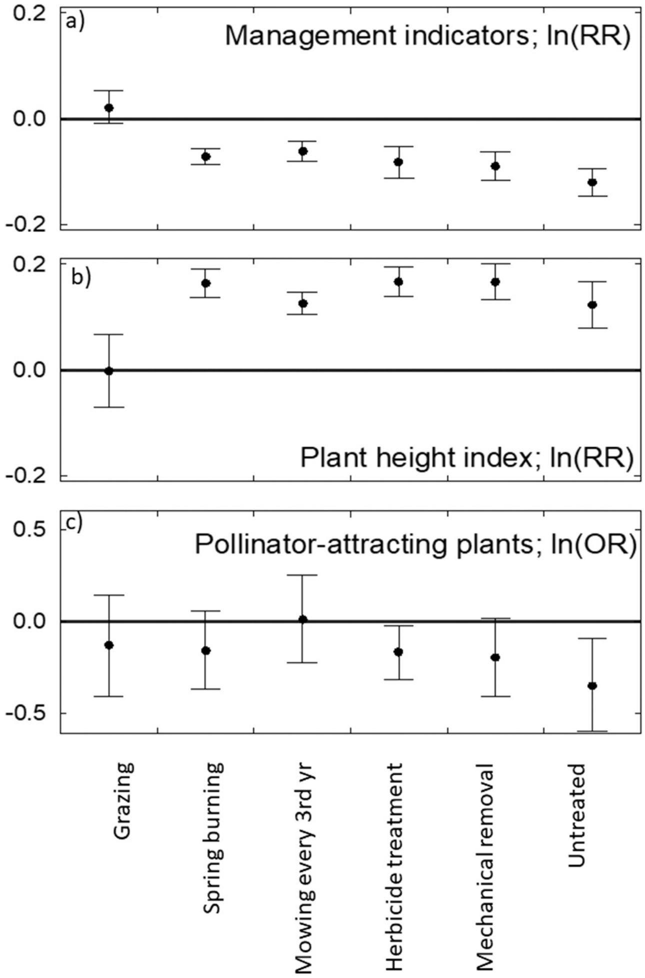

Fig. 4. Results from meta-analyses conducted of response ratios (ln(RR)) or odds ratios (ln(OR)), contrasting treatments with annual mowing in management trials after 12, 13 or 14 years. The average a) management dependence, b) plant height, or c) prevalence of pollinator-attracting plant species, with $CI_{95\%}$. A negative value means higher management dependence, plant height and prevalence of pollinator-attracting plants with annual mowing.

11% lower, and 5–9% lower in treatments with intermediate intensity. Compared to mowing, the APH index was approximately 15% higher, with only small differences between treatments.

The odds of a random species being one that attracts pollinators were the highest under annual mowing and mowing every 3rd year (Fig. 4c). It was significantly lower in the low-intensity treatments than in the control group (Fig. 4c). The effect sizes, with a maximum 50% reduction in the odds, were relatively small (Chen et al., 2010).

3.4. Species composition

To some extent, the species composition responses were similar across treatments, in that one or both high-intensity treatments were differentiated from the other treatments along the first ordination axis (Fig. 5). At five of the least productive sites, the composition of the grazing plots was clearly differentiated from all other treatments along the first axis. Two of the sites were scored as having low grazing intensity (Sättra, Dämkärr), an observation suggesting that grazing there in reality represented an intermediate management intensity rather than the high intensity implied by “grazing”. This was suggested at one site (Sättra) where grazing ended close to the intermediate-intensity treatments in the ordination space, but not at the other site (Dämkärr; Fig. 5).

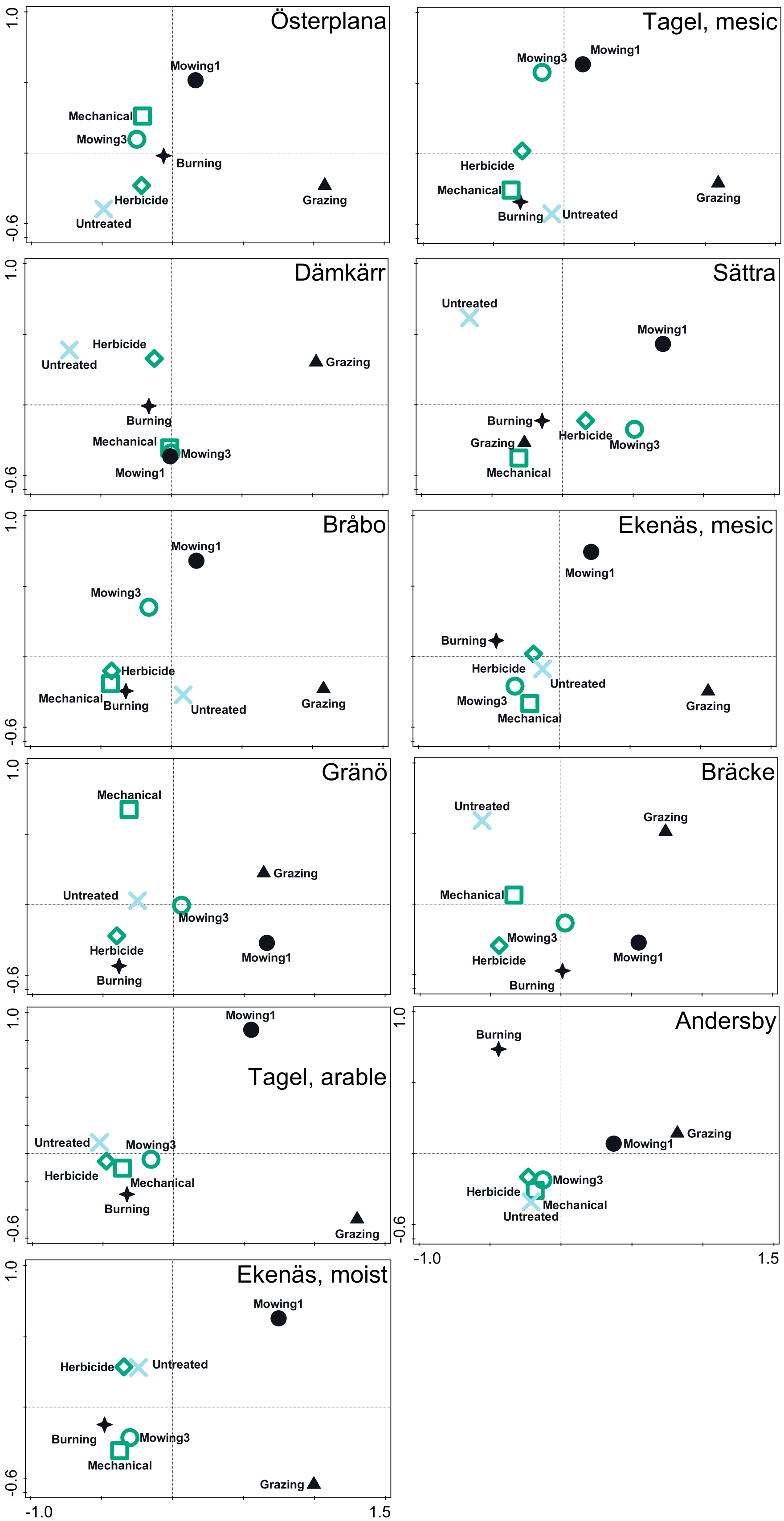

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Fig. 5. RDA of species composition in the seven treatments at the eleven sites, 12, 13 or 14 years after the start of the management trial. Data from each site was subjected to partial RDA, using the two blocks per site as categorical covariables.

There were rarely consistent between-site patterns among the intermediate- or low-intensity treatments, suggesting either a low effect size or that unique site factors may play a substantial role in modulating the treatment effect (Fig. 5). In other words, there were considerable differences in vegetation development among the trials and treatments.

4. Discussion

The best management methods to prevent encroachment of woody plants and to maintain species-rich vegetation containing management-dependent and low-grown species that are attractive to pollinators are annual mowing and grazing, whereas the worst management method is no management. The four treatments of intermediate intensity often performed better than the untreated control but worse than mowing and grazing. This was the expected outcome when the trials were initiated 50 years ago (Steen, 1976), and is further supported by similar trials that were initiated in the 1970 s in Germany and Switzerland (Köhler et al., 2005; Schreiber et al., 2009), as well as other studies (e.g. Isselstein et al., 2005, Gaujour et al., 2012). Therefore, we considered intensive treatments (i.e. grazing and annual mowing) as controls in the current study. Also "no treatment" could be considered a control, allowing us to place the remaining four alternative treatments between the worst and best possible outcome.

4.1. *Preventing encroachment of woody plants*

The four treatments of intermediate intensity in our study turned out to be in-between mowing or grazing and the untreated control when it comes to their ability to prevent encroachment of woody plants. This indicates that higher management intensity is needed to prevent afforestation, as suggested by other studies (Köhler et al., 2005; Schreiber et al., 2009; Calleja et al., 2019; Rupprecht et al., 2022). However, intermediate-intensity treatments could slow the succession from grassland to forest considerably, possibly preventing it for as long as the treatments continue. Nevertheless, there are negative effects of woody species, partly affected by the density of woody plants: Woody species may cause out-shading of low-grown plants (Einarsson and Milberg, 1999), negatively affect seed germination or seedling recruitment (Voigtländer and Jacob, 1987; Roscher et al., 2011), and negatively affect organisms like orthopterans (Bieringer and Zulka, 2003). Under intensive management, out-shading is less likely to occur, as the establishment of woody plants is prevented (Laborde and Thompson, 2013). This is also likely the case with intermittent removal of woody shoots in less intense treatments. However, there are other negative effects of woody shoots unrelated to shading. First, management costs may increase: even if a shoot can be cut, the stumps left might survive and grow to dimensions that cause problems as implements might get stuck or even break down, cutting time might increase, and cutting might be uneven (Per Milberg, personal observation). Secondly, woody materials can decrease fodder quality and cause problems in hay handling (Hejcmanova et al. 2014; Hejcman et al., 2016; Pauler et al., 2020). Hence, irrespective of shading, the occurrence of woody plants is undesirable and should be minimised. If a site has higher densities of woody shoots, less intense management seems ill-advised.

Four of the trials involved initial restoration management where woody plants were removed before the onset of the trial (Andersby, Dämkärr, Sättra, Tagel mesic). Despite annual mowing or grazing for 13 years, woody plants persisted in high numbers in the three least productive trials (Sättra, Dämkärr and Tagel mesic), which has implications for both the management of such sites and for the selection of sites suitable for restoration. First, more intense management (e.g. mowing several times a year) might be needed, at least initially, when many woody shoots are present. Second, when selecting sites for restoration, and when making management priorities among patches within a grassland of high conservation value - a likely future scenario - careful consideration of the presence of woody species is needed. The fact that they may persist for a long time may prohibit the use of less intense management methods, leading to higher management costs.

It is noteworthy that at three sites, after 13 years of no management, woody plants were completely (Tagel arable and Ekenäs moist) or almost completely (Andersby) absent from the untreated control plots. These three trials were also deemed the most productive, indicating that tree and shrub invasions are slow in productive grasslands, presumably because the seedling establishment is hampered by dense grass swards (Voigtländer and Jacob, 1987; Milberg, 1993; Roscher et al., 2011). Hence, it seems productive grassland can remain open for long periods after abandonment, at least if it lacks *Populus tremula* and other species that produce suckers. The most productive sites are often less valuable from the point of view of species conservation (Milberg et al., 2016, 2020), suggesting that more productive sites will retain their openness, while losing few species, under low-intensity treatments, whereas the most valuable sites from the point of view of conservation are most prone to shrub and tree encroachment and loss of species, thereby requiring more intense management.

4.2. *Maintaining vegetation attributes*

4.2.1. *Species richness, management dependence and plant height*

The treatments of high intensity (grazing and annual mowing) consistently resulted in the best outcomes in terms of species richness, management dependence of plant species and plant height, which was in line with expectations and previous publications (Kahmen et al., 2002; Pykälä, 2003; Köhler, Öckinger et al., 2005, 2006; Jacquemyn et al., 2011). While studies have revealed that less intense management (lower frequency of cutting) can result in similar species diversity as more intense management (e.g. Tälle et al., 2018), in the current study, the treatments of intermediate management intensity were only moderately better than the no treatment in terms of preserving species richness or occurrence of management-dependent species. Unsurprisingly, previous analyses of parts of the current data have reached similar conclusions regarding the effects of spring burning (Milberg et al., 2014) and mowing every third year (Milberg et al., 2017).

Tall-grown species can cause the out-shading of low-grown plants; however, this can be prevented under higher management intensities (Liira and Zobel, 2000). Our results revealed that plant heights were similar for intermediate management intensities and no treatment; thus, these were not suitable long-term alternatives. Thus, intermediate-intensity treatments are unlikely to be long-term alternatives to grazing and annual mowing, if the aim is to preserve species richness or the occurrence of management-dependent and short-grown plant species. However, shorter periods of low-intensity treatment might be a way to extend limited resources to larger areas (Milberg et al., 2017).

4.2.2. Pollinator-attracting plants

Fewer plants were attractive to pollinators in the two intermediate-intensity treatments (mechanical removal and chemical treatment) and the untreated control. Thus, within the timeframe of these experiments, despite drastic changes in species composition, there were no changes in the occurrence of pollinator-attracting plant species with spring burning or mowing every third year. This is noteworthy, especially because a similar method applied to observational data from grassland with a 10-year follow-up reported clear declining trends despite continued management (Ehlers et al., 2021). However, studies that have focused directly on the abundance and/or diversity of pollinators have confirmed the benefits of low-intensity management (Potts et al., 2009; Weiner et al., 2011; Millard et al., 2021). Hence, if the density of pollinator-attracting plant species is a key feature, somewhat relaxed management might be an option (see also Milberg et al., 2018).

4.2.3. Species composition

Species composition diverged during the approximately 13 years of differing management practices. This was expected based on similar evaluations of management methods in the same (Milberg, 1995; Hansson and Fogelfors, 2000; Wahlman and Milberg, 2002) as well as other species-rich grasslands (Kahmen et al., 2002; Köhler et al., 2005). The untreated control, where the expected changes were the largest, was often an outlier, but sometimes lined up among the treatments of intermediate intensity. The latter was the case in most species-poor sites (Ekenäs moist, Andersby, Tagel arable and Tagel mesic), demonstrating that the manifestation of a treatment effect varies depending on species richness and composition at a site. In contrast, grazing and mowing were outliers in most trials, indicating the superiority of these treatments to preserve species-rich grasslands. In three of the four least productive sites, grazing stood out as the most diverging treatment (Österplana, Tagel mesic and Dämkärr), whereas mowing stood out at one site (Sättra) where the grazing intensity was low (Hansson, 1991).

4.3. Drivers of change

The competitive exclusion of some low-growth plant species, as management is relaxed, is likely an important driver for the results documented in these trials over their relatively short study duration, as indicated by the increase in the height index. Furthermore, a more detailed analysis of data from these trials (Milberg et al., 2017) revealed that the occurrence of low-growth species decrease when management is relaxed. Finally, according to observational data from southern Sweden, low-grown species are disadvantaged at sites with high productivity, tall grass swards and large amounts of litter (Milberg et al., 2020). In other words, if competitive exclusion is the main driver, we would expect treatments that prevent the encroachment of woody species but otherwise do not affect vegetation (i. e. chemical control and mechanical removal) to be similar to the untreated control. Although this was often the case, at some sites, the conditions in control plots clearly worsened (Tagel Mesic, Dämkärr, Sättra). Notably, these three sites were among the four that were cleared by woody species at onset, indicating a possible additional negative effect of the presence of woody species. On the other hand, these two treatments (chemical control and mechanical removal) involved, especially at sites that had been pre-cleared of woody plants, annual visits for management with trampling not experienced in the control plots. Therefore, although competitive exclusion is likely to be the main driver of compositional change, it may not be the only one.

Shading is a potential driver. The encroachment of woody species eventually causes shading of the ground flora and loss of species as succession proceeds from grassland to forest. This was clearly demonstrated at Sättra in 2022 (personal observation by Per Milberg 2022, Milberg, 1995, Wahlman and Milberg, 2002) and Bråbo in 2012 (Per Milberg, personal observation), where the untreated control plots contained tall and dense canopies of deciduous trees. However, shading by woody species was not an important factor in most of these trials over the time frame considered, because it was only in some of the untreated control plots that woody species had started to form a closing canopy. Therefore, the species loss documented in these trials was not a consequence of tree encroachment. Another aspect of shading occurs within grass swards, where less light penetrates when the sward is taller or denser (Liira et al., 2012; Boob et al., 2021). This would disproportionately affect short-grown species over tall-grown, leading to more tall-grown species, which turned out to be the case under less-intense management in our study. Furthermore, it is worth noting that seedling recruitment can also be negatively affected by less solar radiation at the soil surface (Hautier et al., 2009; DeMalach and Kadmon, 2017) and thus potentially affecting species composition. In conclusion, shading by trees or shrubs is unlikely to have affected the data observed in this study, whereas shading within a denser and taller sward is a more likely driver.

Changes in soil chemistry can also be an important driver of secondary succession (e.g. Maharning et al., 2009, Urbina et al., 2020, Coradini et al., 2022), but in the current trials, plot-wise changes over time were only small and inconsistent (pH, N, P and K; Hansson, 1991). Hence, it seems that such changes are slow and rarely detectable in short-term studies (Broll and Schreiber, 1994, Dupré and

Diekmann, 2001, Schnoor and Olsson, 2010, Rosenthal, 2010). Furthermore, even after 30 years of follow-up in a grassland management trial in Germany, changes in soil chemistry were modest or absent (Schreiber et al., 2009). Hence, on the timescale considered here, vegetation changes caused by changes in soil conditions are unlikely to be drivers of change (but see Pavlů et al., 2022).

4.4. Low management intensity vs rewilding

Although the stated aim of rewilding (Monbiot, 2013; Dehaut, 2023; Hart et al., 2023) might not be to "keep the landscape open", there are some parallels to the 1970 s aim to find cheap means to prevent conversion of grassland to forests (Steen, 1976, Schreiber et al., 2009). Rewilding invariably involves grazing with large herbivores, in large areas of often marginal or abandoned agricultural land. As herbivores differ in grazing preferences (Cromsigt et al., 2018, Zielke et al., 2019), their composition and density, together with whether predators are present, are key issues when launching a rewilding project, both affecting the grazing pressure, making the trajectory of individual projects very different (Hart et al., 2023). Compared with agricultural (or traditional) grazing, there are at least three significant differences with the rewilding paradigm: First, grazing occurs during the full year likely forcing the consumption of woody species even among traditional grazers like horses (Garrido et al., 2021). Second, animals can more freely choose were to graze, causing increasing vegetational heterogeneity (Schulte to Bühne et al., 2022). Third, as rewilding stocking densities are determined by winter conditions (but see Theunissen 2019), grazing pressure during the growing season is presumably lower than under agricultural grazing where densities are adjusted to grass growth in the summer to maximise animal production. As the experimental evidence-base regarding rewilding is slim (Hart et al., 2023), our study might provide some input for such project in northern Europe, where the growing season is short. Grazing hotspots may be kept open in a rewilding project, and especially so in more productive, grass-covered areas where woody species are slow to invade. Forested areas are likely to resemble the intermediate management intensities in the current study. Hence, even if woody plants might be kept down by winter browsing, the vegetation will likely become less species rich.

4.5. Methodological implications

Some methodological issues emerged from this replicated multi-site experiment, which was initiated 50 years ago. First, spatial replication of field experiments is crucial to enable the assessment of the transferability of results (Filazzola and Cahill, 2021). In the current study, the outcomes varied considerably among the 11 trials, as they did in the corresponding series of 14 trials in Germany (Schreiber et al., 2009) and two trials in Switzerland (Köhler et al., 2005). Hence, when analysing a single trial (e.g. Hansson and Fogelfors, 2000, Kahmen et al., 2002, Wahlman and Milberg, 2002), particular attention should be paid to the transferability of the conclusions.

Second, in the current study, we chose to present data per block (Figs. 2, 3) to be able to check for within-site consistency. Local spatial variability in treatment effects turned out to be small at all sites except one (Andersby), and there was rarely a discernible block effect. This clearly places the main part of the variability in responses between, and not within, the sites. Hence, replicating an experiment over several sites appears to be more important than intensive replication within sites.

Third, a challenge when delimiting or communicating the results from an experiment is to specify what is actually being spatially replicated. In the current study, the trial sites were not selected to be true replicates of a single vegetation type, but rather to represent the range of sites likely to be abandoned, approaching what in other fields is called maximum variation sampling (compared with strategic or homogeneous sampling; Cresswell, 1998, Kim et al., 2017). The differing types of "replication" constitute a challenge if the results are to be included in meta-analyses because of the intentional exclusion/inclusion of site variation among studies.

Finally, three attributes of long-term experiments are worth noting, and they probably apply to ecological experiments that span longer times than those normally funded by granting agencies. First, initial questions become less relevant over time as new data emerge. In the current trial, the plan was to run the experiment for at least 20 years. However, funding ceased after approximately 13 years. At one site (Bråbo), management continued for many years, and at another (Sättra), management is still ongoing as a demonstration site, relying on local initiatives in both cases. This is a case where long-term trials come out short in competition for grants as original questions have become outdated (Andersson and Milberg, 1998; Silvertown et al., 2006). Second, in long-term ecological experiments, new methods can emerge that make old ones obsolete, creating inconsistencies in data and limiting their usefulness. Unfortunately, in the present case, changing the method for vegetation sampling during the trials made it more difficult to assess the temporal trend of treatment effects (cf. Köhler et al., 2005) and is why we focused only on uniformly collected data from the final survey. Third, it was possible to expand and introduce new questions to the initial questions in a long-term experiment. In the current study, we have added the prevalence of pollinator-attracting plant species and plant height. It is also possible to turn (parts of) plots into new experiments (Silvertown et al., 2006; plots at Ekenäs mesic were used for a new experiment; Hansson and Persson, 1994).

5. Conclusions

Less intense management methods do not constitute long-term management alternatives to grazing and annual mowing, if the aim is to preserve the typical features of species-rich grasslands. However, they may be short-term alternatives at sites where the recruitment of woody species is absent or rare. Less intensive management might be a more useful alternative in more productive sites, where the recruitment of woody species is slow or inhibited.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data is published at Zenodo https://www.doi.org/10.5281/zenodo.6570242.

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