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Grazing vs. mowing: A meta-analysis of biodiversity benefits for grassland management



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ABSTRACT

To maintain the high biodiversity of semi-natural grasslands, management by grazing or mowing is needed. Given the limited resources and few remaining areas, the best management method should be used. However, only a few studies comparing the effects of mowing and grazing on grassland biodiversity exists. Therefore, the goal of the present review was to extract as much data as possible from the literature and evaluate them using a meta-analysis approach. We searched scientific and grey literature for studies comparing the effects of grazing and annual mowing on outcomes relevant for biodiversity conservation. We identified 35 relevant studies on grazing and annual mowing that provided data suitable for the meta-analysis. We found that grazing generally had a more positive effect on the conservation value of semi-natural grasslands compared to mowing, but effect sizes were generally small to moderate for most contrasts. Furthermore, effects varied across some grassland characteristics e.g. for different grassland types, with grazing and mowing having a similar effect or mowing having a more positive effect in certain cases. Our results suggest, that in most cases grazing should be the preferred management method when managing for grassland conservation.

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1. Introduction

Grasslands are defined as habitats characterized by a mixture of native grasses and dicotyledonous herbs, and with a low proportion of woody species. They cover large areas and occur all over the globe. Generally, grasslands have been formed in climates not suitable for woody vegetation (e.g. steppe or prairie), or by natural disturbances such as fire or herbivory (e.g. savanna). Semi-natural grasslands are defined as grasslands modified by human activities, originating from deforestation or alteration of natural grasslands (Crofts and Jefferson, 1994; Gibson, 2009). In many cases semi-natural grasslands have been created and maintained by traditional agricultural practices since the Neolithic Age (Poschlod et al., 2009). Hence, they have not been modified by intense agricultural practices, like the regular use of inorganic fertilizers or herbicides (Crofts and Jefferson, 1994).

Apart from forage, semi-natural grasslands provide essential ecosystem services such as pollination (Öckinger and Smith, 2007). soil carbon sequestration (De Devn et al., 2011) and erosion regulation (Bazzoffi, 2009). In addition, semi-natural grasslands often maintain a high biodiversity (WallisDeVries et al., 2002; Pärtel et al., 2005; Wilson et al., 2012) and harbour a high number of both plant (e.g. Zhou et al., 2002; Verrier and Kirkpatrick, 2005; Chytrý et al., 2015) and animal species (e.g. Swengel, 1998; D'Aniello et al., 2011; Shi et al., 2014). Some meadows even belong to the most species-rich habitats in the man-made landscape of Central Europe (Poschlod et al., 2009; Wilson et al., 2012). Many of the species present in this habitat type are confined to it and hence highly dependent on it for their survival. Therefore, semi-natural grasslands are widely recognized to be of high conservation value (Crofts and Jefferson, 1994). Substantial resources are spent on their preservation each year, e.g. in Europe by economic subsidies provided by the European Union (European Commission Directorate General for Agriculture and Rural Development, 2005). However, the funds are not sufficient to protect all grasslands of high conservation value.

Management is often required to prevent afforestation of seminatural grasslands (Hansson and Fogelfors, 2000; Wahlman and Milberg, 2002). Furthermore, the removal of above-ground biomass by grazing and mowing promotes the biodiversity of semi-natural grasslands through the depletion of nutrients (Al-Mufti et al., 1977). Therefore, there is a clear association between high species richness, occurrence of rare species and the management of semi-natural grasslands (Pykälä, 2003; Klimek et al., 2007). During the Neolithic Period domestication of livestock resulted in the creation of grasslands as a consequence of grazing of forests or clear cuts adjacent to settlements. The application of mowing was only introduced in the Roman Period. From the Medieval Age onwards, mowing for hay and grazing became a vital part of the mixed farming system that developed in Europe (Poschlod and WallisDeVries, 2002; Poschlod et al., 2009). Hay-making was closely associated with the winter-stabling of livestock, summer grazing and availability of manure for fertilization of arable fields (Pedersen and Widgren, 2011). During the second half of the 20th century agricultural practices were modernized and intensified, with an increasing use of inorganic fertilizers to increase yields. Considerable area of grasslands have been abandoned or been converted to arable land or highyielding grasslands in many areas; in other cases grasslands were converted to forests through tree planting or natural succession, leading to the loss of grasslands and grassland biodiversity (Milberg, 1995; Krebs et al., 1999; Hansson and Fogelfors, 2000; Firbank, 2005; Poschlod et al., 2005; Moller et al., 2008; Briske et al., 2015). As a consequence, many of the species that thrive in this habitat type have become rare and threatened (The IUCN Red List of Threatened Species, 2014).

Maintenance of traditionally managed species-rich grasslands is becoming increasingly difficult, partly due to the high costs of mowing (i.e. cutting and removal of cut plant material) (Schreiber et al., 2009). Furthermore, the number of available grazers are limited as a consequence of the decreasing number of livestock herds (Kumm, 2003) and the increase in the number of potential grazers being kept in stables and fed silage (Poschlod, 2015). Therefore, to optimize the utilization of the limited resources available for biodiversity conservation, it is crucial to improve the management choice to ensure that the "best" management option is used. In spite of this urgent need, relatively few studies have evaluated the benefits and disadvantages of the two most widely applied management methods: grazing and mowing once a year (henceforth termed "annual mowing"). Even fewer studies have compared the two methods and the conclusions have often been contradicting, with more positive effects of grazing (e.g. Cauwer and Reheul, 2009; D'Aniello et al., 2011), mowing (e.g. Wahlman and Milberg, 2002; Grandchamp et al., 2005; Tälle et al., 2015), or positive effects of both grazing and mowing (e.g. Kahmen et al., 2002; Saarinen and Jantunen, 2005). Furthermore, many of the available comparisons are of low quality, often unreplicated and do not span more than a few seasons (Milberg et al., 2014; Milberg and Bergman, 2014). As a result, the effects of the potential management options on biodiversity remain poorly understood, and there is no clear guideline for choosing the most proper conservation measure.

A meta-analysis approach enables a critical evaluation and synthesizing of available studies regarding a specific research question. It can overcome the problem with low quality studies and the lack of conclusive results to some degree, by weighting studies when pooling for effect size (Pullin and Knight, 2001; Milberg, 2014). Our goal was to determine whether grazing or annual mowing is more effective in preserving the biodiversity of seminatural grasslands, by reviewing the literature, and evaluate as much as possible of the available data in meta-analyses. We aimed to determine the best available management method and give direct recommendations for the management of semi-natural grasslands.

2. Methods

2.1. Search strategy

In October 2014 studies, in any language, comparing grazing and mowing were searched for in the databases Scopus, Biological Sciences and Biological Abstract. The search terms used were mow* or scythe*; graz*; grassland*, meadow*, pasture*, fen* or heath* (where * indicates a wild card). In addition we used Agricola, a database containing literature citations relating to all aspects of agriculture, using the search terms mow* and graz*. As our goal was to determine the best management method for preserving the conservation value of grasslands we included all studies comparing grazing and mowing performed in grasslands irrespectively of the grassland type and location. A list of 1024 unique articles resulted from the literature search. From these articles, we selected 11 highly relevant articles which consisted of experimental studies comparing grazing and mowing for the purpose of grassland conservation. We used their reference lists and the papers in which these studies were cited to add articles not previously found in the database search. In total 1770 studies were included for further analysis.

2.2. Study inclusion criteria

First, the studies from the literature search were filtered by title and 639 irrelevant articles were excluded. Second, the abstracts of the 1131 remaining studies were examined, and any study which compared grazing and mowing was kept for the next stage. As mowing with aftermath grazing is a common (and traditional) management method in semi-natural grasslands (Crofts and Jefferson, 1994; Pedersen and Widgren, 2011), studies using this treatment type were also kept for the next stage. We excluded studies comparing grazing and mulching (i.e. cutting of plant material into small pieces which are left in the grassland), as few studies comparing them exist. Furthermore, management using mulching was not comparable with mowing due to the cut material being left in grasslands to decompose as compared to removing it. If the title of an article was ambiguous or the abstract was missing or ambiguous the study was brought forward to the next stage. In the end, the full text of 537 articles remained after the abstract examination. For 12 of these it was impossible to retrieve the full text and they were therefore excluded, leaving 525 papers that were examined in detail.

Third, articles eligible for inclusion in the meta-analysis had to compare grazing vs. mowing or grazing vs. mowing with aftermath grazing. We only included studies where mowing was performed once a year. The traditional mowing regime varies between different regions and for different grassland types, however mowing once a year is the most common mowing regime in species-rich semi-natural grasslands (Kapfer, 2010; Hejcman et al., 2013). We only included studies where the goal was to preserve the high conservation value of grasslands, e.g. management for high species richness. Therefore, studies which only reported e.g. annual yield were excluded from further analysis. To be included, the management had to be considered to directly affect the effect measures e.g. studies only measuring soil nutrients were excluded but not e.g. studies reporting species richness. Furthermore, included studies had to contain data in the form of estimates with a measure of variation (e.g. means and variance) and sample size. In addition, studies containing species lists for both treatments were included. To simplify analysis, we only included studies where the desired outcome was clear e.g. a higher mean species richness. Therefore, studies on e.g. vegetation height or cover were excluded as it is difficult to determine which vegetation height or cover is the most desirable and a higher mean might not be better. We did, however, include studies on mean abundance if the organism studied was desirable in a grassland while studies on e.g. pest species were excluded.

Generally semi-natural grasslands, at least in Europe, have not been modified by regular use of inorganic fertilizers and are cut in late summer. Furthermore, the present goal of grassland management is often preservation of the conservation value (Crofts and Jefferson, 1994). Despite this we included studies where fertilizers had been used (three studies) or grasslands that had been cut in autumn (one study), as these grasslands were characterized as semi-natural by the authors of the study (two studies) or managed specifically for species richness (two studies).

2.3. Data extraction

For the studies that met the inclusion criteria the sample size, the mean and the standard deviation (SD) of the studied features were extracted (or calculated, in the case of another variance measure than SD). If the sample size was not presented or the variance measure was unclear we contacted the authors for this information. However, we only did this for articles published in the last ten years, as we assumed it unlikely for older data to be readily available. Despite this, only half of the contacted authors responded to our queries. Some studies only presented data in figures (mostly bar graphs), in these cases the data were obtained using the program Plot Digitizer (Huwaldt, 2014). Due to time constraints, this was only done for experimental, replicated studies as these were considered to be studies of higher quality.

For studies containing only species lists, the number of species occurring in a treatment and the number of species absent in a treatment was calculated from the number of species only occurring in the other treatment.

In the end, data from 35 studies were used, with varying number of response variables used per study (Appendix A). The high number of excluded studies can mostly be attributed to the fact that no data were presented (190 studies), effect measures irrelevant to the present aim were used (approximately 200 studies) and the lack of presentation of variance measures or data only being presented in figures (approximately 50 studies). One of the included studies comprises of unpublished data (Poschlod, unpublished).

All data were compiled in spreadsheets along with information on study characteristics e.g. grassland type, study quality and previous management. Only information on the characteristics which were explicitly specified in the studies was used. Hence, we abstained from any attempt to, e.g. classify into vegetation types from species lists because of the great variability in how studies and data were presented. The characteristics were used as explanatory variables in the meta-analysis, making it possible to group similar studies together. For all studies that contained data from several years, only data from the most recent inventory were used in the meta-analysis.

2.4. Data synthesis

Before the analysis, the explanatory variables were grouped into four categories: (i) geography and habitat type; (ii) study design; (iii) management; and (iv) other. The categories and explanatory variables were ordered according to a hierarchy where the first variable was considered having the largest effect on the difference between grazing and mowing. Information on the explanatory variables used, their categorization, and their rank in the hierarchy can be found in Table 1. Note that if the grassland type was classified as "semi-natural grassland" in the original study, we categorized it as "semi-natural grassland s.s." (sensu stricto). Furthermore, if the prevailing management in the area before agricultural intensification (hereafter historical management) or the most recently applied management before the onset of the experiment (hereafter recent management) was classified as "unchanged management" the historical or recent management was the same as that used in the study (i.e. no new management was introduced in the grassland). In some cases the recent management was classified as e.g. "Abandonment/mowing" or "Agricultural/grazing". In these cases the grassland had been

Table 1

Explanatory variables used in the meta-analysis. The explanatory variables are ordered according to a hierarchy, where the first variable is considered having the largest effect on the difference between grazing and mowing. The classifications were made from information explicitly specified in the included studies.

Categories and explanatory variables	Description	Classes used
Geography and habitat type		
1. Continent	The continent in which the study was performed	Central Europe, Eastern Asia, Northern Europe, North America, Southern Europe, Western Asia
2. Altitude	Altitude of the study sites. Studies with sites in both lowland and mountainous areas were classified as "Both"	
3. Grassland type	Type of grassland	Calcareous coastal dune, calcareous fen, calcareous semi-natural grassland, dry semi-natural grassland, moorland, prairie, semi-dry semi-natural grassland, semi-natural grassland s.s., steppe, wet semi-natural grassland
Study design		
4. Outcome	The effect measurement used in the study	Abundance, biomass, density, Fisher's alpha, Gini–Simpson index, Shannon evenness, Shannon index, species list, species number
5. Organism	The organism studied. All studies investigating plants of any kind were classified as "Plants"; all studies investigating earthworms of any kind were classified as "Earthworms"; and all studies investigating mosses of any kind were classified as "Bryophytes"	
6. Study duration	The time since the introduction of treatments, either in abandoned or previously grazed and/or mown grasslands	Two years, five years, six years, eight years, 10 years, 11 years, 13 years, 20 years, 30 years, 31 years
Management		
7. Grazer	The grazing animal used in the study. Studies using more than one grazer were classified as "More than 1"	Cattle, horses, sheep, more than 1
8. Fertilization	If fertilizers were used in the study	Fertilization, no fertilization
9. Mowing date	The time of mowing	Autumn, summer
10. Treatment	The treatments compared in the study	Grazing vs. mowing, grazing vs. mowing with aftermath grazing
Other		
Data type	The type of measurement used in the study, either data from species lists or all other measurements	Other responses, species list
Study quality	If the study was pseudoreplicated and/or performed in more than one grassland. See Table 3 for information on the classification	High quality, intermediate quality, low quality
Historical management	The historical management used in the grassland (before agricultural intensification)	Agricultural, grazing, mowing, mowing with aftermath grazing
Recent management	The most recent management used in the grassland	Abandonment, abandonment/grazing, abandonment/mowing, abandonment/unchanged management, agricultural/grazing, grazing, mowing with aftermath grazing, unchanged management

abandoned or used as an arable field until very recently, but was grazed or mowed in the year before the study started; or had been mowed until very recently but had been abandoned for a year or two before the start of the study. In the meta-analysis the explanatory variables were analysed in order, with all studies being grouped by the specific variable. For each of these analyses an overall result was also achieved. For some studies, information on some explanatory variables was unknown (e.g. the type of grazing animal used in the study). If this was the case the study was removed from that specific analysis, but was included in all other analyses. Hence, different numbers of response variables were used for some analyses. To avoid spurious results, any deviating class of explanatory variables was removed from subsequent analyses, if the overall result of the analysis of the explanatory variable differed from the overall result of all studies (i.e. little overlap between studies in the forest plot). If deviating classes of variables contained enough explanatory variables (~20), these were analysed separately. The classes of explanatory variables excluded from analysis can be found in Table 2.

For the meta-analysis of the study duration, a meta-regression was performed with year since start of study as the predictor, to analyse the change in management effect over time. To achieve a single overall result we also performed metaanalysis on all studies and all response variables together, without grouping by explanatory variable. A similar analysis was also conducted but excluding studies containing previously removed explanatory variable classes. In addition we evaluated the quality of the studies by analysing the effect of the response measurement used and study quality (e.g. to what extent there were temporal and spatial replications) (Tables 1 and 3) and the influence of historical management (in the study area), and recent management (i.e. the management that preceded the onset of an experimental study) on the difference between grazing and mowing (Table 1) in separate analyses.

For all analyses the standard difference in means (*d*), using random effects models was calculated. A positive standard difference in means signify a more positive effect of mowing while a negative value signify a more positive effect of grazing and a value around zero signifies similar effects. Results can be considered statistically significant (i.e. rejecting a null hypothesis of no difference) if the confidence interval does not overlap zero. Analyses were made using the software Comprehensive Meta-analysis 2 (Biostat, Inc., 2006).

Table 2

Explanatory variable classes removed from subsequent analyses. The grassland type-classes were removed from analysis of explanatory variables 4–10. Grazer-classes were removed from analysis of explanatory variables 8–10. See Table 1 for information on explanatory variables.

Explanatory variable	Removed class	
Grassland type	Dry semi-natural grassland, semi-dry semi-natural grassland, steppe, wet semi-natural grassland	
Grazer	Sheep	

Table 3

The study design used in studies, with the number of studies, percentage studies and number of response variables of each study design in analysis. Total number of studies was 35.

Study design	Number of studies in analysis	Percentage studies in analysis	Number of response variables in analysis	Description
Low quality	19	54.3	56	Observational or experimental study where one site was used, without proper replication of treatments
Intermediate quality	9	25.7	22	Observational or experimental study where more than one site was used, but without proper replication within sites
High quality	7	20.0	70	Experimental study where one site was used, and where treatments were replicated
Outstanding quality	0	0	0	Experimental study where more than one site was used, and where treatments were replicated

2.5. Sensitivity analysis

Sensitivity analysis is used to test the robustness of the conclusions of a meta-analysis, by assessing the impact of individual studies on the combined effect. If any study has a large impact on the results compared to other studies, the robustness is low (Philibert et al., 2012). We analysed the robustness of our results in three ways. First, we run analyses while removing one study at a time to examine the impact of that study. For all studies providing more than one response variable to the analysis, the overall standard difference in means for that study was used in these analyses. If any such study contained several different categories of the same type of explanatory variable (e.g. several measured outcomes or studied organisms), the study was recategorized as "unknown" for that specific explanatory variable (i.e. was not included in that specific sensitivity analysis). Second. we run analysis while removing one response variable at a time to examine the impact of that response variable. Third, we performed analyses with only one response variable per study site included (randomly selected when there were more than one response per site), to test if the results were influenced by non-independence between response variables from the same study.

If our results were robust, we expected only small differences from the results of the original analyses and the results from the sensitivity analyses, and only modest differences between studies within the analysis of specific explanatory variables.

2.6. Publication bias

Publication bias arises when published work is more likely to be positive or statistically significant than unpublished results, leading to over-estimation of management effects (Stern and Simes, 1997; Dwan et al., 2013). We investigated the presence of publication bias by means of Egger's regression asymmetry test. A publication bias is considered to exist if p < 0.1 (Egger et al., 1997).

3. Results

The overall effect for most explanatory variables (e.g. continent, altitude, organism measured and recent management, but not for e.g. grassland type or treatment) was negative, i.e. grazing had a more positive effect than annual mowing for most explanatory variables. However, effects within explanatory variables differed, with similar effects of grazing and mowing in some cases and more positive effects of mowing in others.

3.1. Geography and habitat type

Our results revealed that the effect of grazing and mowing differed for different continents, grassland types and altitudes (Fig. 1). In some continents (e.g. Southern Europe) mowing

performed better compared to grazing, while in others grazing had a more positive effect (e.g. Central Europe) (Fig. 1a). Grazing had a more positive effect in calcareous coastal dunes (d = -0.266), while grazing and mowing had a similar effect in semi-natural grasslands s.s. (d = 0.064). Four of the vegetation classes deviated from the overall similar effect of grazing and mowing and these were therefore excluded from further analyses as they might otherwise confound the results in subsequent analyses (Table 2 and Fig. 1c). Grazing had a more positive effect in lowland grasslands (d = -0.193) while mowing had a more positive effect in mountainous grasslands (d = 0.185) (Fig. 1d).

3.2. Design

Results differed for different outcomes (i.e. how the effect was estimated) and organisms. For example, mowing and grazing had a similar effect on abundance (d = -0.011) while mowing had a more positive effect when measuring biodiversity as Shannon evenness (d = 0.466) (Fig. 2a). Grazing had a more positive effect on e.g. butterflies while grazing and mowing had a similar effect on plants (d = 0.002) (Fig. 2b). The results from the meta-regression on study duration revealed a positive effect of grazing in the short run and a more positive effect of mowing in long-term studies (slope = 0.0696, intercept = -0.881, n = 78). When only including one response variable per study site the slope was less clear (slope = 0.0116; intercept = -0.142; n = 25).

3.3. Management types

Effects of grazing and mowing differed for different grazers, fertilization levels, mowing dates and treatments. Horse grazing had a more positive effect compared to mowing (d = -0.566) while mowing had a more positive effect compared to sheep grazing (d=0.480) (Fig. 3a). As this result deviated from other grazing animals, studies where only sheep was used for grazing were removed from further analysis on the effect of management types. Grazing had a more positive effect than mowing in fertilized grasslands (d = -0.137), while grazing and mowing had a similar effect in non-fertilized grasslands (d = -0.081) (Fig. 3b). The effect of grazing was more positive than mowing during summer (d = -0.160), while mowing during autumn had a more positive effect compared to grazing (d = 0.532) (Fig. 3c). Grazing and mowing had a similar effect when comparing grazing and mowing with aftermath grazing (d = 0.031). However, grazing had a more positive effect when comparing mowing and grazing (d = -0.202) (Fig. 3d).

3.4. Overall

The analysis of all studies together revealed an overall positive effect of grazing compared to mowing (d = -0.145). The result was the same when analysing all studies except the ones containing

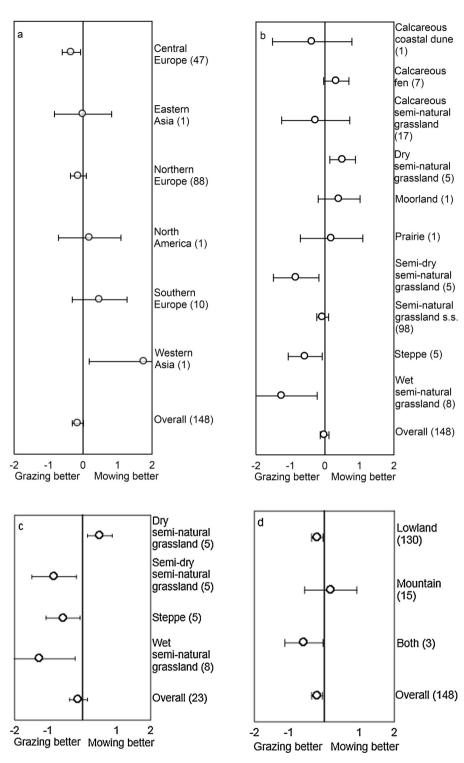


Fig. 1. Forest plots of the standard difference in means when comparing grazing and mowing when grouping by (a) continent, (b) grassland type, (c) deviating grassland type, (d) altitude. Numbers in parenthesis are the number of response variables in the analysis.

removed classes of deviating explanatory variables (d = -0.128) (Fig. 4).

3.5. Study quality

There were no differences in the result when assessing effects using a species list versus any other outcome (Fig. 5a), or regardless of the quality of the study design (Fig. 5b), as the treatments had similar effects on all data types or study qualities.

3.6. Previous management

The effects of grazing and mowing differed for different historical and recent management practices. For some historical management methods (e.g. mowing with aftermath grazing) the effect of mowing was more positive, while the effect of grazing was more positive in historically grazed grasslands (d = -0.134) (Fig. 6a). Grazing had a more positive effect if the recent management was e.g. abandonment and unchanged management, while mowing had a more positive when the previous

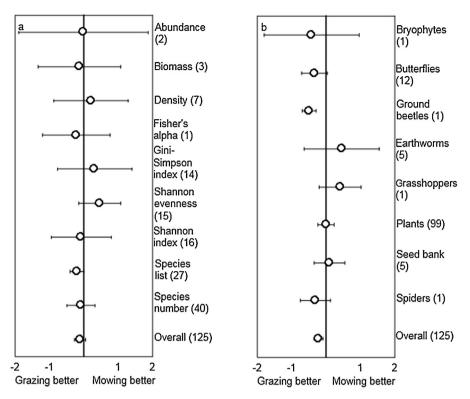


Fig. 2. Forest plots of the standard difference in means when comparing grazing and mowing when grouping by (a) outcome, (b) organism. Numbers in parenthesis are the number of response variables in the analysis.

management was agricultural (e.g. crop field) and mowing (d=0.163), or when there was no change in management method when the study was initiated (d=0.274) (Fig. 6b).

3.7. Sensitivity analysis

Overall, the analyses with one study removed and one response variable removed did not reveal any deviating studies or variables. The effect sizes were positioned within the confidence interval of the original results, and were generally grouped around the original effect size (Appendix B). However, for some explanatory variables one or a few response variables differed from the original effect size (e.g. Fig. B.5b). Furthermore, there were generally only small deviations between the effect sizes of removed studies or response variables for specific explanatory variables. The sensitivity analysis with only one response variable per site did not reveal any large differences compared to the original results (Appendix C). The overall positive effect of grazing compared to mowing became slightly stronger (d = -0.170 compared to d = -0.145) (Fig. C.4). For most explanatory variables the difference in effect of grazing and mowing became larger or slightly weaker. However, for a few explanatory variables the treatment effect was reversed e.g. the effect of grazing became more positive instead of more negative compared to mowing in the analysis of the mowing date (Fig. C.4c). In conclusion, analyses that were based on low number of data points should be interpreted with caution.

3.8. Publication bias

There was no evidence of publication bias (bias = 0.44165, p = 0.11772).

4. Discussion

Despite the considerable impact of management on biodiversity (Klimek et al., 2007) no general recommendation on the preferable management option exists for species-rich grasslands. Single studies comparing mowing and grazing reveal conflicting results (e.g. Schläpfer et al., 1998; Stammel et al., 2003) and to our knowledge there are only a few examples of systematic reviews evaluating the effect of grazing (e.g. Jones, 2000; Newton et al., 2009a) and no reviews comparing grazing and mowing in a wider context (but see Newton et al., 2009b). The results from the present synthesis - comparing data from 35 studies - revealed an overall more positive effect of grazing compared to annual mowing when managing for grassland conservation. The overall effects were similar in the analyses of specific explanatory variables. However, the effect sizes (d) were generally small, ranging between 0.01 and 0.48, most being around 0.15 (an effect size of 0.3 is considered small, 0.5 medium and >0.8 large according to Cohen (1992)). Thus, there were only small differences in the effect of grazing and mowing. The effects within the explanatory variables, however, did vary, which makes it worthwhile to tailor site-specific recommendations from our results.

The mechanisms involved in the difference in effect of grazing and mowing are not completely clear and might differ between explanatory variables. It is apparent that some species traits should be favoured by grazing (e.g. prickliness or poisonousness) and others by mowing (e.g. depressed rosette leaves) (e.g. Catorci et al., 2011). The more gradual and nonintrusive nature of grazing compared to mowing (Oates, 1995) and the fact that grazing promotes openness throughout the growing season (which decreases competition among species) is a possible reason for the more positive effect of grazing on e.g. bryophytes, butterflies and spiders (Fig. 2b) (D'Aniello et al., 2011; Sundberg, 2012). The gradual, but continuous, removal of biomass by grazing (compared to mowing once towards the end of the growing season) might also explain the more positive effect of grazing in fertilized grasslands (Fig. 4b), as increased amount of biomass in fertilized grasslands increases competition for light which can lead to decreases in biodiversity (Hautier et al., 2009). In addition, grazing may

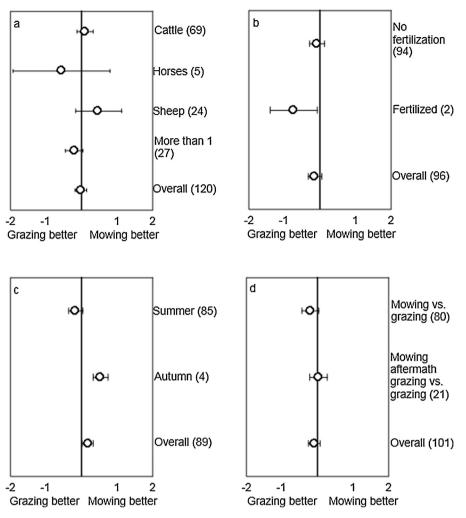


Fig. 3. Forest plot of the standard difference in means when comparing mowing and grazing, when grouping by (a) grazer, (b) fertilization, (c) mowing date, (d) treatment. Numbers in parenthesis are the number of response variables in the analysis.

promote higher plant species richness due to bare patches caused by heavy grazing and trampling, especially around gates and water troughs. Increased availability of micro-sites together with the fact that the grazing animals act as biotic vectors for propagule dispersal (Poschlod and Bonn, 1998; Cousens et al., 2008), improve the chance of seedling emergence, particularly of species with smaller seed size (Reader, 1993). In contrast to grazing, mowing has a uniform effect, even on extended areas, by consistent biomass removal in a short time period, which can lead to homogenization

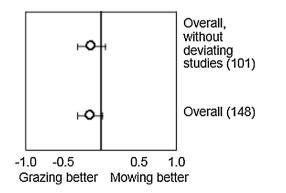


Fig. 4. Forest plot of the standard difference in means when comparing mowing and grazing for the overall results. Numbers in parenthesis are the number of response variables in the analysis.

of the vegetation (Lepš, 2014). By providing a uniform disturbance regime, mowing can decrease the inter- and intraspecific competition supporting the co-existence of numerous species in a small scale, reflected in the fact that evenness tended to be higher after mowing than after grazing (Fig. 2a). On the other hand, uneven spatial and temporal patterns of grazing can support the formation and maintenance of various micro-sites (Olff and Ritchie, 1998). As a consequence grazed swards are more heterogeneous than mown ones (Vickery et al., 2001) which positively affects the biodiversity of the grassland (Palmer, 1992; Dufour et al., 2006). However, grazing may also cause soil compaction and decrease the heterogeneity of the soil, which explain the negative effect of grazing on earthworms (Fig. 2b) (Schlaghamerský et al., 2007). There is no obvious mechanism behind the differences seen in the effect of grazing and mowing for different e.g. continents, grassland types and altitudes (Fig. 1a-c). These differences in the effects of management could be caused by e.g. different climates, species pools and soil types. The differences in the effect of grazer might be a consequence of higher herbage intake and activity of horses providing higher biomass removal and highly selective grazing of sheep, compared to mowing (Fig. 3a) (Duncan et al., 1990; Mitlacher et al., 2002). However, it can also be a consequence of differences in stocking density (Stewart and Pullin, 2006). The results from the analysis of the historical and recent management revealed an overall similar effect of grazing and mowing, indicating that the previous management influence

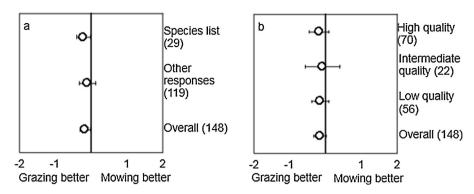


Fig. 5. Forest plot of the standard difference in means when comparing mowing and grazing, when grouping by (a) the type of response measurement used in the study (b) study quality. Numbers in parenthesis are the number of response variables in the analysis.

the effect of grazing and mowing. In specific cases, grazing had a more positive effect compared to mowing (Fig. 6). This is possibly due to the fact that many of the grasslands were grazed prior to study initiation, and mowing was a newly introduced management practice. Studies have shown that the introduction of a new management practice can have a negative effect (e.g. Jantunen, 2003). In grasslands with an agricultural history, i.e. former arable field, the results revealed a large positive effect of mowing (Fig. 6a), suggesting that grazing is not a suitable management practice when converting arable fields to grasslands. The length of a study also seemed to affect the difference between grazing and mowing, with grazing having a more positive effect in shorter studies while mowing have a more positive effect in longer studies according to our results. The mechanisms behind this are more difficult to explain, but it might be a result of vegetation changes due to the alteration of management practices (which was the case in some of the included studies) (Jantunen, 2003).

Some caveats should be considered when interpreting the contrasts between grazing and mowing in the present study. First, we only included grasslands which were mowed once a year in the meta-analysis. However, e.g. wet grasslands are usually rather productive and therefore traditionally cut more than once a year (Schrautzer et al., 1996), which is a possible reason for the large positive effect of grazing in wet semi-natural grasslands. Hence, our conclusions might not be applicable to more productive grasslands, or grasslands with a prolonged growth season, both likely to have been cut more than once a year historically. Second, historical and/or recent management at a study site might complicate matters, e.g. the positive effect of grazing in drier grasslands might be a consequence of this grassland type

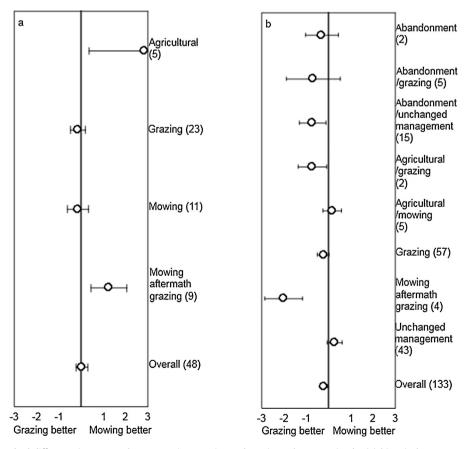


Fig. 6. Forest plot of the standard difference in means when comparing mowing and grazing, when grouping by (a) historical management (i.e. management before agricultural intensification) (b) most recent management. For further details on the variables used see Section 2. Numbers in parenthesis are the number of response variables in the analysis.

traditionally seldom being cut (Dolek and Geyer, 2002) (Fig. 1b). It is also important to note that studies of some grassland types and studies with sheep grazing were excluded from some analyses (Table 2) (but not the overall analysis or analysis of e.g. the study quality; see Section 2). The results might also be influenced by the inclusion of studies where mowing was followed by grazing, as this treatment differs from only annual mowing. However, as the results revealed a similar effect of comparing grazing vs. mowing and grazing vs. mowing with aftermath grazing (Fig. 3d), this is unlikely to challenge the general conclusions. Third, for some explanatory variables the number of analysed response variables were low, e.g. only one study contributed to the comparison of effects in eastern Asia or in prairie grasslands (Fig. 1a and b), meaning these results might poorly represent that continent or grassland type. Fourth, it is important to consider that the results from one grouping of explanatory variables can interact with other explanatory variables. For example, the effect of management on the outcome measured might be connected to the organism that was measured, e.g. as the biomass was only measured for earthworms. Fifth, conclusions might be influenced by many of the studies being of shorter duration (as grazing had a more positive effect in shorter studies). Still, despite these caveats several of which also apply to the primary studies - the strength of a meta-analysis lies in calculating an effect size, and its variation, from many independent studies; in our case 35 studies contributing 148 responses to the overall result. This is an intermediate number of studies used for published meta-analyses (Philibert et al., 2012), and, the sensitivity analyses demonstrated that the outcome was robust to the exclusion of whole studies and response variables (Appendix B), and to the inclusion of several response variables per study (Appendix C). For a few explanatory variables the inclusion of several responses per study resulted in effect sizes which might not be representative of the effect of grazing and mowing e.g. for some grazers or the mowing date (Appendix C, Fig. 3a, c). However, this was likely a result of a large decrease in the number of studies or response variables used for analysis, and these results might therefore not be representative of certain conditions. Furthermore, results were robust to the exclusion of any study or response variable (Appendix B). Not unexpectedly, in analyses comprising of few response variables overall, the effect of a single response variable was larger (e.g. Fig. B.2.a). This highlights the need to include many studies or response variables in metaanalyses, to prevent spurious results, stemming from unrepresentative studies. One study, Schläpfer et al. (1998), had a large impact on the analysis of the study quality (Fig. B.5b); without this study the effect of mowing was positive instead of negative for studies of intermediate quality. The reason for this shift is the substantial negative effect size of this study (d = -6.808), further highlight the need for inclusion of many studies in meta-analyses.

4.1. Practical implications

The general message to managers and policymakers based on our results is that grazing in many cases seems to give the highest biodiversity benefits, but that this benefit is modest to small. Our results also offer more site-specific recommendations, as they reveal differences in the effect of grazing and mowing under different conditions. According to our results, grazing may be a better management option in Central Europe, while mowing may be better suited in Southern Europe (Fig. 1a). The management measures applied should be fitted to the nature conservation aims; e.g. grazing can have a more positive effect on biomass, while mowing is more positive for the grassland evenness (Fig. 2a). For preserving grasshoppers, mowing is more preferable while grazing may have a more positive effect on butterflies (Fig. 2b), conclusions in accordance with studies by Hudewenz et al. (2012) and Pöyry et al. (2004). Furthermore, our results suggest that in the choice between mowing and grazing with sheep, mowing is more preferable in most cases (Fig. 3a). However, in regions where sheep grazing is part of the traditional land use, it can be the best management option for supporting biodiversity (e.g. in short-grass alkali grasslands; Török et al., 2012), explaining why some previous studies found positive (Sýkora et al., 1990) and others negative (Sebastià et al., 2008) effects of sheep grazing.

When determining a suitable management method for the conservation of a grassland, however, not only the effects but also the application circumstances of the management methods need to be considered. The socio-economic situation, livestock availability and the cost and time-consumption may affect the suitability of a treatment in a certain grassland. Livestock availability is decreasing and both grazing and mowing can be costly and time consuming in both smaller and larger grasslands (Kumm, 2003; Schreiber et al., 2009; Valkó et al., 2012). Furthermore, present and historical land-use might affect the suitability of a treatment as the previous management can affect the present species composition (Karlik and Poschlod, 2009). Nevertheless, our results suggest that both grazing and mowing can be suitable management methods regardless of the historic management (Fig. 6a). We found that grazing had a more positive effect regardless of most recent management practices, with a few exceptions (Fig. 6b).

4.2. Research implications

Meta-analyses and systematic reviews are rapidly becoming an important tool in the field of applied ecology as they can support the selection of the best available solution for various management scenarios (Pullin and Knight, 2001; Pullin and Stewart, 2006). To ensure the applicability of the results from systematic reviews, data provided in the included studies should ideally be of high quality. However, as availability of high quality data is low for most management scenarios, data of lower quality should also be used in manager-oriented meta-analyses. We classified more than half of the studies included in the present meta-analysis as of low quality, i.e. they were pseudoreplicated or un-replicated (Table 3). Pseudoreplication can result in false detection of treatment effects or can obscure the true effects due to the underestimation of the influence of spatial variation (Hurlbert, 1984; Heffner et al., 1996). Pseudoreplication has become an often unreflected argument for not publishing data (Davies and Gray, 2015). No doubt, pseudoreplication can be a serious problem for conclusions from individual studies; however we found that the overall results from studies of low quality (many of which involved pseudoreplication) did not differ from high quality studies (i.e. well-replicated experimental studies without pseudoreplication) (Fig. 5b). Several papers, reporting comparisons of outcomes from low and high quality studies, also indicate that systematic differences are often small or lacking (e.g. Benson and Hartz, 2001; Golder et al., 2011). Hence, in the absence of more reliable data, a wealth of poor quality data filtered through meta-analysis can provide useful practical guidelines for management (Sandström et al., 2014). Nevertheless, researchers should carefully elect the experimental design when planning studies and consider how to report the findings to allow inclusion in future meta-analyses (which are likely to apply more strict inclusion criteria than applied in the present study). In Table 4, we propose a number of criteria essential to thoroughly assess study quality, and what the best practice would be for designing and reporting results from primary studies. In addition, the evidence-base on management effects would greatly benefit from e.g. European-wide experiments using the same study design, examining the same type of organisms etc. in different types of grasslands.

Table 4

Information type	Information needed	Best practice
Site information	Detailed information on the study site: climate, altitude, grassland type, soil type, productivity, previous and current management at site	Several study sites, preferably with well-defined or similar site characteristics
Treatment information	Detailed information on treatments investigated: grazing animal, grazing intensity, mowing technique and date(s), fertilization level; and how this relates to the previous management	The same livestock and stocking density, mowing frequency and technique, and fertilization level used across sites and treatments. If the purpose is grassland conservation, no use of fertilizers
Experimental design	Number of sites and replicates used, length of experiment	Replicated experiment repeated over several study sites, with all treatments applied in all sites; experiments of long duration; experimental studies better than observational studies
Data	Data in the form of an effect size estimate with variance and n	Data generally more accessible if presented in tables than in graphs; data placed in data repository

The effect of the study duration on results must also be considered when drawing conclusions. As evident by our results, which revealed a difference in management effect over time, longer studies spanning several growing seasons are needed (see Kahmen et al., 2002; Tälle et al., 2014, 2015). For example, a weak effect might not manifest itself in the early phase of an experiment (e.g. Milberg et al., 2014), or the effect might differ over time. Therefore, using many records from long-term studies may buffer the year-to-year weather differences.

The result of an experiment is affected both by the treatment and by the abiotic conditions (e.g. location, productivity, soil type or soil moisture), meaning that the same treatment can have different effects in different grasslands. Therefore, detailed information regarding the characteristics of the study site(s) and study design is needed. In the present study the primary studies generally provided enough information to enable meta-analysis of specific explanatory variables. However many studies lacked information on the type of grazer, the mowing date or whether fertilizers were used. Even though the grazing intensity is an important driver of vegetation changes (Zhao et al., 2007; García et al., 2009), only one study provided information thereon (Tälle et al., 2015). Furthermore, some classifications of variables became very wide due to lack of information (e.g. grassland type), as we had decided to only use information explicitly specified in the studies for the classification. With more detailed information provided, more specific recommendations could have been given to managers and policymakers.

5. Conclusions

This meta-analysis, comparing the effect of grazing and annual mowing, using studies from several continents, and different types of grasslands and investigating several different organisms important for the conservation value of semi-natural grasslands, revealed an overall positive effect of grazing compared to annual mowing. The results were robust according to sensitivity analyses, but effect sizes were generally modest to weak. Some caveats, e.g. the specifics of the applied treatments and the analysed explanatory variables, should to be considered when interpreting specific results. Our results suggest that the origin of a grassland does not have an effect on the differences, as the effect of grazing and mowing was the same on grasslands formed due to climatic conditions or through deforestation. The general conclusion is therefore that grazing seems to give the highest biodiversity benefits in grasslands. From our results it is also possible to tailor site-specific recommendations on suitable management, based on the analyses of separate explanatory variables. For example, if conservation of butterflies is the main aim, grazing should be the preferred management method. In future primary research, we recommend researchers to strive for high quality studies and to present detailed information on e.g. site conditions and

management intensity, to improve the knowledge-base for future meta-analyses.

Studies used in the metaanalyses but not cited above

Bakker (1985), Catorci et al. (2014), Cernusca and Nachuzrišvili (1983), Debinski and Babbit (1997), During and Willems (1984), Fritch et al. (2011), Gao et al. (2014), Herbst et al. (2013), Jacquemyn et al. (2003), Koncz et al. (2014), Lithner (2005), Louault et al. (2005), Malt and Perner (2002), Mikola et al. (2009), Penksza et al. (2005), Perner and Malt (2002), Poschlod et al. (2011), Radlmair and Laußmann (1997), Rūsiņa et al. (2013), Schaich and Barthelmes (2012), Tamm (1956), Thyen (1997), WallisDeWries and Rademakers (2001), Wellstein et al. (2007) and Willhelm (1997).

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Appendices A, B & C. Supplementary information

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