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Mowing and warming effects on grassland species richness and harvested biomass: meta-analyses

Francesca Piseddu¹ · Gianni Bellocchi¹ · Catherine Picon-Cochard¹

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Abstract

Climate and management affect grassland plant diversity but studies vary regarding the magnitude of changes in plant species richness. Here we develop a comprehensive understanding of species richness modification due to management (mowing) and climate (warming) variations worldwide, and present the results of two meta-analyses from 999 and 1793 records (articles). Recorded articles had at least one experiment with a case-control design. The results show that both mowing (43 articles) and warming (34 articles) modify species richness, which on average increased by *c.* 32% with once-a-year mowing (against no mowing) and declined by *c.* 13% with warming (against ambient temperature). Our meta-analysis on the mowing regime supports the humped-back model, with one or two cuts per year being the level of disturbance optimising species richness. We also observed that warming-induced reduction in species richness is lower in dry climates ($< 300 \text{ mm yr}^{-1}$) and at low elevations ($< 1000 \text{ m a.s.l.}$). Where available, we accounted for harvested biomass as a concomitant variable and we found that overall it decreased by *c.* 21% (mowing) and increased by *c.* 11% (warming). The evidence provided of an opposite response of species richness and harvested biomass to disturbance is consistent with the competitive-exclusion hypothesis of negatively correlated patterns between the two outcomes (high taxonomic diversity with low biomass production, and vice versa). The reported difficulties in finding representative studies in previous meta-analyses and in the present ones highlight the need to orient future research towards long-term experiments on the combined effects of mowing and warming for a more robust inference of environmental and management constraints on grassland performance.

Keywords Biodiversity · Ecosystem services · Environmental pressure · Grassland ecosystems · Management intensity

1 Introduction

The intensification of agricultural practices from the twentieth century onwards is partly responsible for the reduction of areas covered by grassland ecosystems, notably with a considerable loss of semi-natural grasslands and a decrease of their biodiversity in different regions worldwide (e.g., Fakarayi et al. 2015; Münch et al. 2017; Schirpke et al. 2017; Gibson et al. 2018). Plant species' richness (Fig. 1) was also observed to decrease with the current warming trend (White et al. 2014), especially in climates that are becoming more arid and less productive (Harrison et al. 2015). These changes affect the human population broadly and may

actually have a great socio-economic impact (Dunford et al. 2015). In fact, not only grassland replacement and biodiversity erosion alter the continuity of the forage production supporting livestock agriculture but also the delivery of a broad set of ecosystem services essential to society (Loreau 2010; Bengtsson et al. 2019) like carbon storage, pollination and the maintenance of the general aesthetic of landscapes (e.g., Oertel et al. 2016; Tribot et al. 2018). These services are related to the plant diversity of grasslands (Turnbull et al. 2016), whose high biodiversity is not only consisting of plants, but also of mammals, arthropods and microorganisms (Plantureaux et al. 2005; Baur et al. 2006; van Klink et al. 2015). This biodiversity is recognized as an ecological and evolutionary insurance (after Yachi and Loreau 1999) thanks to the stabilizing effect of species diversity on aggregate ecosystem properties through fluctuations of component species (e.g., phenotypic changes, Norberg et al. 2001). Different components of plant diversity (e.g., species richness, functional diversity, assemblage structures)

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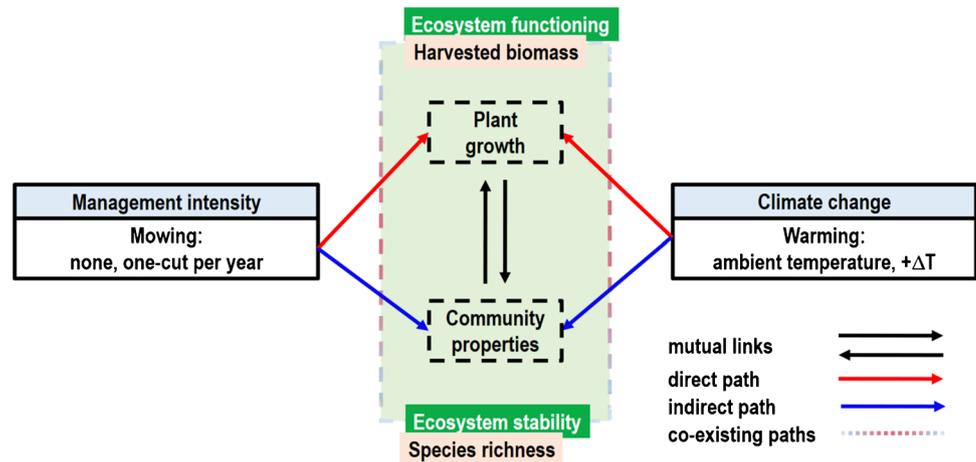
Fig. 1 Wildflowers and grasses in a species-rich grassland. Photograph by Célia Pouget (PhD student at Université Clermont Auvergne, INRAE, VetAgro Sup, UREP, Clermont-Ferrand, France in 2018–2021).

would also make grasslands more resilient to hazards and extreme weather events (such as prolonged droughts, e.g., Vogel et al. 2012; Craven et al. 2016) and would be able to stabilize forage production and maintain overall ecosystem services (Cleland 2011). It is thus essential to preserve these open spaces in order to preserve their biodiversity and the associated services, but also to study them to better appreciate their evolution under different constraints (Zeller et al. 2017). In hay meadows, which typically occur where the environmental constraints are less important compared to high-elevation pastures, the management practices and their intensity tend to be the main drivers of plant diversity (Pittarello et al. 2020), whose changes reflect the evolution of both environmental conditions (pedo-climate) and management practices (Pontes et al. 2015). While the effects of increased temperature on grassland production are systematically studied and understood (e.g., Parton et al. 1995; Song et al. 2019), the effects of warming on plant diversity is an evolving and multifaceted challenge (Cowles et al. 2018). This is because temperature changes are dynamic and their effects on grassland communities depend on a number of other factors like moisture and nutrient availability (e.g., Zavaleta et al. 2003). Likewise, the effects of cutting events on the botanical composition of a sward are related to environmental conditions (e.g., Wen and Jiang 2005).

Studies that have reported the response of grassland plant diversity to climate and management conditions (e.g., Su et al. 2019) indicate that the pattern of responses is complex and needs additional analyses based on quantitative assessments. An objective assessment is increasingly important as grasslands continue being vulnerable to warming conditions (e.g., Gao et al. 2018), and halting grassland abandonment is an emerging topic of interest (e.g., Lasanta et al. 2017), especially in mountain regions (Haddaway et al. 2014). The

proportion of grassland plant species tends to decline following abandonment (Riedener et al. 2014) and plant species decline due to abandonment could not easily be reversed (and grasslands restored) by mowing alone (Stampfli and Zeiter 1999). However, the variability in the reported results is also likely due to the different challenges associated with the quantification of impacts on plant diversity. In particular, there is no standardized mode of conducting the experimental design and setup of control versus the experimental dataset (Christie et al. 2019). In the wake of diverse findings and conclusions, and because of the availability of an increasing number of peer-reviewed publications as well as the maturity of the results, there are science questions relevant to the issue of plant diversity modifications, e.g., is warming or mowing modifying species richness and, if yes, by what amount and under which conditions? We performed two meta-analyses using species richness as an indicator of plant diversity conditions. In fact, despite the growing knowledge about grassland modifications induced by temperature increase and mowing regime, quantitative assessments and analyses are still limited (e.g., Tälle et al. 2016; Gruner et al. 2017). Here, we provide a conceptual framework (Fig. 2) of the direct and indirect effects of mowing (one cut per year versus abandonment) and climate change (warming) on the grassland ecosystem (after Li et al. 2018), using harvested biomass and species richness as expressions of functioning and stability (e.g., species richness can promote community stability through increases in asynchronous dynamics across species; Zhang et al. 2018). We highlight that the type of inference presented in Fig. 2 (which represents a simplified view of the grassland ecosystem) depends on the extent to which the meta-analysis can establish causality between the outcomes of interest and the hypothesized related factors. This means that for only a subset of the above questions, it may be possible to find consistency in the set of bibliographic data to code into the state-of-the-art literature and develop meta-analyses of the extracted data. Specific objectives were to analyse (1) the mean effect of mowing (first meta-analysis: one mowing event per year versus abandonment) and (2) the mean effect of warming (second meta-analysis: warming versus ambient temperature), both conducted on species richness in grasslands (and concomitant harvested biomass when available). In this way, we have pursued standardized meta-analyses to review fragmented results in a common framework. For the impact of mowing on plant diversity worldwide, our study complements previous reports from Tälle et al. (2018) on the effects of different mowing frequency on the conservation value of semi-natural grasslands in Europe. It also completes the assessment with a meta-analysis on the effect of warming on the biodiversity of different ecosystems including plant terrestrial ecosystems (Gruner et al. 2017).

Fig. 2 Conceptual framework of this study. Direct (blue arrows) and indirect (red arrows) effects of climate change (i.e., warming) and management (i.e., mowing) jointly determine (coloured hatched line) the functioning (expressed by harvested biomass) and stability (expressed by species diversity) of grassland ecosystems, as mediated by plant growth and community properties.



2 Materials and methods

2.1 Literature search method

Our meta-analysis method quantitatively combines and summarizes research results across individual and independent studies performed worldwide and published in peer-review journals (grey literature was not included in our meta-analyses). The first step was to find all the pertinent articles on the topic. We used a keyword search and expert recommendations to find the related articles in two international bibliographic databases. The literature search was initiated using the ISI Web of Science (WoS, (<http://apps.webofknowledge.com>)) with the following topic search terms:

(Title)TI=(grassland OR meadow OR pasture OR pampa OR steppe OR prairie OR savanna OR tundra). AND (Topic)TS=(diversity OR diverse OR richness OR evenness OR cover OR abundance AND plant OR "functional type*"). AND (Title)TI=(cut OR mow OR clip OR treatment OR management). NOT (Title)TI=(forest OR tree OR shrub*)

TI=(temperature* OR warm* OR air OR heat* OR stress* OR "extreme temperature") AND TI=(grassland* OR meadow* OR pasture* OR pampa* OR steppe* OR prairie* OR savanna* OR tundra*) NOT TI=(forest* OR tree* OR shrub*) AND TS=(diversity* OR diverse* OR richness OR evenness OR cover OR abundance* AND plant* OR "functional type*")

Searches were also undertaken with Scopus (<http://www.scopus.com>) in order to pick up publications that were not indexed in the WoS database:

TITLE (grassland OR meadow OR pasture OR pampa OR steppe OR prairie OR savanna OR tundra) AND TITLE-ABS-KEY (diversity OR diverse OR richness OR even-

ness OR cover OR abundance AND plant OR "functional type*") AND TITLE (cut OR mow OR clip OR treatment OR management) AND NOT TITLE (forest OR tree OR shrub*) AND LANGUAGE (English) AND DOCTYPE (ar).

(TITLE (temperature* OR warm* OR air OR heat* OR stress* OR "extreme temperature") AND TITLE (grassland* OR meadow* OR pasture* OR pampa* OR steppe* OR prairie* OR savanna* OR tundra*) AND NOT TITLE (forest* OR tree* OR shrub*) AND TITLE-ABS-KEY (diversity* OR diverse* OR richness OR evenness OR cover OR abundance* AND plant* OR "functional type*") AND LANGUAGE (english)) AND DOCTYPE (ar OR re) AND PUBYEAR > 1984 AND PUBYEAR < 2021 AND (LIMIT-TO (SUBJAREA, "AGRI") OR LIMIT-TO (SUBJAREA, "ENVI") OR LIMIT-TO (LIMIT-TO (SUBJAREA, "MATE") OR LIMIT-TO (SUBJAREA, "EART") OR LIMIT-TO (SUBJAREA, "BIOC") OR LIMIT-TO (SUBJAREA, "MULT"))

This review covers articles published from 1985 to 2020. The cut-off date for data collection was 31 December 2019, which ensured including 2020 articles web published in 2019. We also added other pertinent articles from peer-review journals to the extent that we are aware of them. In particular, for the effect of warming, we used part of the bibliography of a meta-analysis made by Gruner et al. (2017).

2.2 Inclusion criteria and data extraction

Care was taken to standardize and document the process of data extraction. The quantitative review followed a structured protocol, which included pre-setting objectives and the inclusion criteria for studies, approach for data collection, and the analyses to be done (Pullin and Stewart 2006). To facilitate the capture, organization and elimination of duplicate records from electronic WoS and Scopus databases

searching, bibliographic records were imported into End-Note reference manager (<https://endnote.com>) and outputted in BIBTeX format (Lorenzetti and Ghali 2013). Data extracted from articles were recorded on carefully designed spreadsheets and accompanying tables with details of the study characteristics, data quality, relevant outcomes, level of replication and variability measures.

Using PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses; Liberati et al. 2009) diagrams depicting the flow of information through the different phases of the literature review, we mapped out the number of records identified, included and excluded, and the reasons for exclusions. Any single article had at least one experiment with a case-control design. The control was defined as being identical to the experimental treatment (case) with regard to all variables apart from the type of factor applied. Here, the mowing and warming experiments included ambient temperature (no warming) and abandonment (no mowing) as controls, respectively. The articles from the literature search were filtered by title and abstract, discarding obviously irrelevant studies (e.g., when species richness referred to other organisms than grassland plant species). After the examination of abstracts, the full text of the remaining articles was examined in detail. Articles that quantitatively reported effects of mowing (or clipping or cutting) or warming on species richness (SR as species conservation metric) were selected. When available, concomitant harvested biomass (HB as provisioning service metric, g DM m⁻²) determinations were also considered in the analyses. Articles had to contain data in the form of experimental determinations together with a measure of variation (e.g., means and variance). Articles with unreported outcomes (e.g., no species richness available), ineligible experimental design (e.g., lack of control) and missing essential statistics (e.g., standard deviations or related variability metrics) were discarded. In our meta-analyses, experiments with and without fertilisation were pooled. We also took into account only the effect of mowing (one cut per year) even if there was a previous grazing period. Mowing once per year is the most commonly used mowing frequency in species-rich grasslands (e.g., Hejman et al. 2013) and was used as a treatment in all included experiments regardless of the timing of the mowing event during the year. Articles comparing more frequent cuts during the same year were excluded from the meta-analysis, as these comparisons (often using once-a-year mowing, not abandonment, as control) were outside the scope of the present study, but their results were used as complementary elements to improve the discussion of our results.

For the articles that met the inclusion criteria, the sample size, mean and standard deviation (*sd*) of the response variables were extracted (or calculated where a variability measure other than *sd* was provided, e.g., standard error). With sample data collected at different dates, mean and *sd*

were used as practical descriptors of time-series central tendency and spread. Critical appraisals were performed by two authors independently, i.e., the above data were extracted and ~ 50% of the extracted data were randomly cross-checked by another author. In case of disagreement on data extraction, a consensus was reached through discussion among all authors. As some studies had not reported the exact values for relevant variables and experimental design details, more than 10 disagreements on the most appropriate inference for these missing data were discussed within the team.

2.3 Effect sizes

The goal of any meta-analysis is to provide an outcome estimate (or overall effect size) that is representative of all study-level findings. Effect sizes were characterized by the response ratio (*RR*), which is frequently used to quantify the proportion of changes due to experimental manipulations and thus provide a measure of the experimental effects (Hedges et al. 1999; Nagakawa and Santos 2012). This is calculated as the ratio of the average values of a treatment (\bar{X}_T) and its control (\bar{X}_C). Then, log-response ratio (*LRR*) values, $\ln\left(\frac{\bar{X}_T}{\bar{X}_C}\right)$, are calculated as these are the size effects used in ecological meta-analyses, primarily because they tend to be normally distributed around zero for small samples. This means that a size effect with a value of zero represents no difference between the groups being compared (treatment vs. control). Meta-analysis, by pooling *LRR* values from several studies, also assigns a weight to each *LRR* that is inversely proportional to its sampling variance, equal to $\text{var}(LRR) = \frac{(sd_T)^2}{N_T \bar{X}_T^2} + \frac{(sd_C)^2}{N_C \bar{X}_C^2}$, where *sd* and *N* are the standard deviation and sample size of \bar{X}_T and \bar{X}_C , respectively (e.g., Lajeunesse 2011). The percent change (%) in the level of the outcome from baseline to the treatment is $100 \cdot [\exp(LRR) - 1]$.

2.4 Meta-analysis models

To perform the two meta-analyses, we referred to the set of dedicated functions of the *metafor* package (Viechtbauer 2010), implemented within the statistical software RStudio (<https://www.rstudio.com>) for R version 3.5.3 x64. Meta-analysis models determine if an effect (*y*) is significant or not in a given experiment (*i*). In mathematical form, this is expressed as $y_i = \theta_i + e_i$, where θ and *e* indicate the unknown true effect and the known sampling error, respectively. Once effect sizes are extracted from the primary studies, they are pooled by applying a fixed- or random-effects model. A random-effects model was used in our meta-analysis, because the fixed-effects model assumes that there is only one underlying population effect size and that the observed effect sizes

deviate from this population effect only because of sampling variation (an unrealistic scenario of heterogeneity among the population effect sizes). A random-effects model assumes that each study has its own population effect, i.e., effect sizes vary due to sampling variation and also due to systematic differences among studies. In this model, not only is the combined effect size estimated, but also the variance of the overall effect among studies. The mixed-effects model was also applied to explain heterogeneity in the data with the use of moderators (covariates). In this case, it is a challenge for the meta-analyst to find moderating variables (moderator) that explain the variation in effect sizes among studies. Mixed-effects analyses were only conducted if at least half of the studies reported information on moderators.

The Q -statistic (or multiple significance testing across means; weighted squared deviations) was used to evaluate heterogeneity through $0 < I^2 < 100$, which quantifies the proportion of total variability that is due to heterogeneity rather than sample variations: $I^2 > 75\%$ means high heterogeneity; values between 50 and 75% are considered as moderate heterogeneity; if the I^2 is between 25 and 50%, it is considered as low heterogeneity; below 25%, it is considered as no heterogeneity (e.g., Gianfredi et al. 2019). When p -values for the Q -test and effect sizes (random-effect model) were less than 0.1, homogeneity and no-effect assumptions were considered invalid. After quantifying variation among effect sizes beyond sampling variation (I^2), we examined the effects of moderators (covariates) that might explain this additional variation. The significance of moderators was tested using the probability (P) of an omnibus test (i.e., the Q_m statistic). For that, in addition to SR and HB determinations, we recorded information on moderators that may affect the response variables - from the k articles ($k \leq n$) and experiments (j) for which this information was available. Plot size (S, m²), duration of the study (D, number of years), year of publication of articles (Y), site elevation (E, m a.s.l.) and two site-specific climatic variables (mean annual air temperature: T, °C; mean annual precipitation total: R, mm) were chosen as moderators of the SR and HB responses in the mixed-effects model. Year of publication of the studies can be a potential source of bias because changes in study methods and characteristics occurring over time can correlate to effect sizes (e.g., Jennions and Møller 2002). As well, since vegetation within smaller plots tends to be more homogeneous than within larger plots, plot size may influence the number of recorded species and the estimate of SR (Chytrý 2001). Some authors also found that as the duration of the study increased so did the plant species diversity and productivity (e.g., Cardinale et al. 2007; Pallett et al. 2016). Then, plant community composition can change along elevation gradients (e.g., Ohdo and Takahashi 2020), with global warming pushing species towards higher elevations (e.g., Engler et al. 2009), and temperature and rainfall are the climatic variables most used to explore the relationships between

climate and plant community data (e.g., Harrison et al. 2020). For the effect of mowing, the cutting height (H, cm) was also considered because it can affect the community characteristics and biomass production (e.g. Wan et al. 2016). The temperature difference between control and warming treatments (ΔT , °C) was instead used as moderator in the meta-analysis of the effects of warming because divergent effects may be due to different warming treatments among experiments and different temperature sensitivities of various plant species (e.g., Llorens et al. 2004). As well, the heating technique (M, 0: open-top chambers; 1: heaters) used in vegetation warming experiments (a categorical moderator) may lead to potential differences in plant responses for: (i) the different control on temperatures of passive (e.g., open-top chambers) and active (e.g., infrared heating) warming methods (e.g., De Boeck and Nijs 2011), and (ii) the size of the device, open-top chambers used in field experiments being generally relatively small (i.e. ≤ 3 m in diameter), allowing the establishment of a well-controlled and essentially homogeneous environment (e.g., Cunningham et al. 2013).

2.5 Potential data analysis bias and results

Possible publication biases were tested, either visually by means of funnel plots, which show the observed effect sizes on the x -axis against a measure of precision (standard error) of the observed effect sizes on the y -axis, or statistically by means of the test for plot asymmetry (Egger et al. 1997). The results of meta-analysis were displayed in forest plots for each outcome, where individual experiments were plotted sequentially on the y -axis. The x -axis shows outcome measures (log-ratio and 0.95 confidence interval for each study). Point estimates are represented by square boxes, where the weight of a study is reflected by the size of the square. The point estimates are accompanied by a line, which represents their associated 0.95 confidence interval. A vertical midline (line-of-no-effect) divides the diagram into two parts. A confidence interval that crosses the line-of-no-effect indicates a statistically non-significant difference, whereas a confidence interval that does not cross the midline indicates a significant difference for either the treatment or control, depending on whether it is located at the left side or the right side of the midline. That is, right-sided (left-sided) result estimates ($LRR > 0$) for our two outcomes of interest, SR and HB, are higher (lower) in the treatment than in the control (and vice versa).

3 Results and discussion

3.1 Literature search

The heuristic search of the state-of-the art literature in the WoS and Scopus bibliometric databases yielded 999 articles

for the effects of mowing (Fig. 3a) and 1793 articles for the effect of warming (Fig. 3b), after removing 467 and 411 duplicates from the original set of 1466 and 2204 records (with pairwise observations in the control and treatments), respectively. The two bulks of articles were reviewed, and initially screened, for their relevance to the study topic. After applying the criteria to the original set of articles and adding 31 articles from other sources, 43 and 34 articles (46 and 42 experiments, respectively) met the criteria and were selected to quantify the effects on SR of mowing or warming, respectively (Supplementary material). In 16 articles for mowing (18 experiments) and 17 articles (22 experiments) for warming the same analysis was performed to assess the effect of the same factors on HB.

Table S1 and Table S2 show the characteristics of the articles included in the meta-analysis on the effects of mowing and warming, respectively. The current literature did not provide a robust sample of articles and quantitative results corresponding to different subclasses (e.g., abandonment versus management with two, three, etc. mowing events associated with fertiliser supply gradients; warming under gradients of atmospheric CO₂ concentration and water status levels). The included studies report on grassland research conducted in 46 mowing experiments in 18 countries from Asia, Europe, North America and Oceania, and 42 warming experiments in nine countries from Asia, Europe and

North America (Fig. 4). Using the Köppen-Geiger climate classification (Peel et al. 2007), our research shows an uneven geographical distribution of the selected studies for the effect of mowing (Table S1), with most articles focusing on temperate-oceanic (44%) and warm- or hot-summer continental (37%) climate zones of the northern hemisphere (with the exception of one study from the southern hemisphere in the temperature-oceanic climatic zone of Australia). Studies from cold (12%), Mediterranean (2%), and subtropical (5%) areas remain rare. Climate zones only in part reflect the distinctive characteristics of grassland systems, which varied widely in environmental conditions, mowing regimes and experimental settings. All recorded articles on the effect of warming document studies carried out on grasslands in the northern hemisphere (Table S2): 15 in China, 10 in the USA, and nine in central and northern Europe. Most of them (41%) are from regions with ice cap and tundra climates, showing that manipulation studies focusing on the effects of warming on grassland systems are not gaining interest in the Mediterranean and developing regions of the world. They are all unfertilised treatments and include two main devices to simulate the experimental climate warming and to study plant responses, i.e., open-top chambers and infrared heaters. As with articles on the effects of mowing, the types and designs varied considerably also within the same study.

Fig. 3 PRISMA-flow diagram of studies' selection process on the effect of mowing and warming on species richness (n , number of articles). Some articles included more than one experiment and, in this case, these experiments (j) were considered as separate experiments ($j = 46$ with mowing, $j = 42$ with warming). Subsets of the identified records also included the effect of mowing (16 articles, 18 experiments) or warming (17 articles, 22 experiments) on harvested biomass.

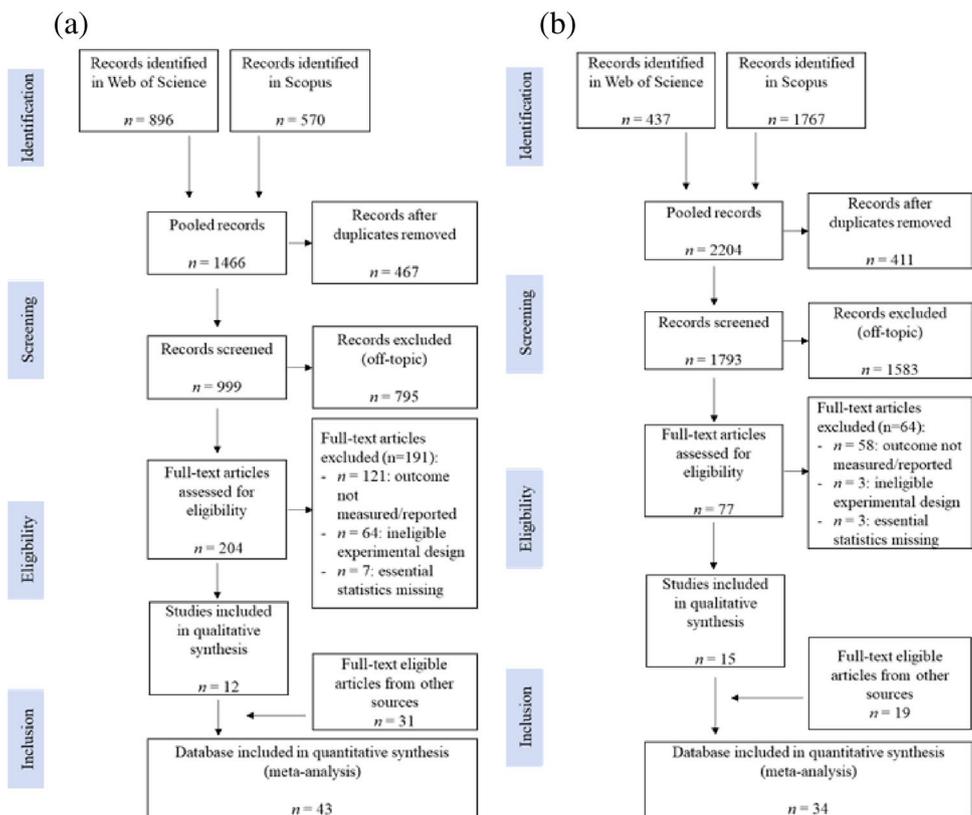
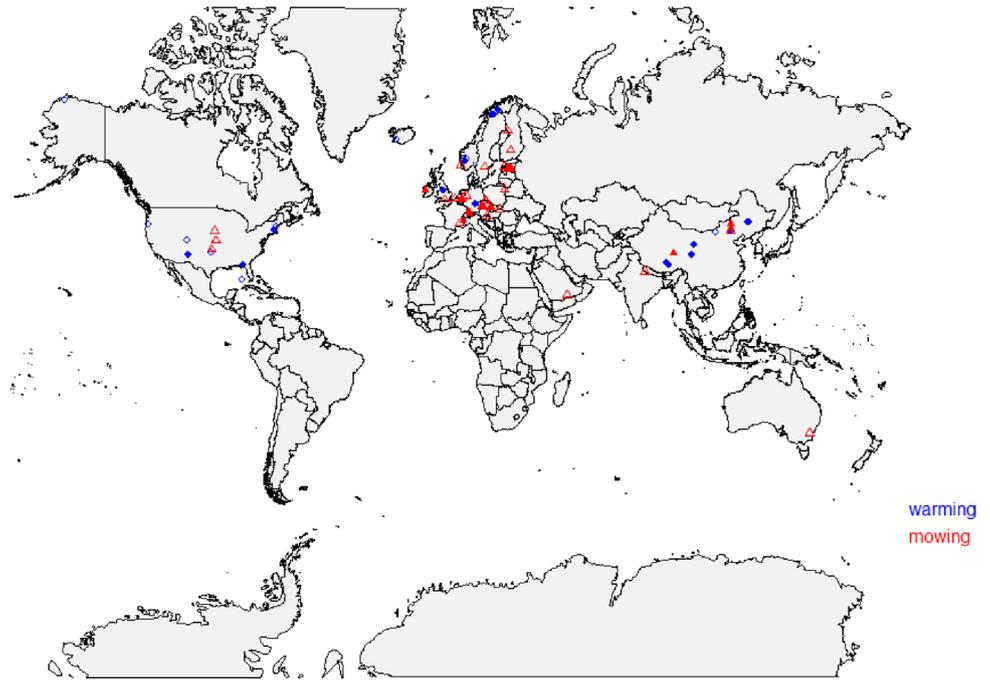


Fig. 4 Global map of study sites that provided data for meta-analysis of the effects of mowing (red triangles) or warming (blue dots) on species richness only (empty markers) or on species richness and harvested biomass (solid markers).



3.2 Potential data analysis bias

The statistical distributions of *LRR* values were determined to be nearly normal according to quantile plots (Fig. S1).

For mowing, high heterogeneity was found with both SR ($I^2 = 92\%$; $Q = 499$, $p < 0.01$) and HB ($I^2 = 66\%$; $Q = 55$, $p < 0.01$) determinations. However, no evidence of publication bias was found in our meta-analysis for the effect of mowing on SR and HB that would reflect bias toward not reporting small positive or negative effect sizes, as demonstrated by the substantial symmetry of the funnel plots (SR: $z = -1.06$, $p > 0.10$; HB: $z = -2.00$, $p = \sim 0.05$). The points falling outside both funnels (Fig. S2, top graphs) are located on both sides of the funnel, hence indicating no clear-cut direction in the bias. For SR, Fig. S2 (left) shows that the majority of the data are clustered in one-point cloud (same order of magnitude), with the exception of the study of Lanta et al. (2009), whose high variability is found in the forest plot (Fig. 5a). For warming, significant results with both SR ($I^2 = 92\%$; $Q = 815$, $p < 0.01$) and HB ($I^2 = 55\%$; $Q = 60$, $p < 0.01$) are taken as evidence of heterogeneity. The overall funnel plots are however relatively symmetric (Fig. S2, bottom graphs) and consistent with low likelihood of publication bias (SR: $z = 1.40$, $p > 0.10$; HB: $z = -0.94$, $p > 0.10$).

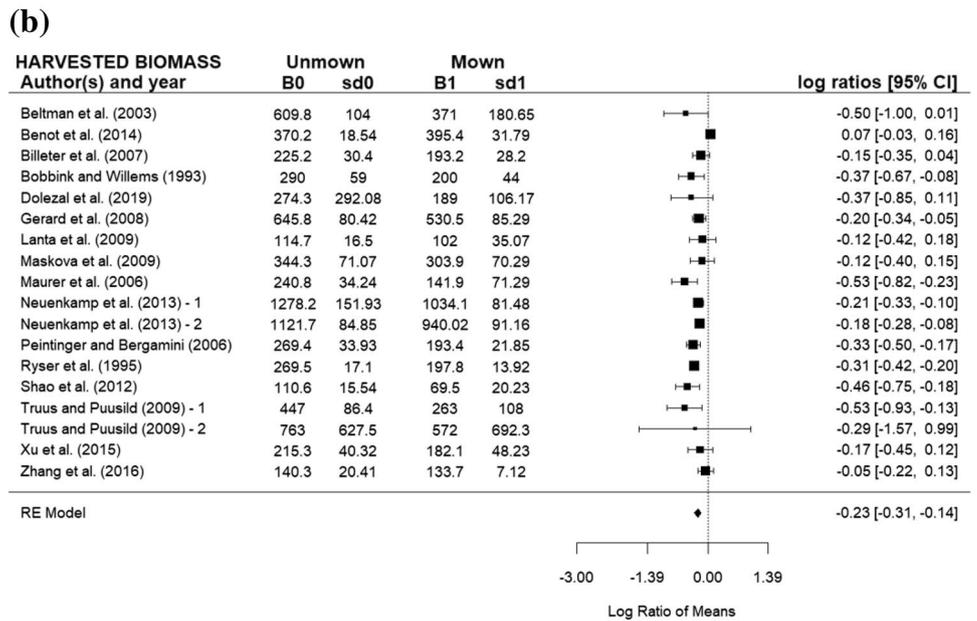
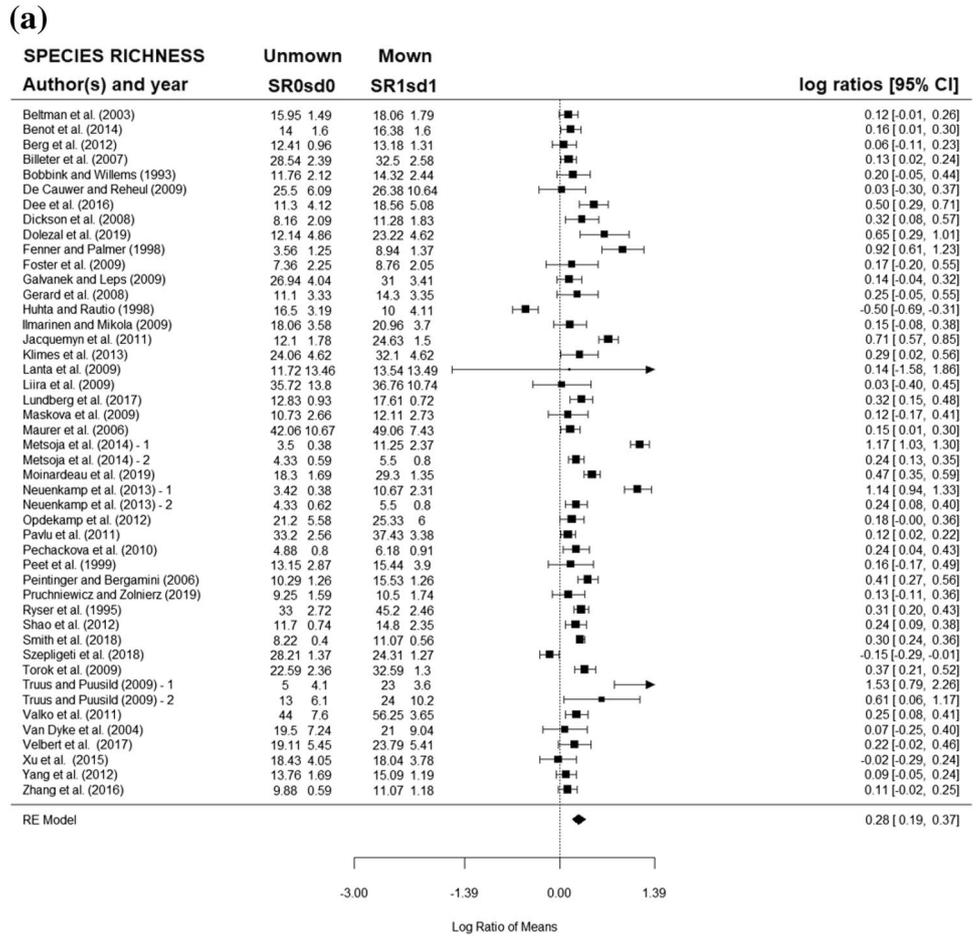
3.3 Effect of mowing on SR and HB

A forest plot for all 43 recorded articles combined (46 experiments) indicates a significantly positive effect of mowing (one cutting event per year) on SR compared to abandonment (Fig. 5a): pooled *LRR* = 0.28 (c. 32% increase), 0.95

confidence interval from 0.19 to 0.37 ($p < 0.01$). There are however three studies, which showed an opposite effect. This was distinctly observed in Finnish meadow patches (*LRR* = -0.50, Huhta and Rautio 1998), where an increase in SR due to a successional change may have only been apparent, plausibly related to short-term effects and creating (according to authors) the illusion that abandonment is more desirable than management. In fact, early succession was characterized by a transient loss of plant species diversity (Velbert et al. 2017) in wet meadows of north-west Germany (*LRR* = 0.22). While in the Qinghai-Tibetan plateau (Xu et al. 2015) SR was observed not to be sensitive to the short-term effects of mowing (*LRR* = -0.02), in a mesic hay meadow of Western Hungary (near the Slovenian border), Szépligeti et al. (2018) noted that mowing once a year may not be efficiently preventing (*LRR* = -0.15) the spread of tall goldenrod (*Solidago gigantea* Ait.) and control native competitive species (which hinder the growth of rare and less competitive species).

Without including the unmanaged option in their analysis, Tälle et al. (2018) observed small differences in the effects of different mowing intensities on the SR of European semi-natural grasslands (*LRR* < 0.13, with 0.1 representing the difference between a SR of two communities consisting of 10 and 11 species, respectively). The authors highlighted that while lower and higher mowing frequency can be expected to have both positive and negative effects on plant diversity at the same time, they concurred with other authors (e.g., Batáry et al. 2010; Tóth et al. 2018) that any kind of management which is actually applied tends to be more important than the intensity of the management itself. We

Fig. 5 Forest plots of the meta-analysis (log-response ratios and 0.95 confidence limits) comparing species richness, SR (a) and harvested biomass, HB, in g DM m⁻² (b) in unmown (0, control) and once-a-year mown (1, treatment) grasslands, with the relative standard deviations (sd). RE model stands for random-effects model.



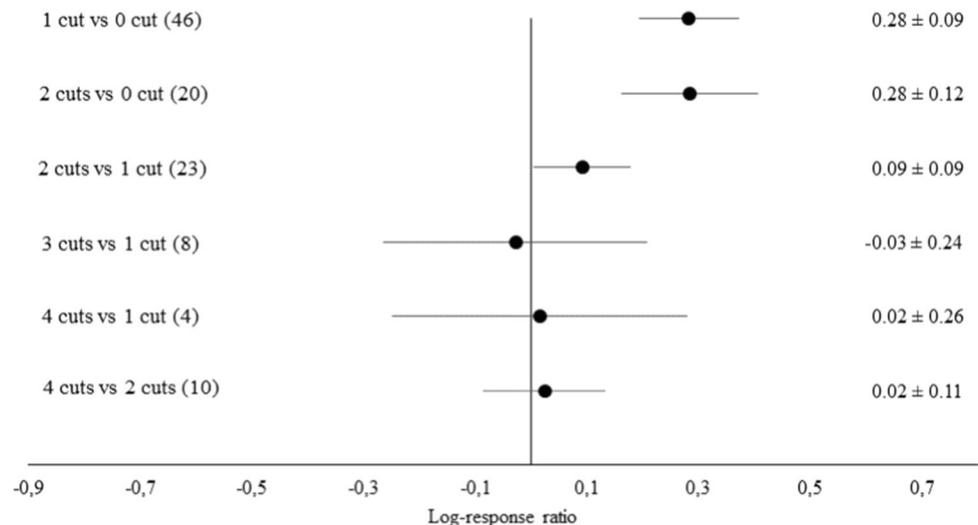
show that the difference can indeed be high when moving from abandoned fields to once-a-year mowing. The highest estimated mean effect size of $LRR = 1.53$ (wet experiment from Truus and Puusild 2009), in particular, reflects the substantial decrease in SR on long-abandoned floodplain grasslands, which is likely a consequence of increased light competition and the accumulation of dense litter layers, as several low-growing plant species are outcompeted by strong competitors during succession or germination and establishment are inhibited by litter layers.

In addition to the results of our meta-analysis, some results by individual studies were also informative on the effect of alternative mowing schemes on SR. Figure 6 shows the changes in the SR of grassland plants under combinations of mowing frequency beyond one cut per year versus no cut, which were identified in the systematic review and in additional sources (section “References of the review on the effect of different mowing regimes”), and not included in the meta-analysis. Overall, it appears that a moderate mowing intensity of one or two cuts per year is positive for maintaining or enhancing a high plant SR. With two cuts per year over abandonment, we observe a similar mean response ($LRR = 0.28$) but greater variability across studies compared to just one cut (that is the core of this meta-analysis), likely associated with the influence of varying situations of soil fertility. In fact, the more a grassland is harvested, the more intensively it must be fertilised to remain productive. Significant interactions are often observed between cutting and fertilisation treatments, with maximum counts detected in unfertilized plots and the total number of plant species decreasing along with increasing fertilization rates (e.g., Hejzman et al. 2007). The addition of nitrogen, in particular, significantly influences the increase of plant biomass and height, leading to a decrease in species diversity (Tilman 1987; Silvertown et al. 2006). Then, the potential benefits

of mowing on SR are progressively lost with more frequent cuts (i.e., three to four cutting events per year compared to one cut). It is known that regular disturbance by mowing can trigger niche partitioning, leading to higher species diversity (e.g., Mason et al. 2011), but too frequent harvests may threaten the long-term survival of certain plant species (e.g., Loydi et al. 2013) by suppressing their seed stock. Our results can be interpreted in terms of the humped-back model (Huston 1979), a dynamic equilibrium model predicting that taxonomic richness may be greatest at intermediate biomass production and at intermediate levels of available resources (stress) and disturbance factors (Pierce 2014). In fact, a hump-shaped relationship between vegetation biomass and SR, based on the balance between competition and abiotic stress, has been found in a large number of case studies (van Klink et al. 2017), and with SR likely peaking at intermediate productivity levels (Boch et al. 2019). Consistently with the pattern predicted by the intermediate disturbance hypothesis, SR may be maintained by extensive agricultural practices (Uchida and Ushimaru 2014). By alleviating understory light limitation through the removal of plant biomass, both mowers and grazers play an important role in maintaining plant diversity in grassland ecosystems, where they increase ground-level light availability (Borer et al. 2014).

However, even if mowing frequency only marginally affecting plant diversity measures like SR might still affect the species composition in a grassland and, considering that mowing is costly, it is important to find a balance between mowing frequency and conservation benefits beyond SR (Tälle et al. 2018). The most suitable mowing frequency can be highly site-specific because the mechanisms linking mowing to conservation value are complex, and there is often no need or no resource for a second cut (beneficial for the feeding of herbivores), or weather conditions may

Fig. 6 Log-response ratios (LRR) and 0.95 confidence bars comparing species richness for different mowing regimes (number of cuts per year). The number of studies for these data is given in brackets (to the left). For LRR , the values of the mean and standard deviation are on the right-hand side of the plot. The reference articles are listed in the section “References of the review on the effect of different mowing regimes.”



make hay making difficult in autumn (Szépligeti et al. 2018). The level of detail of the present study, aiming at assessing the overall SR, does not allow to refer to the richness (and abundance) of plant species of nature conservation interest (which would be a more valuable indicator than the overall richness). Studying the effects of disturbances requires measures of species abundance, rather than just their presence, and an experimental approach to complete the understanding of the mechanisms involved (e.g., Debussche et al. 1996). For instance, it is possible that the abundance of each plant species decreases or the plant species turnover increases while the SR remains the same. In this case, different results would be expected when assessing biodiversity outcomes taking species abundance into account, e.g., Shannon diversity, which is calculated on the proportion of each species relative to the total number of species (Milberg et al. 2017).

A possibly important factor not taken into account in the present study is the timing of mowing during the year (either this information was not available for some included studies or too small subgroups would have been created by including this factor). In fact, the effects can be different depending on whether the harvest occurs early or late in the growing season. Early mowing can have negative effects on plant species with late seed-setting. In combination with more frequent harvesting this can affect the ability of species to re-grow back (e.g., Humbert et al. 2012). Then, the two American studies of the review (Dickson and Foster 2008; Foster et al. 2009) in which fertilisers were used during the study period, were also combined in the meta-analysis.

In the study of Lanta et al. (2009), the estimate of *LRR* = 0.14 was obtained with a wide confidence interval (from -1.58 to 1.86), likely due to the wide variation in the original dataset. We also note that five experiments showed effects that are about three- to five-fold higher (*LRR* from 0.71 to 1.53) than the average. Fenner and Palmer (1998) in Belgium (*LRR* = 0.92), and Jacquemyn et al. (2011) in United Kingdom (*LRR* = 0.71), noticed that several small herbs and rosette plants were quickly lost in abandoned plots, with mowing reducing the proportion of tall-growing plants and increasing light penetration to the ground surface. As Truus and Puusild (2009), with *LRR* = 1.53 (wet experiment), Metsoja et al. (2014) - *LRR* = 1.17 (tall forb meadow) - and Neuenkamp et al. (2013) - *LRR* = 1.14 (tall forb meadow) - observed that mowing had a distinct role in activating the soil seed bank in Estonian flooded, well drained meadows dominated by tall forb meadow communities. These are highly productive communities (e.g., ~ 1000 g m⁻² in Neuenkamp et al. 2013), where plant SR is determined primarily by light and litter rather than nutrient availability.

Opposite to SR, over the 16 independent studies (18 experiments) for the effect of mowing on HB (Fig. 5b), the pooled *LRR* value equal to -0.23, or c. -21% (0.95 confidence

interval from -0.31 to -0.14, $p < 0.01$) suggests an overall negative influence of disturbance. In the included studies, mowing (which had a positive effect on SR) distinctly had a negative effect on HB. Although this is undoubtedly a trade-off between a provisioning service (forage production) and biodiversity-mediated ecosystem services (e.g., pollination, pest control, soil fertility and yield stability), there are studies which indicate that vegetation density and biomass production may be reduced in unmanaged treatments because litter accumulated on the sward surface prevents plants sprouting (as observed, for instance, in Czech Republic by Pavlů et al. 2016). A stimulating effect of cutting on grassland productivity was also observed by Sasaki et al. (2011) in temperate Japan, which was attributed to the over-compensatory growth because of changes in floristic composition owing to the mowing treatment. There is indeed a body of literature (as reviewed, for instance, by Sonkoly et al. 2019) that shows that HB increases when SR increases, mainly from experiments with grasslands sown along gradients of a limited number of plant species compared to monocultures.

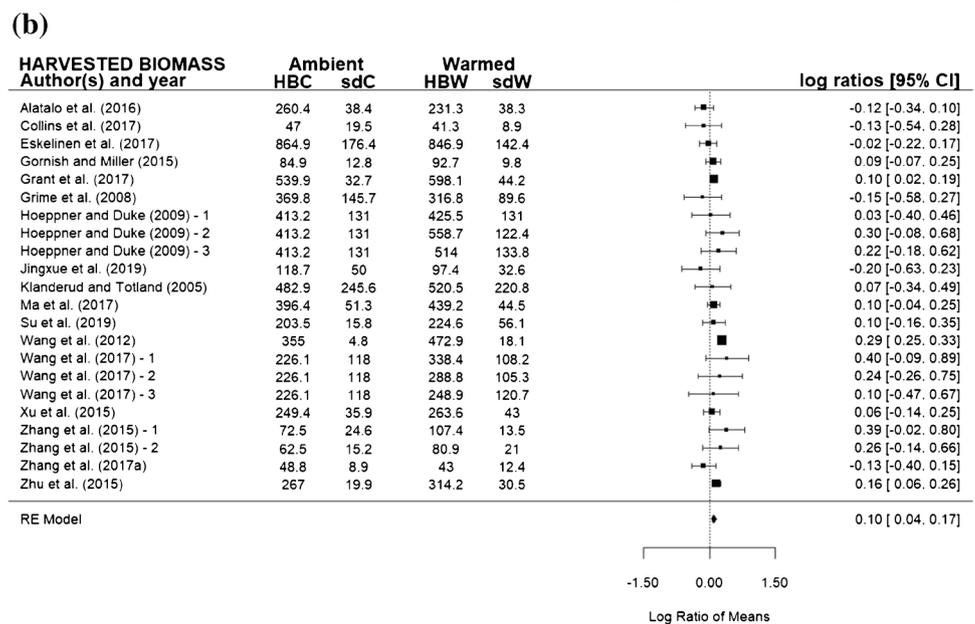
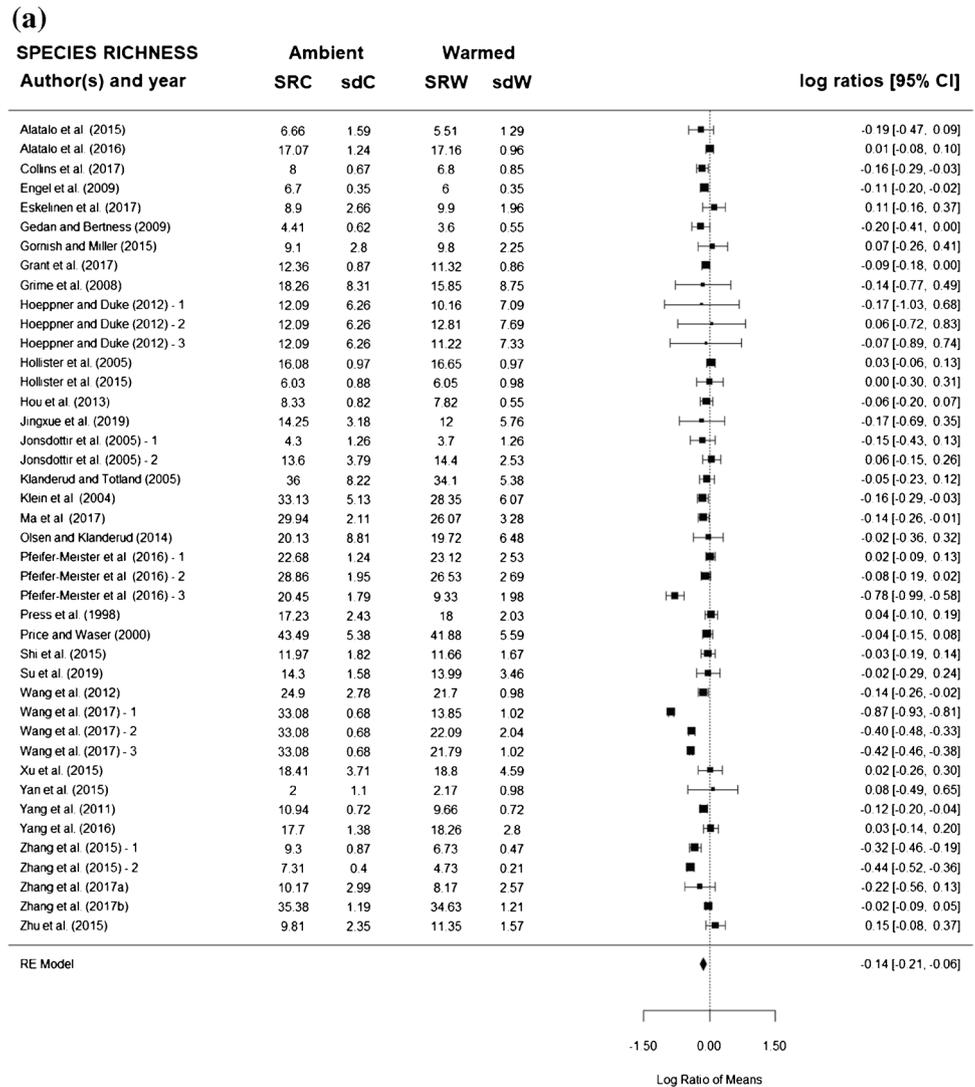
In the mixed-effects model, planned moderators were mostly not significant ($p > 0.10$). When a grassland is abandoned, changes in SR can be expected as a function of time since abandonment (vegetation succession; e.g., Tasser and Tappeiner 2002) but we could not confirm an effect of the duration of the experiment. Only the year of publication was a significant moderator ($p < 0.05$) of the effect of mowing on HB ($k = 16$, $j = 18$) when this covariate was assessed alone (with more negative *LRR* values observed in the oldest experiments, i.e., mean *LRR* of about -0.20 in 2010-2019 and -0.31 in 1993-2009). The covariate explained ~ 33% of the heterogeneity (Table S3) but the effect was not significant ($P > 0.05$) when different moderators were assessed together.

3.4 Effect of warming on SR and HB

A forest plot for all 34 recorded articles combined (42 experiments) indicates a significantly negative effect of warming (different treatments) on SR compared to control (Fig. 7a): pooled *LRR* = -0.14 (c. -13%), 0.95 confidence interval from -0.21 to -0.06 ($p < 0.01$). The decline in SR, observed here for an average temperature increase of 1.8 ± 0.9 °C (range: 0.15 to 4.10 °C), is consistent with the response of terrestrial ecosystems (-10.5% of SR) as observed by Gruner et al. (2017) for an average warming of 3 °C. It cannot be excluded that short-term simulation of warming, without considering temporal adaptation, has exacerbated the warming effect on terrestrial ecosystems (Leuzinger et al. 2011).

The results of the mixed-effects model showed that SR was somewhat significantly moderated by the year of publication ($p \sim 0.05$) when this moderator, which explained only

Fig. 7 Forest plots of the meta-analysis (log-response ratios and 0.95 confidence limits) comparing species richness, SR **(a)** and harvested biomass, HB, in g DM m⁻² **(b)** in ambient (C, control) and warmed (W, treatment) grasslands, with the relative standard deviations (sd). RE stands for random-effects model.



~ 9% of the heterogeneity (Table S3), was assessed alone ($k = 34, j = 42$). We note that more recently published studies were more numerous and yielded larger effect sizes, with an imbalance with only eight studies published prior to 2010 (giving an average LRR of -0.05). This could be due to the widespread use of small, low-cost open-top chambers (passive warming) in climate change experiments, especially on short-statured vegetation like grassland steppe and temperate grasslands (Frei et al. 2020). According to Leuzinger et al. (2011), a diminishing effect size is expected with a longer duration and a larger spatial scope of experiments. In light of this, we would have expected an influence of the experimental methodology on SR/HB responses since infrared heaters (active heating) can be applied to larger plots than open-top chambers. The three experiments of Wang et al. (2017) do indeed indicate that a smaller open-top chamber of different sizes could have an impact on the response to warming on both SR (which tends to become even more negative, $LRR = -0.87$, with a smaller chamber) and HB (which, conversely, tends to become more positive, $LRR = 0.40$, with a smaller chamber). The duration of experiments could also have had an influence on the grassland response to warming since SR changes slowly (e.g., Galvánek and Lepš 2008), but we have no confirmation of these effects in our study.

Site elevation ($p < 0.05$) and annual rainfall ($p < 0.01$) emerged as significant moderators when all moderators were included in the mixed-effects model ($P < 0.05$; $k = 22, j = 30$). The latter explained ~ 36% of the heterogeneity (Table S3). We note that smaller size effects of warming on SR (lesser plant diversity loss) tend to be associated with dry areas (< 300 mm precipitation per year, with LRR of about -0.01 on average). In fact, the response of SR to warming was observed to be stronger the lower the aridity (e.g. Peñuelas et al. 2007). Similarly, less negative LRR values (i.e., more limited decline in plant diversity) were found for grassland sites below 1000 m a.s.l. (about -0.06 on average), where SR is generally lower (e.g., Dengler et al. 2014). The more pronounced decline of SR in high-elevation grasslands may reflect that plant species that are adapted to cold areas tend to be more sensitive to warming. It can be assumed that the thermal niche of plant species may be narrower than at low altitudes, which considerably hinders adaptation/acclimation in the short-term (e.g., Löffler and Pape 2020). While changes in species cover and the composition of plant communities indicate an acceleration of the transformation towards more heat-demanding vegetation, this colonisation process could take place at a slower pace than the continued decrease in cryophilic species, thus favouring periods of accelerated species decline (Lamprecht et al. 2018).

Of the few experiments in which $LRR > 0$ (i.e., increased SR under higher temperatures), the one from Zhu et al. (2015), with $LRR = 0.15$, is consistent with the situation of a meadow steppe dominated by a perennial rhizome grass

species – *Leymus chinensis* (Trin.) Tzvelev (Chinese rye grass) – which is the first to germinate each year. A higher accumulation of plant community biomass in the warmed plots leads to more plant litter, which suppresses the germination and regrowth of *L. chinensis*, reducing its dominance and allowing other species (annual forbs) to quickly colonize the plant community. In Eskelinen et al. (2017), warmer climate increased SR ($LRR = 0.11$) via recruitment in conditions where competition with the residents was relaxed (e.g., in disturbed sites), where herbivores kept vegetation open and in habitats with relatively low nutrient availability.

Over the 17 recorded articles (22 experiments) for the effect of warming on HB (Fig. 7b), the pooled LRR value equal to 0.10, or c. 11% increase (0.95 confidence interval from 0.04 to 0.17), suggests an overall positive influence of increasing temperatures ($p < 0.05$). This is in accordance with Song et al. (2019) for terrestrial ecosystems and Liang et al. (2013) who, in a meta-analysis, found that across warming experiments conducted worldwide, warming overall had positive effects on plant photosynthetic rates of terrestrial plants, with varying effects depending on plant functional types. Similarly, Wu et al. (2011) reported in a meta-analysis that experimental warming has led to an overall increase in aboveground biomass production of terrestrial ecosystems. However, plant gas exchanges can be constrained by other environmental factors (e.g., water availability) that can inhibit photosynthetic and transpiration rates (Song et al. 2016). In fact, warming-induced soil water deficit indirectly affects biomass production by decreasing soil moisture availability (e.g., Wagle and Kakani 2014). In Hoepfner and Duke (2009), the maximum HB was obtained with $+2.7$ °C ($LRR = 0.30$), while with $\Delta T = +4.0$ °C the increase in HB was smaller ($LRR = 0.22$). The mixed-effects model with year of publication, site elevation and heating method as moderators ($k = 15, j = 20$) was significant ($P < 0.05$) and explained ~ 63% of the heterogeneity (Table S3), but only year of publication was significant ($p < 0.05$). In fact, negative effects of warming on HB were mostly observed in experiments conducted after 2015, reducing the LRR values for the period 2015-2019 (which nevertheless remained positive on average, i.e., ~ 0.04). In our meta-analysis, the most negative effect of warming on HB ($LRR = -0.20$) was obtained in a Tibetan alpine steppe (Jingxue et al. 2019), where experimental warming ($+2$ °C) under ambient precipitation significantly caused reductions in biomass because of induced water deficit. Xu et al. (2015) also showed in an alpine meadow on the Qinghai-Tibetan Plateau (arid and cold area) how warming and mowing combined (a treatment not included in our meta-analysis) negatively affected HB ($LRR = -0.08$) and positively affected SR ($LRR = 0.04$), indicating the dominant role of management (which tends to favour SR and limit HB) over an environmental change (which, conversely, is supposed to favour HB and

limit SR). Higher biomass production under warming conditions could explain the decline in SR, through competitive exclusion, for which all environmental conditions likely to favour high levels of HB could lead to a decline of SR. However, as warming increases evapotranspiration, greater drought conditions could dampen the biomass response, thus reducing competitive exclusion, which favours the stability of SR. In fact, the adverse effects of warming caused by increased heat stress and water scarcity could, in the long term, counteract the positive effect of mowing on SR, especially in temperate grasslands (e.g., De Boeck et al. 2008).

4 Conclusion

Using a meta-analytical methodology, we generated an integrated analysis of a large amount of observation data from different regions of the world, which better reflect the general patterns of grassland response than several fragmented studies performed so far. First, we found higher SR and lower HB in plots that were mown, suggesting the importance of management practices based on the application of disturbances such as prescribed mowing to enhance plant species diversity. Second (and opposite to the first result), we found that HB can be higher in plots that are exposed to higher temperatures while warming tends to decrease the number of plant species. The opposite responses of SR and HB to disturbances in the two meta-analyses suggest possible competitive exclusion mechanisms, which have not been investigated in this study. This is supported by the importance of site elevation (narrow thermal niche preventing plant species from adapting quickly at high altitudes) and annual rainfall (competitive exclusion in humid areas) in explaining the response of SR to warming. However, the present results of meta-analyses have some limitations. First, SR and HB are kinds of ecosystem response influenced by multiple factors and there are complex interactions between them that we have not considered due to lack of adequate data. Second, even if publication bias was substantially avoided, we have no access to unpublished researches or studies published in other language than English, which may have influenced our results. Despite some limitations, the present meta-analyses provide the latest evidence regarding the positive effect of moderate physical disturbance (i.e., limited mowing) on the creation and maintenance of highly diverse, ecologically and agriculturally valuable grasslands. In parallel to that, our results confirm the importance of considering plant species' response to environmental stresses together with competition when predicting community dynamics under warming scenarios. Further quantitative analysis of these relations may contribute to improve grassland simulation models addressing the dynamics of

plant diversity. Overall, we argue for long-term, two-factor warming and mowing experiments that incorporate both SR and HB assessment to guide discussions of how best to meet the relevant goal of improving our understanding of grassland responses to global changes.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s13593-021-00722-y>.

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Authors' contributions Conceptualisation: C.P.C.; Methodology: C.P.C. and F.P.; Formal analysis: F.P. and C.P.C.; Investigation: F.P. and C.P.C.; Writing—original draft: G.B. and F.P.; Writing—review and editing: G.B. F.P. and C.P.C.; Supervision: G.B. and C.P.C.; Funding acquisition: G.B. and C.P.C.

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Data availability Supplementary files are available online (<https://doi.org/10.15454/M9P0TT>) as 'database_mowing_meta-analysis_one_cut.tab', 'database_mowing_review_different_cuts.tab' and 'database_warming_meta-analysis.tab' at Data INRAE portal (<https://data.inrae.fr>). Additional data that support the findings of this study are available upon request from the authors.

Code availability Not applicable.

Declarations

Ethics approval Not applicable.

Consent to participate All authors agree to participate in this paper.

Consent for publication All authors agree to the publication of this paper.

Conflict of interest The authors declare no competing interests.

References

- Batáry P, Báldi A, Sárosspataki M, Kohler F, Verhulst J, Knop E, Herzog G, Kleijn D (2010) Effect of conservation management on bees and insect-pollinated grassland plant communities in three European countries. *Agric. Ecosyst. Environ.* 136:35–39. <https://doi.org/10.1016/j.agee.2009.11.004>
- Baur B, Cremene C, Groza G, Rakosy L, Schileyko AA, Baur A, Stoll P, Erhardt A (2006) Effects of abandonment of subalpine hay meadows on plant and invertebrate diversity in Transylvania. *Romania. Biol. Conserv.* 132:261–273. <https://doi.org/10.1016/j.biocon.2006.04.018>
- Bengtsson J, Bullock M, Egoh B, Everson C, Everson T, O'Connor T, O'Farrell PJ, Smith HG, Lindborg R (2019) Grasslands - more important for ecosystem services than you might think. *Ecosphere* 10:e02582. <https://doi.org/10.1002/ecs2.2582>
- Boch S, Bedolla A, Ecker KT, Ginzler C, Graf U, Kuchler H, Nobis MP, Holderegger R, Bergamini A (2019) Threatened and specialist species suffer from increased wood cover and productivity in Swiss steppes. *Flora* 258:151444. <https://doi.org/10.1016/j.flora.2019.151444>
- Borer ET, Seabloom EW, Gruner DS, Harpole WS, Hillebrand H, Lind EM, Adler PB, Alberti J, Anderson TM, Bakker JD, Biederman LA, Blumenthal D, Brown CS, Brudvig LA, Buckley YM, Cadotte M, Chu C, Cleland EE, Crawley MJ et al (2014) Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* 508:517–520. <https://doi.org/10.1038/nature13144>
- Cardinale BJ, Wright JP, Cadotte MW, Carroll IT, Hector A, Srivastava DS, Loreau M, Weis JJ (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proc. Natl. Acad. Sci. U. S. A.* 104:18123–18128. <https://doi.org/10.1073/pnas.0709069104>
- Christie AP, Amano T, Martin P, Shackelford G, Simmons BI, Sutherlands WJ (2019) Simple study designs in ecology produce inaccurate estimates of biodiversity responses. *J. Appl. Ecol.* 56:2742–2754. <https://doi.org/10.1111/1365-2664.13499>
- Chytrý M (2001) Phytosociological data give biased estimates of species richness. *J. Veg. Sci.* 12:439–444. <https://doi.org/10.1111/j.1654-1103.2001.tb00190.x>
- Cleland EE (2011) Biodiversity and ecosystem stability. *Nature Education Knowledge* 3:14
- Cowles J, Boldgiv B, Liancourt P, Petraitis PS, Casper BB (2018) Effects of increased temperature on plant communities depend on landscape location and precipitation. *Ecol. Evol.* 8:5267–5278. <https://doi.org/10.1002/ece3.3995>
- Craven D, Isbell F, Manning P, Connolly J, Bruelheide H, Ebelng A, Roscher C, van Ruijven J, Weigelt A, Wilsey B, Beierkuhnlein C, de Luca E, Griffin JN, Hautier Y, Hector A, Jentsch A, Kreyling J, Lanta V, Loreau M et al (2016) Plant diversity effects on grassland productivity are robust to both nutrient enrichment and drought. *Philos. T. R. Soc. B* 371:20150277. <https://doi.org/10.1098/rstb.2015.0277>
- Cunningham P, Linn RR, Koo E, Wilson CJ (2013) Large-eddy simulations of air flow and turbulence within and around low-aspect-ratio cylindrical open-top chambers. *J. Appl. Meteorol. Climatol.* 52: 1716–1737. <https://doi.org/10.1175/JAMC-D-12-041.1>
- De Boeck HJ, Lemmens CMHM, Gielen B, Malchair S, Carnol M, Merckx R, Van den Berge J, Ceulemans R, Nijs I (2008) Biomass production in experimental grasslands of different species richness during three years of climate warming. *Biogeosciences* 5:585–594. <https://doi.org/10.5194/bg-5-585-2008>
- De Boeck HJ, Nijs I (2011) An alternative approach for infrared heater control in warming and extreme event experiments in terrestrial ecosystems. *J. Ecol.* 99:724–728. <https://doi.org/10.1111/j.1365-2745.2011.01799.x>
- Debussche M, Escarré J, Lepart J, Houssard C, Lavorel S (1996) Changes in Mediterranean plant succession: Old-fields revisited. *J. Veg. Sci.* 7:519–526. <https://doi.org/10.2307/3236300>
- Dengler J, Janišová M, Török P, Wellstein C (2014) Biodiversity of Palaearctic grasslands: a synthesis. *Agric. Ecosyst. Environ.* 182:1–14. <https://doi.org/10.1016/j.agee.2013.12.015>
- Dickson TL, Foster BL (2008) The relative importance of the species pool, productivity and disturbance in regulating grassland plant species richness: a field experiment. *J. Ecol.* 96:937–946. <https://doi.org/10.1111/j.1365-2745.2008.01420.x>
- Dunford RW, Smith AC, Harrison PA, Hanganu D (2015) Ecosystem service provision in a changing Europe: adapting to the impacts of combined climate and socio-economic change. *Landscape Ecol.* 30:443–461. <https://doi.org/10.1007/s10980-014-0148-2>
- Egger M, Davey Smith G, Schneider M, Minder C (1997) Bias in meta-analysis detected by a simple, graphical test. *BMJ* 315:629–634. <https://doi.org/10.1136/bmj.315.7109.629>
- Engler R, Randin C, Vittoz P, Czárka T, Beniston M, Zimmermann N, Guisan A (2009) Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? *Ecography* 32:34–45. <https://doi.org/10.1111/j.1600-0587.2009.05789.x>
- Eskelinen A, Kaarlejärvi E, Olofsson J (2017) Herbivory and nutrient limitation protect warming tundra from lowland species' invasion and diversity loss. *Global Change Biol.* 23:245–255. <https://doi.org/10.1111/gcb.13397>
- Fakarayi T, Mashapa C, Gandiwa E, Kativu S (2015) Pattern of land-use and land cover changes in Driefontein grassland important bird area. Zimbabwe. *Trop. Conserv. Sci.* 8:274–283. <https://doi.org/10.1177/194008291500800120>
- Fenner M, Palmer L (1998) Grassland management to promote diversity: creation of a patchy sward by mowing and fertiliser regimes. *Field Stud.* 9:313–324
- Foster BL, Kindscher K, Houseman GR, Murphy CA (2009) Effects of hay management and native species sowing on grassland community structure, biomass, and restoration. *Ecol. Appl.* 19:1884–1896. <https://doi.org/10.1890/08-0849.1>
- Frei ER, Schnell L, Vitasse Y, Wohlgemuth T, Moser B (2020) Assessing the effectiveness of *in-situ* active warming combined with open top chambers to study plant responses to climate change. *Front. Plant Sci.* 11:539584. <https://doi.org/10.3389/fpls.2020.539584>
- Galvánec D, Lepš J (2008) Changes of species richness pattern in mountain grasslands: abandonment versus restoration. *Biodivers. Conservat.* 17:3241. <https://doi.org/10.1007/s10531-008-9424-2>
- Gao J, Jiao K, Wu S (2018) Quantitative assessment of ecosystem vulnerability to climate change: methodology and application in China. *Environ. Res. Lett.* 13:094016. <https://doi.org/10.1088/1748-9326/aadd2e>
- Gianfredi V, Nucci D, Salvatori T, Dallagiocoma G, Fatigoni C, Moretti M, Realdon S (2019) Rectal cancer: 20% risk reduction thanks to dietary fibre intake. Systematic review and meta-analysis. *Nutrients* 11: 1579. <https://doi.org/10.3390/nu11071579>
- Gibson L, Münch Z, Palmer A, Mantel S (2018) Future land cover change scenarios in South African grasslands - implications of altered biophysical drivers on land management. *Heliyon* 4:e00693. <https://doi.org/10.1016/j.heliyon.2018.e00693>
- Gruner DS, Bracken MES, Berger SA, Eriksson BK, Gamfeldt L, Matthiessen B, Moorthi S, Sommer U, Hillebrand H (2017) Effects of experimental warming on biodiversity depend on ecosystem type and local species composition. *Oikos* 126:8–17. <https://doi.org/10.1111/oik.03688>
- Haddaway NR, Styles D, Pullin AS (2014) Evidence on the environmental impacts of farm land abandonment in high altitude/mountain regions: a systematic map. *Environ. Evid.* 3:1–19. <https://doi.org/10.1186/2047-2382-3-17>

- Harrison SP, Gornish ES, Copeland S (2015) Climate-driven diversity loss in a grassland community. *Proc. Natl. Acad. Sci. U. S. A.* 112:8672–8677. <https://doi.org/10.1073/pnas.1502074112>
- Harrison S, Spasojevic MJ, Li D (2020) Climate and plant community diversity in space and time. *Proc. Natl. Acad. Sci. U. S. A.* 117:4464–4470. <https://doi.org/10.1073/pnas.1921724117>
- Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. *Ecology* 80:1150–1156. <https://doi.org/10.2307/177062>
- Hejman M, Klaudivsova M, Schellberg J, Honsova D (2007) The Rengen grassland experiment: Plant species composition after 64 years of fertilizer application. *Agric. Ecosyst. Environ.* 122:259–266. <https://doi.org/10.1016/j.agee.2006.12.036>
- Hejman M, Hejmanová P, Pavlů V, Beneš J (2013) Origin and history of grasslands in Central Europe - a review. *Grass Forage Sci.* 68:345–363. <https://doi.org/10.1111/gfs.12066>
- Huhta AP, Rautio P (1998) Evaluating the impacts of mowing: a case study comparing managed and abandoned meadow patches. *Annales Botanici Fennici* 35:85–99
- Humbert J-Y, Pellet J, Buri P, Arlettaz R (2012) Does delaying the first mowing date benefit biodiversity in meadowland? *Environ. Evid.* 1:9. <https://doi.org/10.1186/2047-2382-1-9>
- Huston M (1979) A general hypothesis of species diversity. *Am. Nat.* 113:81–101. <https://doi.org/10.1086/283366>
- Jacquemyn H, Van Mechelen C, Brys R, Honnay O (2011) Management effects on the vegetation and soil seed bank of calcareous grasslands: an 11-year experiment. *Biol. Conserv.* 144:416–422. <https://doi.org/10.1016/j.biocon.2010.09.020>
- Jennions MD, Møller AP (2002) Relationships fade with time: a meta-analysis of temporal trends in publication in ecology and evolution. *Proc. Royal Soc. B* 269:43–48. <https://doi.org/10.1098/rspb.2001.1832>
- Jingxue Z, Tianxiang L, Haixia W, Zhaoheng D, Xiang L, Ruicheng L, Yanhong T (2019) Increased precipitation offsets the negative effect of warming on plant biomass and ecosystem respiration in a Tibetan alpine steppe. *Agric. For. Meteorol.* 279:107761. <https://doi.org/10.1016/j.agrformet.2019.107761>
- Lajeunesse MJ (2011) On the meta-analysis of response ratios for studies with correlated and multi-group designs. *Ecology* 92:2049–2055. <https://doi.org/10.1890/11-0423.1>
- Lamprecht A, Semenchuk R, Steinbauer K, Winkler M, Pauli H (2018) Climate change leads to accelerated transformation of high-elevation vegetation in the central Alps. *New Phytol.* 220:447–459. <https://doi.org/10.1111/nph.15290>
- Lanta V, Doležal J, Lantová P, Kelišek J, Mudrák O (2009) Effects of pasture management and fertilizer regimes on botanical changes in species-rich mountain calcareous grassland in Central Europe. *Grass Forage Sci.* 64:443–453. <https://doi.org/10.1111/j.1365-2494.2009.00709.x>
- Lasanta T, Arnáez J, Pascua NE, Ruiz-Flaño P, Errea MP, Lana-Renault N (2017) Space–time process and drivers of land abandonment in Europe. *Catena* 149:810–823. <https://doi.org/10.1016/j.catena.2016.02.024>
- Leuzinger S, Luo Y, Beier C, Dieleman W, Vicca S, Körner C (2011) Do global change experiments overestimate impacts on terrestrial ecosystems? *Trends Ecol. Evo.* 26:236–241. <https://doi.org/10.1016/j.tree.2011.02.011>
- Liang JY, Xia JY, Liu LL, Wan S (2013) Global patterns of the responses of leaf-level photosynthesis and respiration in terrestrial plants to experimental warming. *J. Plant Ecol.* 6:437–447. <https://doi.org/10.1093/jpe/rtt003>
- Liberati A, Altman DG, Tetzlaff J, Mulrow C, Gøtzsche PC, Ioannidis JPA, Clarke M, Devereaux PJ, Kleijnen J, Moher D (2009) The PRISMA statement for reporting systematic reviews and meta-analyses of studies that evaluate health care interventions: explanation and elaboration. *PLOS Medicine* 6:e1000100. <https://doi.org/10.1371/journal.pmed.1000100>
- Li W, Li X, Zhao Y, Zheng S, Bai Y (2018) Ecosystem structure, functioning and stability under climate change and grazing in grasslands: current status and future prospects. *Current Opinion in Environmental Sustainability* 33:124–135. <https://doi.org/10.1016/j.cosust.2018.05.008>
- Llorens L, Peñuelas J, Beier C, Emmett B, Estiarte M, Tietema A (2004) Effects of an experimental increase of temperature and drought on the photosynthetic performance of two ericaceous shrub species along a north-south European gradient. *Ecosystems* 7:613–624. <https://doi.org/10.1007/s10021-004-0180-1>
- Loreau M (2010) Linking biodiversity and ecosystems: towards a unifying ecological theory. *Philos. T. R. Soc. B* 365:49–60. <https://doi.org/10.1098/rstb.2009.0155>
- Lorenzetti DL, Ghali WA (2013) Reference management software for systematic reviews and meta-analyses: an exploration of usage and usability. *BMC Medical Research Methodology* 13:141. <https://doi.org/10.1186/1471-2288-13-141>
- Loydi A, Eckstein RL, Otte A, Donath TW (2013) Effects of litter on seedling establishment in natural and semi-natural grasslands: a meta-analysis. *J. Ecol.* 101:454–464. <https://doi.org/10.1111/1365-2745.12033>
- Löffler J, Pape R (2020) Thermal niche predictors of alpine plant species. *Ecology* 101:e02891. <https://doi.org/10.1002/ecy.2891>
- Mason NWH, de Bello F, Doležal J, Lepš J (2011) Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. *J. Ecol.* 99:788–796. <https://doi.org/10.1111/j.1365-2745.2011.01801.x>
- Metsoja JA, Neuenkamp L, Zobel M (2014) Seed bank and its restoration potential in Estonian flooded meadows. *Appl. Veg. Sci.* 17:262–273. <https://doi.org/10.1111/avsc.12057>
- Milberg P, Tälle M, Fogelfors H, Westerberg L (2017) The biodiversity cost of reducing management intensity in species-rich grasslands: mowing annually vs. every third year. *Basic Appl. Ecol.* 22:61–74. <https://doi.org/10.1016/j.baae.2017.07.004>
- Münch Z, Okoye PI, Gibson L, Mantel S, Palmer A (2017) Characterizing degradation gradients through land cover change analysis in rural Eastern Cape, South Africa. *Geosci. J.* 7:1–7. <https://doi.org/10.3390/geosciences7010007>
- Nakagawa S, Santos ESA (2012) Methodological issues and advances in biological meta-analysis. *Evol. Ecol.* 26:1253–1274. <https://doi.org/10.1007/s10682-012-9555-5>
- Neuenkamp L, Metsoja JA, Zobel M, Hölzel N (2013) Impact of management on biodiversity-biomass relations in Estonian flooded meadows. *Plant Ecol.* 214:845–856. <https://doi.org/10.1007/s11258-013-0213-y>
- Norberg J, Swaney DP, Dushoff J, Lin J, Casagrandi R, Levin SA (2001) Phenotypic diversity and ecosystem functioning in changing environments: A theoretical framework. *Proc. Natl. Acad. Sci. U. S. A.* 98:11376–11381
- Oertel C, Matschullat J, Zurba K, Zimmermann F, Erasmí S (2016) Greenhouse gas emissions from soils - A review. *Geochemistry* 76:327–352. <https://doi.org/10.1016/j.chemer.2016.04.002>
- Ohdo T, Takahashi K (2020) Plant species richness and community assembly along gradients of elevation and soil nitrogen availability. *AoB Plants* 12: plaa014. <https://doi.org/10.1093/aobpla/plaa014>
- Pallett DW, Pescott OL, Schäfer SM (2016) Changes in plant species richness and productivity in response to decreased nitrogen inputs in grassland in southern England. *Ecol. Indic.* 68:73–81. <https://doi.org/10.1016/j.ecolind.2015.12.024>
- Parton WJ, Scurlock JMO, Ojima DS, Schimel DS, Hall DO (1995) Impact of climate change on grassland production and soil

- carbon worldwide. *Global Change Biol.* 1:13–22. <https://doi.org/10.1111/j.1365-2486.1995.tb00002.x>
- Pavlu L, Gaisler J, Hejzman M, Pavlu VV (2016) What is the effect of long-term mulching and traditional cutting regimes on soil and biomass chemical properties, species richness and herbage production in *Dactylis glomerata* grassland? *Agric. Ecosyst. Environ.* 217:13–21. <https://doi.org/10.1016/j.agee.2015.10.026>
- Peel MC, Finlayson BL, McMahon TA (2007) Updated world map of the Köppen-Geiger climate classification. *Hydrol. Earth Syst. Sci.* 11:1633–1644. <https://doi.org/10.5194/hess-11-1633-2007>
- Peñuelas J, Prieto P, Beier C, Cesaraccio C, De Angelis P, De Dato G, Emmett BA, Estiarte M, Garadnai J, Gorissen A, Láng EK, Kröel-Dulay G, Llorens L, Pellizzaro G, Riis-Nielsen T, Schmidt IK, Sirca C, Sowerby A, Spano D, Tietema A (2007) Response of plant species richness and primary productivity in shrublands along a north-south gradient in Europe to seven years of experimental warming and drought: reductions in primary productivity in the heat and drought year of 2003. *Global Change Biol.* 13:2563–2581. <https://doi.org/10.1111/j.1365-2486.2007.01464.x>
- Pierce S (2014) Implications for biodiversity conservation of the lack of consensus regarding the humped-back model of species richness and biomass production. *Funct. Ecol.* 28:253–257. <https://doi.org/10.1111/1365-2435.12147>
- Pittarello M, Lonati M, Ravetto Enri S, Lombardi G (2020) Environmental factors and management intensity affect in different ways plant diversity and pastoral value of alpine pastures. *Ecol. Indic.* 115:106429. <https://doi.org/10.1016/j.ecolind.2020.106429>
- Plantureux S, Peeters A, McCracken D (2005) Biodiversity in intensive grasslands: Effect of management, improvement and challenges. *Agron. Res* 3:153–164
- Pontes LS, Maire V, Schellberg J, Louault F (2015) Grass strategies and grassland community responses to environmental drivers: a review. *Agron. Sustain. Dev.* 35:1297–1318. <https://doi.org/10.1007/s13593-015-0314-1>
- Pullin AS, Stewart GB (2006) Guidelines for systematic review in conservation and environmental management 20:1647–1656. <https://doi.org/10.1111/j.1523-1739.2006.00485.x>
- Riedener E, Rusterholz HP, Baur B (2014) Land-use abandonment owing to irrigation cessation affects the biodiversity of hay meadows in an arid mountain region. *Agric. Ecosyst. Environ.* 185:144–152. <https://doi.org/10.1016/j.agee.2013.12.023>
- Schirpke U, Kohlera M, Leitinger G, Fontana V, Tasser E, Tappeiner U (2017) Future impacts of changing land-use and climate on ecosystem services of mountain grassland and their resilience. *Ecosyst. Serv.* 26:79–94. <https://doi.org/10.1016/j.ecoser.2017.06.008>
- Silvertown J, Poulton P, Johnston E, Edwards G, Heard M, Biss P (2006) The Park Grass Experiment 1856–2006; its contribution to ecology. *J. Ecol.* 94:801–814. <https://doi.org/10.1111/j.1365-2745.2006.01145>
- Song B, Niu S, Wan S (2016) Precipitation regulates plant gas exchange and its long-term response to climate change in a temperate grassland. *J. Plant Ecol.* 9:531–541. <https://doi.org/10.1093/jpe/rtw010>
- Song J, Wan S, Piao S, Knapp AK, Classen AT, Vicca S, Ciais P, Hovenden MJ, Leuzinger S, Beier C, Kardol P, Xia J, Liu Q, Ru J, Zhou Z, Luo Y, Guo D, Adam Langley J, Zscheischler J et al (2019) A meta-analysis of 1,119 manipulative experiments on terrestrial carbon-cycling responses to global change. *Nature Ecol. Evol.* 3:1309–1320. <https://doi.org/10.1038/s41559-019-0958-3>
- Sonkoly J, Kelemen A, Valkó O, Deák B, Kiss R, Tóth K, Miglécz T, Tóthmérész B, Török P (2019) Both mass ratio effects and community diversity drive biomass production in a grassland experiment. *Sci. Rep.* 9:1848. <https://doi.org/10.1038/s41598-018-37190-6>
- Stampfli A, Zeiter M (1999) Plant species decline due to abandonment of meadows cannot easily be reversed by mowing. A case study from the southern Alps. *J. Veg. Sci.* 10:151–164. <https://doi.org/10.2307/3237137>
- Su F, Wei Y, Wang F, Guo J, Zhang J, Wang Y, Guo H, Hu S (2019) Sensitivity of plant species to warming and altered precipitation dominates the community productivity in a semiarid grassland on the Loess Plateau. *Ecol. Evol.* 9:7628–7638. <https://doi.org/10.1002/ece3.5312>
- Tälle M, Deák B, Poschlod P, Valkó O, Westerberg L, Milberg P (2016) Grazing vs. mowing: a meta-analysis of biodiversity benefits for grassland management. *Agric. Ecosyst. Environ.* 222:200–212. <https://doi.org/10.1016/j.agee.2016.02.008>
- Tälle M, Deák B, Poschlod P, Valkó O, Westerberg L, Milberg P (2018) Similar effects of different mowing frequencies on the conservation value of semi-natural grasslands in Europe. *Biodivers. Conserv.* 27:2451–2475. <https://doi.org/10.1007/s10531-018-1562-6>
- Tasser E, Tappeiner U (2002) Impact of land use changes on mountain vegetation. *Appl. Veg. Sci.* 5:173–184. <https://doi.org/10.1111/j.1654-109X.2002.tb00547.x>
- Tilman D (1987) Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecol. Monogr.* 57:189–214. <https://doi.org/10.2307/2937080>
- Tóth E, Deák B, Valkó O, Kelemen A, Miglécz T, Tóthmérész B, Török P (2018) Livestock type is more crucial than grazing intensity: traditional cattle and sheep grazing in short-grass steppes. *Land Degrad. Dev.* 29:231–239. <https://doi.org/10.1002/ldr.2514>
- Tribot A-S, Deter J, Mouquet N (2018) Integrating the aesthetic value of landscapes and biological diversity. *Proc. Royal Soc. B* 285:20180971. <https://doi.org/10.1098/rspb.2018.0971>
- Truus L, Puusild E (2009) Species richness, biomass production and recent vegetation changes or estonian floodplain. *Pol. J. Ecol.* 1:33–45
- Turnbull LA, Isbell F, Purves DW, Loreau M, Hector A (2016) Understanding the value of plant diversity for ecosystem functioning through niche theory *Proc. Royal Soc. B* 14: 283. [101098/rspb20160536](https://doi.org/10.1098/rspb.2016.0536)
- Uchida K, Ushimaru A (2014) Biodiversity declines due to abandonment and intensification of agricultural lands: patterns and mechanisms. *Ecol. Monogr.* 84:637–658. <https://doi.org/10.1890/13-2170>
- van Klink R, Boch S, Buri P, Rieder NS, Humbert JY, Arlettaz R (2017) No detrimental effects of delayed mowing or uncut grass refuges on plant and bryophyte community structure and phytomass production in low-intensity hay meadows. *Basic Appl. Ecol.* 20:1–9. <https://doi.org/10.1016/j.baae.2017.02.003>
- van Klink R, van der Plas F, van (Toos) Noordwijk CGE, Wallis-DeVries MF, Olff H (2015) Effects of large herbivores on grassland arthropod diversity *Biol Rev* 90: 347–366 [101111/brv12113](https://doi.org/10.1111/brv.12113)
- Viechtbauer W (2010) Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.* 36: 1–48 [1018637/jssv036i03](https://doi.org/10.18637/jssv036i03)
- Vogel A, Scherer-Lorenzen M, Weigelt A (2012) Grassland resistance and resilience after drought depends on management intensity and species richness. *PLOS ONE* 7:e36992. <https://doi.org/10.1371/journal.pone.0036992>
- Wan Z, Yang J, Gu R, Liang Y, Yan Y, Gao Q, Yang J (2016) Influence of different mowing systems on community characteristics and the compensatory growth of important species of the *Stipa grandis* steppe in Inner Mongolia. *Sustainability* 8:1121. <https://doi.org/10.3390/su8111121>
- Wang C, Wang G, Wang Y, Zi H, Lerdau M, Liu W (2017) Effects of long-term experimental warming on plant community properties and soil microbial community composition in an alpine meadow.

- Isr. J. Ecol. Evol. 63:85–96. <https://doi.org/10.1080/15659801.2017.1281201>
- Wen Y, Jiang HF (2005) Cutting effects on growth characteristics, yield composition, and population relationships of perennial ryegrass and white clover in mixed pasture. *New Zeal. J. Agr. Res.* 48:349–358. <https://doi.org/10.1080/00288233.2005.9513666>
- White SR, Bork EW, Cahill JF Jr (2014) Direct and indirect drivers of plant diversity responses to climate and clipping across northern temperate grassland. *Ecology* 95:3093–3103. <https://doi.org/10.1890/14-0144.1>
- Xu M, Peng F, You Q, Guo J, Tian X, Liu M, Xue X (2015) Effects of warming and clipping on plant and soil properties of an alpine meadow in the Qinghai-Tibetan Plateau, China. *J. Arid Land* 7:189–204. <https://doi.org/10.1007/s40333-014-0010-z>
- Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci. U. S. A.* 96:1463–1468. <https://doi.org/10.1073/pnas.96.4.1463>
- Zavaleta ES, Shaw MR, Chiariello NR, Mooney HA, Field CB (2003) Additive effects of simulated climate changes, elevated CO₂, and nitrogen deposition on grassland diversity. *Proc. Natl. Acad. Sci. U. S. A.* 100:7650–7654. <https://doi.org/10.1073/pnas.0932734100>
- Zeller U, Starik N, Göttert T (2017) Biodiversity, land use and ecosystem services - An organismic and comparative approach to different geographical regions. *Glob. Ecol. Conserv.* 10:114–125. <https://doi.org/10.1016/j.gecco.2017.03.001>
- Zhang Y, Loreau M, He N, Wang J, Pan W, Bai Y, Han X-G (2018) Climate variability decreases species richness and community stability in a temperate grassland. *Oecologia* 188:183–192. <https://doi.org/10.1007/s00442-018-4208-1>
- Zhu H, Zou X, Wang D, Wan S, Wang L, Guo L (2015) Responses of community-level plant-insect interactions to climate warming in a meadow steppe. *Sci. Rep.* 5:18654. <https://doi.org/10.1038/srep18654>
- plant species richness: a field experiment. *J. Ecol.* 96:937–946. <https://doi.org/10.1111/j.1365-2745.2008.01420.x>
- Doležal J, Lanta V, Mudrák O, Lepš J (2019) Seasonality promotes grassland diversity: Interactions with mowing, fertilization and removal of dominant species. *J. Ecol.* 107:203–215. <https://doi.org/10.1111/1365-2745.13007>
- Fenner M, Palmer L (1998) Grassland management to promote diversity: creation of a patchy sward by mowing and fertiliser regimes. *Field Stud.* 9:313–324
- Foster BL, Kindscher K, Houseman GR, Murphy CA (2009) Effects of hay management and native species sowing on grassland community structure, biomass, and restoration. *Ecol. Appl.* 19:1884–1896. <https://doi.org/10.1890/08-0849.1>
- Galvánek D, Lepš J (2009) How do management and restoration needs of mountain grasslands depend on moisture regime? Experimental study from north-western Slovakia (Western Carpathians). *Appl. Veg. Sci.* 12:273–282. <https://doi.org/10.1111/j.1654-109X.2009.01022.x>
- Gerard M, El Kahloun M, Rymen J, Beauchard O, Meire P (2008) Importance of mowing and flood frequency in promoting species richness in restored floodplains. *J. Appl. Ecol.* 45:1780–1789. <https://doi.org/10.1111/j.1365-2664.2008.01572.x>
- Huhta AP, Rautio P (1998) Evaluating the impacts of mowing: a case study comparing managed and abandoned meadow patches. *Annales Botanici Fennici* 35:85–99
- Ilmarinen K, Mikola J (2009) Soil feedback does not explain mowing effects on vegetation structure in a semi-natural grassland. *Acta Oecol.* 35:838–848. <https://doi.org/10.1016/j.actao.2009.08.008>
- Jacquemyn H, Van Mechelen C, Brys R, Honnay O (2011) Management effects on the vegetation and soil seed bank of calcareous grasslands: an 11-year experiment. *Biol. Conserv.* 144:416–422. <https://doi.org/10.1016/j.biocon.2010.09.020>
- Klimeš HM, Mudrák O, Dančák M, Preislerová Z, Hájková P, Jongepierová I, Klimešová J (2013) Effects of changes in management on resistance and resilience in three grassland communities. *Appl. Veg. Sci.* 16:640–649. <https://doi.org/10.1111/avsc.12032>
- Lanta V, Doležal J, Lantová P, Kelíšek J, Mudrák O (2009) Effects of pasture management and fertilizer regimes on botanical changes in species-rich mountain calcareous grassland in Central Europe. *Grass Forage Sci.* 64:443–453. <https://doi.org/10.1111/j.1365-2494.2009.00709.x>
- Liira J, Issak M, Jõgar Ü, Mändoja M, Zobel M (2009) Restoration management of a floodplain meadow and its cost-effectiveness - the results of a 6-year experiment. *Annales Botanici Fennici* 46:397–408. <https://doi.org/10.5735/085.046.0504>
- Lundberg A, Kapfer J, Måren IE (2017) Reintroduced mowing can counteract biodiversity loss in abandoned meadows. *Erdkunde*, 127-142. <https://doi.org/10.3112/erdkunde.2017.02.03>
- Mašková Z, Doležal J, Květ J, Zemek F (2009) Long-term functioning of a species-rich mountain meadow under different management regimes. *Agric. Ecosyst. Environ.* 132:192–202. <https://doi.org/10.1016/j.agee.2009.04.002>
- Maurer K, Weyand A, Fischer M, Stöcklin J (2006) Old cultural traditions, in addition to land use and topography, are shaping plant diversity of grasslands in the Alps. *Biol. Conserv.* 130:438–446. <https://doi.org/10.1016/j.biocon.2006.01.005>
- Metsoja JA, Neuenkamp L, Zobel M (2014) Seed bank and its restoration potential in Estonian flooded meadows. *Appl. Veg. Sci.* 17:262–273. <https://doi.org/10.1111/avsc.12057>
- Moinardeau C, Mesléard F, Ramone H, Dutoit T (2019) Short-term effects on diversity and biomass on grasslands from artificial dykes under grazing and mowing treatments. *Environ. Conserv.* 46:132–139. <https://doi.org/10.1017/S0376892918000346>
- Neuenkamp L, Metsoja JA, Zobel M, Hölzel N (2013) Impact of management on biodiversity-biomass relations in Estonian

References of the meta-analysis (effect of mowing)

- Beltman B, van den Broek T, Martin W, ten Cate M, Güsewell S (2003) Impact of mowing regime on species richness and biomass of a limestone hay meadow in Ireland. *Bull. Geobot. Inst. ETH* 69:17–30
- Benot ML, Saccone P, Pautrat E, Vicente R, Colace MP, Grigulis K, Clément JC, Lavorel S (2014) Stronger short-term effects of mowing than extreme summer weather on a subalpine grassland. *Ecosystems* 17:458–472. <https://doi.org/10.1007/s10021-013-9734-4>
- Berg M, Joyce C, Burnside N (2012) Differential responses of abandoned wet grassland plant communities to reinstated cutting management. *Hydrobiologia* 692:83–97. <https://doi.org/10.1007/s10750-011-0826-x>
- Billeter R, Peintinger M, Diemer M (2007) Restoration of montane fen meadows by mowing remains possible after 4–35 years of abandonment. *Bot. Helv.* 117:1–13. <https://doi.org/10.1007/s00035-007-0743-9>
- Bobbink R, Willems JH (1993) Restoration management of abandoned chalk grassland in the Netherlands. *Biodivers. Conserv.* 2:616–626. <https://doi.org/10.1007/BF00051962>
- De Cauwer B, Reheul D (2009) Impact of land use on vegetation composition, diversity and potentially invasive, nitrophilous clonal species in a wetland region in Flanders. *Agron. Sustain. Dev.* 29:277–285. <https://www.x-mol.com/paperRedirect/1225023804092760067>
- Dickson TL, Foster BL (2008) The relative importance of the species pool, productivity and disturbance in regulating grassland

- flooded meadows. *Plant Ecol.* 214:845–856. <https://doi.org/10.1007/s11258-013-0213-y>
- Opdekamp W, Beauchard O, Backx H, Franken F, Cox TJS, Van Diggelen R, Meire P (2012) Effects of mowing cessation and hydrology on plant trait distribution in natural fen meadows. *Acta Oecol.* 39:117–127. <https://doi.org/10.1016/j.actao.2012.01.011>
- Pavlu L, Pavl V, Gaisler J, Hejcman M, Mikulka J (2011) Effect of long-term cutting versus abandonment on the vegetation of a mountain hay meadow (*Polygono-Trisetion*) in Central Europe. *Flora* 206:1020–1029. <https://doi.org/10.1016/j.flora.2011.07.008>
- Pecháčková S, Hadincová V, Münzbergová Z, Herben T, Krahulec F (2010) Restoration of species-rich, nutrient-limited mountain grassland by mowing and fertilization. *Restor. Ecol.* 18:166–174. <https://doi.org/10.1111/j.1526-100X.2009.00615.x>
- Peet NB, Watkinson AR, Bell DJ, Sharma UR (1999) The conservation management of *Imperata cylindrica* grassland in Nepal with fire and cutting: an experimental approach. *J. Appl. Ecol.* 36:374–387. <https://doi.org/10.1046/j.1365-2664.1999.00405.x>
- Peintinger M, Bergamini A (2006) Community structure and diversity of bryophytes and vascular plants in abandoned fen meadows. *Plant Ecol.* 185:1–17. <https://doi.org/10.1007/s11258-005-9079-y>
- Pruchniewicz D, Żolnierz L (2019) The effect of different restoration treatments on the vegetation of the mesic meadow degraded by the expansion of *Calamagrostis epigejos*. *Int J Agric Biol* 22:347–354. <https://doi.org/10.17957/IJAB/15.1070>
- Ryser P, Langenauer R, Gigon A (1995) Species richness and vegetation structure in a limestone grassland after 15 years management with six biomass removal regimes. *Folia Geobot.* 30:157–167. <https://doi.org/10.1007/BF02812095>
- Shao C, Chen J, Li L, Zhang L (2012) Ecosystem responses to mowing manipulations in an arid Inner Mongolia steppe: an energy perspective. *J. Arid Environ.* 82:1–10. <https://doi.org/10.1016/j.jaridenv.2012.02.019>
- Smith AL, Barrett RL, Milner RN (2018) Annual mowing maintains plant diversity in threatened temperate grasslands. *Appl. Veg. Sci.* 21:207–218. <https://doi.org/10.1111/avsc.12365>
- Szépligeti M, Kőrösi Á, Szentirmai I, Házi J, Bartha D, Bartha S (2018) Evaluating alternative mowing regimes for conservation management of Central European mesic hay meadows: a field experiment. *Plant Biosyst.* 152:90–97. <https://doi.org/10.1080/11263504.2016.1255268>
- Török P, Arany I, Prommer M, Valkó O, Balogh A, Vida E, Tóthmérész B, Matus G (2009) Vegetation, phytomass and seed bank of strictly protected hay-making Molinion meadows in Zemplén Mountains (Hungary) after restored management. *Thaiszia J. Bot.* 19:67–77
- Truus L, Puusild E (2009) Species richness, biomass production and recent vegetation changes or estonian floodplain. *Pol. J. Ecol.* 1:33–45
- Valkó O, Török P, Tóthmérész B, Matus G (2011) Restoration potential in seed banks of acidic fen and dry-mesophilous meadows: can restoration be based on local seed banks? *Restor. Ecol.* 19:9–15. <https://doi.org/10.1111/j.1526-100X.2010.00679.x>
- Van Dyke F, Van Kley SE, Page CE, Van Beek JG (2004) Restoration efforts for plant and bird communities in tallgrass prairies using prescribed burning and mowing. *Restor. Ecol.* 12:575–585. <https://doi.org/10.1111/j.1061-2971.2004.00352.x>
- Velbert F, Kleinebecker T, Mudrák O, Schwartz P, Hölzel N (2017) Time lags in functional response to management regimes—evidence from a 26-year field experiment in wet meadows. *J. Veg. Sci.* 28:313–324. <https://doi.org/10.1111/jvs.12497>
- Xu M, Peng F, You Q, Guo J, Tian X, Liu M, Xue X (2015) Effects of warming and clipping on plant and soil properties of an alpine meadow in the Qinghai-Tibetan Plateau, China. *J. Arid Land* 7:189–204. <https://doi.org/10.1007/s40333-014-0010-z>
- Yang H, Jiang L, Li L, Li A, Wu M, Wan S (2012) Diversity-dependent stability under mowing and nutrient addition: Evidence from a 7-year grassland experiment. *Ecol. Lett.* 15:619–626. <https://doi.org/10.1111/j.1461-0248.2012.01778.x>
- Zhang J, Huang Y, Chen H, Gong J, Qi Y, Yang F, Li E (2016) Effects of grassland management on the community structure, above-ground biomass and stability of a temperate steppe in Inner Mongolia, China. *J. Arid Land* 8:422–433. <https://doi.org/10.1007/s40333-016-0002-2>

References of the meta-analysis (effect of warming)

- Alatalo JM, Jägerbrand AK, Molau U (2016) Impacts of different climate change regimes and extreme climatic events on an alpine meadow community. *Sci. Rep.* 6:1–12. <https://doi.org/10.1038/srep21720>
- Alatalo JM, Little CJ, Jägerbrand AK, Molau U (2015) Vascular plant abundance and diversity in an alpine heath under observed and simulated global change. *Sci. Rep.* 5:1–11. <https://doi.org/10.1038/srep10197>
- Collins SL, Ladwig LM, Petrie MD, Jones SK, Mulhouse JM, Thibault JR, Pockman WT (2017) Press–pulse interactions: effects of warming, N deposition, altered winter precipitation, and fire on desert grassland community structure and dynamics. *Glob. Change Biol.* 23:1095–1108. <https://doi.org/10.1111/gcb.13493>
- Engel EC, Weltzin JF, Norby RJ, Classen AT (2009) Responses of an old-field plant community to interacting factors of elevated [CO₂], warming, and soil moisture. *J. Plant Ecol.* 2:1–11. <https://doi.org/10.1093/jpe/rtn026>
- Eskelinen A, Kaarlejärvi E, Olofsson J (2017) Herbivory and nutrient limitation protect warming tundra from lowland species' invasion and diversity loss. *Glob. Change Biol.* 23:245–255. <https://doi.org/10.1111/gcb.13397>
- Gornish ES, Miller TE (2015) Plant community responses to simultaneous changes in temperature, nitrogen availability, and invasion. *PLOS ONE* 10:e0123715. <https://doi.org/10.1371/journal.pone.0123715>
- Grant K, Kreyling J, Beierkuhnlein C, Jentsch A (2017) Importance of seasonality for the response of a mesic temperate grassland to increased precipitation variability and warming. *Ecosystems* 20:1454–1467. <https://doi.org/10.1007/s10021-017-0122-3>
- Grime JP, Fridley JD, Askew AP, Thompso K, Hodgson JG, Bennett CR (2008) Long-term resistance to simulated climate change in an infertile grassland. *Proc. Natl. Acad. Sci. U.S.A.* 105:10028–10032. <https://doi.org/10.1073/pnas.0711567105>
- Hoepfner SS, Dukes JS (2012) Interactive responses of old-field plant growth and composition to warming and precipitation. *Glob. Change Biol.* 18:1754–1768. <https://doi.org/10.1111/j.1365-2486.2011.02626.x>
- Hollister RD, Webber PJ, Tweedie CE (2005) The response of Alaskan arctic tundra to experimental warming: Differences between short- and long-term responses. *Glob. Change Biol.* 11:525–536. <https://doi.org/10.1111/j.1365-2486.2005.00926.x>
- Hollister RD, May JL, Kremers KS, Tweedie CE, Oberbauer SF, Liebig JA, Botting TF, Barrett RT, Gregory JL (2015) Warming experiments elucidate the drivers of observed directional changes in tundra vegetation. *Ecol. Evol.* 5:1881–1895. <https://doi.org/10.1002/ece3.1499>
- Hou Y, Zhou G, Xu Z, Liu T, Zhang X (2013) Interactive effects of warming and increased precipitation on community structure and composition in an annual forb dominated desert steppe. *PLOS ONE* 8:e70114. <https://doi.org/10.1371/journal.pone.0070114>
- Jingxue Z, Tianxiang L, Haixia W, Zhaoheng D, Xiang L, Ruicheng L, Yanhong T (2019) Increased precipitation offsets the negative effect of warming on plant biomass and ecosystem respiration

- in a Tibetan alpine steppe. *Agric. For. Meteorol.* 279:107761. <https://doi.org/10.1016/j.agrformet.2019.107761>
- Jónsdóttir IS, Magnússon B, Guðmundsson J, Elmarsdóttir Á, Hjartarson H (2005) Variable sensitivity of plant communities in Iceland to experimental warming. *Glob. Change Biol.* 11:553–563. <https://doi.org/10.1111/j.1365-2486.2005.00928.x>
- Klanderud K, Totland Ø (2005) Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. *Ecol.* 86:2047–2054. <https://doi.org/10.1890/04-1563>
- Klein JA, Harte J, Zhao XQ (2004) Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecol. Lett.* 7:1170–1179. <https://doi.org/10.1111/j.1461-0248.2004.00677.x>
- Ma Z, Liu H, Mi Z, Zhang Z, Wang Y, Xu W, Jiang L, He JS (2017) Climate warming reduces the temporal stability of plant community biomass production. *Nat. Commun.* 8:1–7. <https://doi.org/10.1038/ncomms15378>
- Olsen SL, Klanderud K (2014) Exclusion of herbivores slows down recovery after experimental warming and nutrient addition in an alpine plant community. *J. Ecol.* 102:1129–1137. <https://doi.org/10.1111/1365-2745.12292>
- Pfeifer-Meister L, Bridgman SD, Reynolds LL, Goklany ME, Wilson HE, Little CJ, Ferguson A, Johnson BR (2016) Climate change alters plant biogeography in Mediterranean prairies along the West Coast. *USA. Glob. Change Biol.* 22:845–855. <https://doi.org/10.1111/gcb.13052>
- Press MC, Potter JA, Burke MJW, Callaghan TV, Lee JA (1998) Responses of a subarctic dwarf shrub heath community to simulated environmental change. *J. Ecol.* 86:315–327. <https://doi.org/10.1046/j.1365-2745.1998.00261.x>
- Price MV, Waser NM (2000) Responses of subalpine meadow vegetation to four years of experimental warming. *Ecol. Appl.* 10:811–823. [https://doi.org/10.1890/1051-0761\(2000\)010\[0811:ROSMVT\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0811:ROSMVT]2.0.CO;2)
- Shi Z, Sherry R, Xu X, Hararuk O, Souza L, Jiang L, Xia J, Liang J, Luo Y (2015) Evidence for long-term shift in plant community composition under decadal experimental warming. *J. Ecol.* 103:1131–1140. <https://doi.org/10.1111/1365-2745.12449>
- Su F, Wei Y, Wang F, Guo J, Zhang J, Wang Y, Guo H, Hu S (2019) Sensitivity of plant species to warming and altered precipitation dominates the community productivity in a semiarid grassland on the Loess Plateau. *Ecol. Evol.* 9:7628–7638. <https://doi.org/10.1002/ece3.5312>
- Wagle P, Kakani VG (2014) Confounding effects of soil moisture on the relationship between ecosystem respiration and soil temperature in switchgrass. *BioEnergy Res.* 7:789–798. <https://doi.org/10.1007/s12155-014-9434-8>
- Wang C, Wang G, Wang Y, Zi H, Lerdau M, Liu W (2017) Effects of long-term experimental warming on plant community properties and soil microbial community composition in an alpine meadow. *Isr. J. Ecol. Evol.* 63:85–96. <https://doi.org/10.1080/15659801.2017.1281201>
- Wang S, Duan J, Xu G, Wang Y, Zhang Z, Rui Y, Luo C, Xu B, Zhu X, Chang X, Cui X (2012) Effects of warming and grazing on soil N availability, species composition, and ANPP in an alpine meadow. *Ecol.* 93:2365–2376. <https://doi.org/10.1890/11-1408.1>
- Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA (2011) Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biol.* 17:927–942. <https://doi.org/10.1111/j.1365-2486.2010.02302.x>
- Xu M, Peng F, You Q, Guo J, Tian X, Liu M, Xue X (2015) Effects of warming and clipping on plant and soil properties of an alpine meadow in the Qinghai-Tibetan Plateau, China. *J. Arid Land* 7:189–204. <https://doi.org/10.1007/s40333-014-0010-z>
- Yan X, Ni Z, Chang L, Wang K, Wu D (2015) Soil warming elevates the abundance of *Collembola* in the Songnen plain of China. *Sustainability* 7:1161–1171. <https://doi.org/10.3390/su7021161>
- Yang Z, Jiang L, Su F, Zhang Q, Xia J, Wan S (2016) Nighttime warming enhances drought resistance of plant communities in a temperate steppe. *Sci. Rep.* 6:1–9. <https://doi.org/10.1038/srep23267>
- Yang H, Wu M, Liu W, Zhang ZHE, Zhang N, Wan S (2011) Community structure and composition in response to climate change in a temperate steppe. *Glob. Change Biol.* 17:452–465. <https://doi.org/10.1111/j.1365-2486.2010.02253.x>
- Zhang Y, Gao Q, Dong S, Liu S, Wang X, Su X, Li Y, Tang L, Wu X, Zhao H (2015) Effects of grazing and climate warming on plant diversity, productivity and living state in the alpine rangelands and cultivated grasslands of the Qinghai-Tibetan Plateau. *Rangel. J.* 37:57–65. <https://doi.org/10.1071/RJ14080>
- Zhang X, Johnston ER, Li L, Konstantinidis KT, Han X (2017) Experimental warming reveals positive feedbacks to climate change in the Eurasian Steppe. *ISME J.* 11:885–895. <https://doi.org/10.1038/ismej.2016.180>
- Zhang C, Willis CG, Klein JA, Ma Z, Li J, Zhou H, Zhao X (2017) Recovery of plant species diversity during long-term experimental warming of a species-rich alpine meadow community on the Qinghai-Tibet plateau. *Biol. Conserv.* 213:218–224. <https://doi.org/10.1016/j.biocon.2017.07.019>
- Zhu H, Zou X, Wang D, Wan S, Wang L, Guo J (2015) Responses of community-level plant-insect interactions to climate warming in a meadow steppe. *Sci. Rep.* 5:1–11. <https://doi.org/10.1038/srep18654>

References of the review on the effect of different mowing regimes

Two versus zero cuts per year

- Antonsen H, Olsson PA (2005) Relative importance of burning, mowing and species translocation in the restoration of a former boreal hayfield: responses of plant diversity and the microbial community. *J. Appl. Ecol.* 42:337–347. <https://doi.org/10.1111/j.1365-2664.2005.01023.x>
- Bakker JP, Elzinga JA, De Vries Y (2002) Effects of long-term cutting in a grassland system: perspectives for restoration of plant communities on nutrient-poor soils. *Appl. Veg. Sci.* 5:107–120. <https://doi.org/10.1111/j.1654-109X.2002.tb00540.x>
- Beltman B, van den Broek T, Martin W, ten Cate M, Güsewell S (2003) Impact of mowing regime on species richness and biomass of a limestone hay meadow in Ireland. *Bull. Geobot. Inst. ETH* 69:17–30
- Bobbink R, Willems JH (1993) Restoration management of abandoned chalk grassland in the Netherlands. *Biodivers. Conserv.* 2:616–626. <https://doi.org/10.1007/BF00051962>
- Gaisler J, Pavlů L, Nwaogu C, Pavlů K, Hejcman M, Pavlů VV (2019) Long-term effects of mulching, traditional cutting and no management on plant species composition of improved upland grassland in the Czech Republic. *Grass Forage Sci.* 74:463–475. <https://doi.org/10.1111/gfs.12408>
- Gaisler J, Pavlů V, Pavlů L, Hejcman M (2013) Long-term effects of different mulching and cutting regimes on plant species composition of *Festuca rubra* grassland. *Agric. Ecosyst. Environ.* 178:10–17. <https://doi.org/10.1016/j.agee.2013.06.010>
- Han W, Luo Y, Du G (2007) Effects of clipping on diversity and above-ground biomass associated with soil fertility on an alpine meadow in the eastern region of the Qinghai-Tibetan Plateau. *New Zealand*

- J. Agric. Res. 50:361–368. <https://doi.org/10.1080/00288230709510304>
- Házi J, Bartha S, Szentes S, Wichmann B, Penksza K (2011) Seminatural grassland management by mowing of *Calamagrostis epigejos* in Hungary. *Plant Biosyst.* 145:699–707. <https://doi.org/10.1080/11263504.2011.601339>
- Ilmarinen K, Mikola J (2009) Soil feedback does not explain mowing effects on vegetation structure in a semi-natural grassland. *Acta Oecol.* 35:838–848. <https://doi.org/10.1016/j.actao.2009.08.008>
- Klimeš L, Hájek M, Mudrák O, Dančák M, Preislerová Z, Hájková P, Jongepierová I, Klimešová J (2013) Effects of changes in management on resistance and resilience in three grassland communities. *Appl. Veg. Sci.* 16:640–649. <https://doi.org/10.1111/avsc.12032>
- Oomes MJM, Mooi H (1981) The effect of cutting and fertilizing on the floristic composition and production of an *Arrhenatherion elatioris* grassland. In: *Vegetation dynamics in grasslands, healthlands and mediterranean ligneous formations*. Springer, Dordrecht, pp 233–239
- Pavlu L, Gaisler J, Hejcman M, Pavlu VV (2016) What is the effect of long-term mulching and traditional cutting regimes on soil and biomass chemical properties, species richness and herbage production in *Dactylis glomerata* grassland? *Agric. Ecosyst. Environ.* 217:13–21. <https://doi.org/10.1016/j.agee.2015.10.026>
- Pruchniewicz D, Żolnierz L (2019) The effect of different restoration treatments on the vegetation of the mesic meadow degraded by the expansion of *Calamagrostis epigejos*. *Int. J. Agric. Biol.* 22:347–354. <https://doi.org/10.17957/IJAB/15.1070>
- Smith H, Feber RE, Morecroft MD, Taylor ME, Macdonald DW (2010) Short-term successional change does not predict long-term conservation value of managed arable field margins. *Biol. Conserv.* 143:813–822. <https://doi.org/10.1016/j.biocon.2009.12.025>
- Squires VR, Dengler J, Hua L, Feng H (2018) Grasslands of the world: diversity, management and conservation. CRC Press, Boca Raton
- Stybnarova M, Hakl J, Bilosova H, Micova P, Latal O, Pozdisek J (2016) Effect of cutting frequency on species richness and dry matter yield of permanent grassland after grazing cessation. *Arch. Agron. Soil Sci.* 62:1182–1193. <https://doi.org/10.1080/03650340.2015.1132839>
- Szépligetű M, Körösi Á, Szentirmai I, Házi J, Bartha D, Bartha S (2018) Evaluating alternative mowing regimes for conservation management of Central European mesic hay meadows: a field experiment. *Plant Biosyst.* 152:90–97. <https://doi.org/10.1080/11263504.2016.1255268>
- van Tooren BF, Odé B, During HJ, Bobbink R (1990) Regeneration of species richness in the bryophyte layer of Dutch chalk grasslands. *Lindbergia* 16:153–160
- Velbert F, Kleinebecker T, Mudrák O, Schwartz P, Hölzel N (2017) Time lags in functional response to management regimes—evidence from a 26-year field experiment in wet meadows. *J. Veg. Sci.* 28:313–324. <https://doi.org/10.1111/jvs.12497>
- Wan Z, Yang J, Gu R, Liang Y, Yan Y, Gao Q, Yang J (2016) Influence of different mowing systems on community characteristics and the compensatory growth of important species of the *Stipa grandis* steppe in Inner Mongolia. *Sustainability* 8:1121. <https://doi.org/10.3390/su8111121>
- biomass of a limestone hay meadow in Ireland. *Bull. Geobot. Inst. ETH* 69:17–30
- Bobbink R, Willems JH (1991) Impact of different cutting regimes on the performance of *Brachypodium pinnatum* in Dutch chalk grassland. *Biol. Conserv.* 56:1–21. [https://doi.org/10.1016/0006-3207\(91\)90085-N](https://doi.org/10.1016/0006-3207(91)90085-N)
- Bobbink R, Willems JH (1993) Restoration management of abandoned chalk grassland in the Netherlands. *Biodivers. Conserv.* 2:616–626. <https://doi.org/10.1007/BF00051962>
- Fynn RW, Morris CD, Edwards TJ (2004) Effect of burning and mowing on grass and forb diversity in a long-term grassland experiment. *Appl. Veg. Sci.* 7:1–10. <https://doi.org/10.1111/j.1654-109X.2004.tb00589.x>
- Han W, Luo Y, Du G (2007) Effects of clipping on diversity and above-ground biomass associated with soil fertility on an alpine meadow in the eastern region of the Qinghai-Tibetan Plateau. *New Zealand J. Agric. Res.* 50:361–368. <https://doi.org/10.1080/00288230709510304>
- Ilmarinen K, Mikola J (2009) Soil feedback does not explain mowing effects on vegetation structure in a semi-natural grassland. *Acta Oecol.* 35:838–848. <https://doi.org/10.1016/j.actao.2009.08.008>
- Klimeš L, Hájek M, Mudrák O, Dančák M, Preislerová Z, Hájková P, Jongepierová I, Klimešová J (2013) Effects of changes in management on resistance and resilience in three grassland communities. *Appl. Veg. Sci.* 16:640–649. <https://doi.org/10.1111/avsc.12032>
- Marini L, Fontana P, Scotton M, Klimek S (2008) Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. *J. Appl. Ecol.* 45:361–370. <https://doi.org/10.1111/j.1365-2664.2007.01402.x>
- Oloff H, Bakker JP (1991) Long-term dynamics of standing crop and species composition after the cessation of fertilizer application to mown grassland. *J. Appl. Ecol.* 1040–1052. <https://doi.org/10.2307/2404224>
- Oomes MJM, Mooi H (1981) The effect of cutting and fertilizing on the floristic composition and production of an *Arrhenatherion elatioris* grassland. In: *Vegetation dynamics in grasslands, healthlands and mediterranean ligneous formations*. Springer, Dordrecht, pp 233–239
- Pavlu L, Gaisler J, Hejcman M, Pavlu VV (2016) What is the effect of long-term mulching and traditional cutting regimes on soil and biomass chemical properties, species richness and herbage production in *Dactylis glomerata* grassland? *Agric. Ecosyst. Environ.* 217:13–21. <https://doi.org/10.1016/j.agee.2015.10.026>
- Pruchniewicz D, Żolnierz L (2019) The effect of different restoration treatments on the vegetation of the mesic meadow degraded by the expansion of *Calamagrostis epigejos*. *Int. J. Agric. Biol.* 22:347–354. <https://doi.org/10.17957/IJAB/15.1070>
- Smith H, Feber RE, Morecroft MD, Taylor ME, Macdonald DW (2010) Short-term successional change does not predict long-term conservation value of managed arable field margins. *Biol. Conserv.* 143:813–822. <https://doi.org/10.1016/j.biocon.2009.12.025>
- Socher SA, Prati D, Boch S, Müller J, Klaus VH, Hölzel N, Fischer M (2012) Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. *J. Ecol.* 100:1391–1399. <https://doi.org/10.1111/j.1365-2745.2012.02020.x>
- Socher SA, Prati D, Boch S, Müller J, Baumbach H, Gockel S, Hemp A, Schöning I, Wells K, Buscot F, Kalko EKV, Linsenmair KE, Schulze ED, Weisser WW, Fischer M (2013) Interacting effects of fertilization, mowing and grazing on plant species diversity of 1500 grasslands in Germany differ between regions. *Basic Appl. Ecol.* 14:126–136. <https://doi.org/10.1016/j.baae.2012.12.003>
- Squires VR, Dengler J, Hua L, Feng H (2018) Grasslands of the world: diversity, management and conservation. CRC Press, Boca Raton FL

Two versus one cuts per year

- Bakker JP, Elzinga JA, De Vries Y (2002) Effects of long-term cutting in a grassland system: perspectives for restoration of plant communities on nutrient-poor soils. *Appl. Veg. Sci.* 5:107–120. <https://doi.org/10.1111/j.1654-109X.2002.tb00540.x>
- Beltman B, van den Broek T, Martin W, ten Cate M, Güsewell S (2003) Impact of mowing regime on species richness and

- Stybnarova M, Hakl J, Bilosova H, Micova P, Latal O, Pozdisek J (2016) Effect of cutting frequency on species richness and dry matter yield of permanent grassland after grazing cessation. *Arch. Agron. Soil Sci.* 62:1182–1193. <https://doi.org/10.1080/03650340.2015.1132839>
- Szépligeti M, Kőrösi Á, Szentirmai I, Házi J, Bartha D, Bartha S (2018) Evaluating alternative mowing regimes for conservation management of Central European mesic hay meadows: a field experiment. *Plant Biosyst.* 152:90–97. <https://doi.org/10.1080/11263504.2016.1255268>
- van Tooren BF, Odé B, During HJ, Bobbink R (1990) Regeneration of species richness in the bryophyte layer of Dutch chalk grasslands. *Lindbergia* 16:153–160
- Velbert F, Kleinebecker T, Mudrák O, Schwartz P, Hölzel N (2017) Time lags in functional response to management regimes—evidence from a 26-year field experiment in wet meadows. *J. Veg. Sci.* 28:313–324. <https://doi.org/10.1111/jvs.12497>
- Wan Z, Yang J, Gu R, Liang Y, Yan Y, Gao Q, Yang J (2016) Influence of different mowing systems on community characteristics and the compensatory growth of important species of the *Stipa grandis* steppe in Inner Mongolia. *Sustainability* 8:1121. <https://doi.org/10.3390/su811121>
- Zechmeister HG, Schmitzberger I, Steurer B, Peterseil J, Wrba T (2003) The influence of land-use practices and economics on plant species richness in meadows. *Biol. Conserv.* 114:165–177. [https://doi.org/10.1016/S0006-3207\(03\)00020-X](https://doi.org/10.1016/S0006-3207(03)00020-X)

Three versus one cuts per year

- Fynn RW, Morris CD, Edwards TJ (2004) Effect of burning and mowing on grass and forb diversity in a long-term grassland experiment. *Appl. Veg. Sci.* 7:1–10. <https://doi.org/10.1111/j.1654-109X.2004.tb00589.x>
- Klimek S, Hofmann M, Isselstein J (2007) Plant species richness and composition in managed grasslands: the relative importance of field management and environmental factors. *Biol. Conserv.* 134:559–570. <https://doi.org/10.1016/j.biocon.2006.09.007>
- Pavlu L, Gaisler J, Hejman M, Pavlu VV (2016) What is the effect of long-term mulching and traditional cutting regimes on soil and biomass chemical properties, species richness and herbage production in *Dactylis glomerata* grassland? *Agric. Ecosyst. Environ.* 217:13–21. <https://doi.org/10.1016/j.agee.2015.10.026>
- Rose L, Coners H, Leuschner C (2012) Effects of fertilization and cutting frequency on the water balance of a temperate grassland. *Ecophysiol. Hydrobiol.* 5:64–72. <https://doi.org/10.1002/eco.201>
- Socher SA, Prati D, Boch S, Müller J, Klaus VH, Hölzel N, Fischer M (2012) Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. *J. Ecol.* 100:1391–1399. <https://doi.org/10.1111/j.1365-2745.2012.02020.x>
- Socher SA, Prati D, Boch S, Müller J, Baumbach H, Gockel S, Hemp A, Schöning I, Wells K, Buscot F, Kalko EKV, Linsenmair KE, Schulze ED, Weisser WW, Fischer M (2013) Interacting effects of fertilization, mowing and grazing on plant species diversity of 1500 grasslands in Germany differ between regions. *Basic Appl. Ecol.* 14:126–136. <https://doi.org/10.1016/j.baae.2012.12.003>
- Stybnarova M, Hakl J, Bilosova H, Micova P, Latal O, Pozdisek J (2016) Effect of cutting frequency on species richness and dry matter yield of permanent grassland after grazing cessation. *Arch. Agron. Soil Sci.* 62:1182–1193. <https://doi.org/10.1080/03650340.2015.1132839>
- Zechmeister HG, Schmitzberger I, Steurer B, Peterseil J, Wrba T (2003) The influence of land-use practices and economics on plant species richness in meadows. *Biol. Conserv.* 114:165–177. [https://doi.org/10.1016/S0006-3207\(03\)00020-X](https://doi.org/10.1016/S0006-3207(03)00020-X)

Four versus one cuts per year

- Bobbink R, Willems JH (1993) Restoration management of abandoned chalk grassland in the Netherlands. *Biodivers. Conserv.* 2:616–626. <https://doi.org/10.1007/BF00051962>
- Socher SA, Prati D, Boch S, Müller J, Klaus VH, Hölzel N, Fischer M (2012) Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. *J. Ecol.* 100:1391–1399. <https://doi.org/10.1111/j.1365-2745.2012.02020.x>
- Squires VR, Dengler J, Hua L, Feng H (2018) Grasslands of the world: diversity, management and conservation. CRC Press, Boca Raton
- van Tooren BF, Odé B, During HJ, Bobbink R (1990) Regeneration of species richness in the bryophyte layer of Dutch chalk grasslands. *Lindbergia* 16:153–160

Four versus two cuts per year

- Bobbink R, Willems JH (1993) Restoration management of abandoned chalk grassland in the Netherlands. *Biodivers. Conserv.* 2:616–626. <https://doi.org/10.1007/BF00051962>
- Hejman M, Schellberg J, Pavlu V (2010) Long-term effects of cutting frequency and liming on soil chemical properties, biomass production and plant species composition of *Lolium-Cynosuretum* grassland after the cessation of fertilizer application. *Appl. Veg. Sci.* 13:257–269. <https://doi.org/10.1111/j.1654-109X.2010.01077.x>
- Knop EVA, Kleijn D, Herzog F, Schmid B (2006) Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. *J. Appl. Ecol.* 43:120–127. <https://doi.org/10.1111/j.1365-2664.2005.01113.x>
- Kramberger B, Podvršnik M, Gselman A, Šuštar V, Kristl J, Muršec M, Lešnik M, Škorjanc D (2015) The effects of cutting frequencies at equal fertiliser rates on bio-diverse permanent grassland: Soil organic C and apparent N budget. *Agric. Ecosyst. Environ.* 212:13–20. <https://doi.org/10.1016/j.agee.2015.06.001>
- Pavlu V, Schellberg J, Hejman M (2011) Cutting frequency vs. N application: effect of a 20-year management in *Lolium-Cynosuretum* grassland. *Grass Forage Sci.* 66:501–515. <https://doi.org/10.1111/j.1365-2494.2011.00807.x>
- Sasaki T, Yoshihara Y, Suyama Y, Nakashizuka T (2011) Clipping stimulates productivity but not diversity in improved and semi-natural pastures in temperate Japan. *Agric. Ecosyst. Environ.* 142:428–431. <https://doi.org/10.1016/j.agee.2011.06.009>
- Sinkovč T (2009) Plant diversity and species richness of Ljubljana marsh grasslands under the influence of different cutting and fertilizing regimes. *Acta Agron. Hung.* 57:197–203. <https://doi.org/10.1556/AAgr.57.2009.2.11>
- Socher SA, Prati D, Boch S, Müller J, Klaus VH, Hölzel N, Fischer M (2012) Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. *J. Ecol.* 100:1391–1399. <https://doi.org/10.1111/j.1365-2745.2012.02020.x>
- Squires VR, Dengler J, Hua L, Feng H (2018) Grasslands of the world: diversity, management and conservation. CRC Press, Boca Raton
- Stybnarova M, Hakl J, Bilosova H, Micova P, Latal O, Pozdisek J (2016) Effect of cutting frequency on species richness and dry matter yield of permanent grassland after grazing cessation. *Arch. Agron. Soil Sci.* 62:1182–1193. <https://doi.org/10.1080/03650340.2015.1132839>
- van Tooren BF, Odé B, During HJ, Bobbink R (1990) Regeneration of species richness in the bryophyte layer of Dutch chalk grasslands. *Lindbergia* 16:153–160

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