Abandoning grassland management negatively influences plant but not bird or insect biodiversity in Europe

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Abstract
Grasslands are globally distributed and naturally occurring; however, in Europe, most grasslands are anthropogenically created or altered by livestock grazing or mowing. Low-intensity use and management have led to species-rich communities in European grasslands. The intensification of crop production and livestock farming with stabling throughout the year has led to an abandonment of grasslands that are no longer economically profitable. In this study, we looked at the influence of grassland abandonment on biodiversity. We hypothesized that abandonment of grasslands decreases the overall biodiversity, but has different effects depending on the focal taxonomic group (i.e., vascular plants, insects, or birds). We also hypothesized that the type of management before abandonment, the type of grassland, and the time after abandonment would influence grassland biodiversity. We conducted a Web of Science search, with pre-defined terms, to find articles that compared biodiversity of managed and abandoned grasslands in Europe.

Tessa Elliott and Amibeth Thompson shared first authorship.

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We screened the articles and included 39 studies in a subsequent meta-analysis. We found that overall biodiversity was reduced after abandonment; however, the biodiversity reduction in the grasslands differed among taxonomic groups. Plant species diversity was significantly lower after abandonment (plant summary effect size: $-0.25 \pm -0.34; -0.16$), whereas the diversity of insects and birds showed no significant trend, but a visual trend toward an increase. None of the other environmental variables (type of management, type of grassland, or the time after abandonment) had a significant influence on the biodiversity of the grasslands. We conclude that maintaining grassland management is crucial to support biodiversity conservation in European grasslands.

**KEYWORDS**

bird, insect, meadow, meta-analysis, pasture, plant, species-richness

## 1 | INTRODUCTION

Grasslands are globally distributed and occur naturally if precipitation and temperature are within a given range (Dixon et al., 2014; Wilson et al., 2012; Woodward et al., 2004). In Europe, most grasslands have been anthropogenically used over centuries for agricultural production (Bardgett et al., 2021; Dengler et al., 2014; Feurdean et al., 2018; Pärtel et al., 2005; Pereira & Navarro, 2015; Vrahnakis et al., 2013). Grasslands are predominantly used for fodder production or direct livestock grazing (Hejcman et al., 2013; Valkó et al., 2018; Wiezik et al., 2011). Low-intensity managed grasslands in Europe are not only important for the production of fodder, but can also contribute to biodiversity conservation (Dengler et al., 2014; Janišová et al., 2020). Along with anthropogenic grassland management, plant communities and diversity of higher trophic levels, such as herbivorous insects, have evolved to diverse systems (Cerabolini et al., 2016). Grasslands are habitats for many endemic or endangered plant species across different regions in Europe (Stoate et al., 2009). Supporting their conservation, numerous grassland types have been listed in the Annex I of the Habitats Directive (92/43/EEC), the main policy instrument for site protection at the EU level, such as mountain hay meadows and swards of Mat-grass (*Nardus stricta* L.; Evans & Roekarts, 2019; Henle et al., 2008).

Biodiversity in European grasslands is threatened most particularly by rapid and severe changes in agricultural production since the beginning of industrialization around 1830 (Habel et al., 2013; Mupepele et al., 2021; Queiroz et al., 2014). The invention of artificial fertilizer production has led to an intensification in grassland productivity, which favored herbaceous plant species, such as grasses. The additional nutrients from fertilizers reduce plant biodiversity and shift competition to other limited resources such as light (Grace et al., 2016; Harpole et al., 2016). Livestock farming was equally industrialized and globalized with fodder production far beyond the local scale. The overall grassland area was reduced and fragmented by conversion to cropland or urban areas (Aune et al., 2018; Bengtsson et al., 2019; Pärtel et al., 2005; Schoof et al., 2019; Walcher et al., 2019).

Apart from the intensification and a general loss of grassland area, there is further a widespread trend of grassland abandonment in Europe, which has received less scientific attention (Henle et al., 2008; Nikolov, 2010). Abandonment occurs particularly on lands for which management no longer appears economically profitable, for instance due to difficult accessibility, trafficability, or rural population decline (Joyce, 2014; Valkó et al., 2018; Walcher et al., 2019). A consequence of management abandonment is a succession toward denser and taller vegetation (Tanneberger et al., 2008, 2010), and ultimately shrubby and forest vegetation (Bonanomi et al., 2013; Gibson, 2009; Shugart, 2013). Such an encroachment can in turn reduce grassland-associated species communities and their biodiversity (Azcárate & Peco, 2012; Facioni et al., 2019; Pärtel et al., 2005; Pereira & Navarro, 2015). In other cases, management abandonment led to habitat regeneration and increased biodiversity (Azcárate & Peco, 2012; Kuhn et al., 2021; Laiolo et al., 2004; Skórka et al., 2007). Thus, succession can be progressive, leading to increased biodiversity, structural complexity, and stability, or retrogressive, changing an ecosystem in the opposite direction and reducing biodiversity (Shugart, 2013). Abandonment has been known to both decrease (Azcárate & Peco, 2012; Pärtel et al., 2005) and increase biodiversity (Azcárate & Peco, 2012), but a comprehensive quantitative synthesis of these findings and their difference between management, time since abandonment, or habitat characteristics is still missing.
Based on the previous findings that management, such as mowing and subsequent biomass removal in low intensities, is a key aspect for maintaining biodiversity in grasslands (Cerabolini et al., 2016; Dengler et al., 2014; Valkó et al., 2018), we hypothesized that overall, abandonment of grasslands decreases the biodiversity and has differential effects depending on the taxonomic group studied. We also expected that the type of management, the type of grassland, and the years after abandonment would influence the biodiversity of grasslands. To identify an overall change in biodiversity potentially influenced by environmental variables, we synthesized the existing information of biodiversity on abandoned grasslands in Europe in the form of a meta-analysis to address the following research questions:

1. Does the abandonment of grassland in Europe have an impact on overall biodiversity?
2. Does the effect of abandonment on biodiversity differ among taxonomic groups?
3. What other factors, such as the type of previous management, for example, mowing or grazing, the type of grassland ranging from dry to moist, or the time after abandonment, influence biodiversity changes in abandoned European grasslands?

### 2 | METHODS

#### 2.1 | Literature search

Studies published between 1995 and 2021 comparing biodiversity on managed and abandoned grasslands in Europe were searched in Clarivate Web Of Science (WOS, https://www.webofscience.com) in July 2021. We used search terms related to “biodiversity,” “grassland,” “abandonment,” and “Europe” (full search string in Appendix S1), which resulted in 1079 potentially relevant studies. Studies revealed by the WOS search had to fulfill additional inclusion criteria, namely the study (i) was conducted in Europe, (ii) looked at the biodiversity of a grassland (grassland definition based on Dengler et al., 2014), and (iii) compared abandoned with managed (control) grassland sites (full list of criteria in Table 1). The 1079 potentially relevant articles resulting from the WOS search were screened to identify whether they fulfilled all inclusion criteria. According to general systematic review standards, we first screened title and abstract and discarded studies not fulfilling the inclusion criteria (e.g., if the abstract revealed that the study was conducted outside of Europe). In a second screening, the full-text was read and studies not fulfilling the inclusion criteria were again discarded. After the screenings, 39 studies were again discarded. After the screenings, 39 studies were included in this review.

<table>
<thead>
<tr>
<th>Criteria</th>
<th>Eligibility</th>
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<tbody>
<tr>
<td>Study location</td>
<td>Study sites located within Europe</td>
<td>Study sites located outside of Iceland to the Ural Mountains and from Norway to the Mediterranean Sea and the Black Sea</td>
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<tr>
<td>Study was conducted in a grassland which means densely-covered herbaceous vegetation dominated by grasses (Dengler et al., 2014)</td>
<td>Study was conducted in a different type of habitat or in a grassland not as defined</td>
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<td>Language</td>
<td>In English or German</td>
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<td>Accessibility</td>
<td>Article accessible through the subscriptions held by the University of Freiburg or personal communication with the authors</td>
<td>Articles inaccessible through the subscription or by personal communication</td>
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<td>Study design</td>
<td>Study recorded data on a grassland on which management had been abandoned as well as on a control site with management in the form of biomass removal</td>
<td>Sites on which management had recently changed, for example, by adding irrigation or fertilizer, or which were restored after a period of abandonment</td>
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<td>The management on the abandoned grassland and control grassland are clearly described and replicable</td>
<td>The differentiation of abandoned and managed grassland based solely on visual characteristics such as “degree of shrub encroachment”</td>
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<td>Study measured average species richness or other quantifiable biodiversity measures, such as Shannon diversity, and data are extractable</td>
<td>Study did not measure biodiversity or the measure was not extractable</td>
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(Continues)
were left that met all inclusion criteria (see Table 1, Appendix S2). Environmental variables (type of management, type of grassland, or the time after abandonment) and the biodiversity metrics (species richness [preferential], Shannon-Diversity-Index, species density) with sample size and standard deviation, were extracted, each for an abandoned grassland (treatment) and a managed grassland (control). Unique control–treatment combinations of control types, taxonomic groups, and study site locations were extracted, which meant that some studies provided several combinations. We extracted a total of 90 control–treatment combinations, that is, 90 effect sizes, out of the 39 studies, and, if possible, their concordant environmental variables (see Appendix S3 and S4). WebPlotDigitizer was used to extract data points from figures (Rohatgi, 2021). If standard deviation was not given, but other variance measures, such as standard error, they were converted to standard deviation (Higgins et al., 2021). If no information about variance or sample size was given and the study was published within the last 10 years, we contacted the authors via e-mail and asked for further information that would allow us to compute the standard deviation. Some studies used a nested design with several data points on a larger plot so that information about the diversity on a small scale plot level, for example, 1 m², and a larger scale site level, for example, 1 km² were available. Only a few studies (9 from 39) provided information on the size of the area, so that the influence of the spatial scale could not be included in the analysis. If diversity was given on several scales, only the largest scale was included in the analysis. For studies that provided data over several years after the abandonment, only the last data point in a time series was used to guarantee an equal weighting for all study sites across the meta-analysis.

### 2.3 | Statistical analysis

The log response ratio was chosen as an effect size to compare the biodiversity of abandoned grasslands (“treatment”) with grasslands managed, for example, by mowing or grazing (“control”) in a meta-analysis (Gurevitch et al., 2018; Koricheva et al., 2013). A log response ratio below zero reflects a decrease in biodiversity after management abandonment. The log response ratio was chosen as we were interested in the proportional change of biodiversity, reflected in ratios (Hillebrand & Gurevitch, 2016). Log response ratios can further be used if measurement units differ between studies, such as in our case, in which we had effect sizes derived from species richness or Shannon diversity. The summary effect size was estimated based on a three-level random-effects model (Konstantopoulos, 2011; Nakagawa & Santos, 2012). This model was chosen to incorporate the hierarchies and dependencies in the dataset resulting from the fact that some effect sizes originated from the same study. A three-level random-effect model assumes three sources of variance with sampling error as well as two sources of heterogeneity (Konstantopoulos, 2011; Nakagawa & Santos, 2012). To identify whether there was a high amount of variance attributed to between-study variability (heterogeneity) or within-study variability two approaches were used: (i) a Q-test, which can be seen as an
ANOVA counterpart in meta-analysis and reflects the distance of effect sizes from primary studies to the mean effects size, and (ii) the index $I^2$, specifying the proportion of the between-study variability in relation to the total variance, was used (Assink & Wibbelink, 2016). To consider variables possibly explaining the between-study variability, we used mixed-effects models and a subsequent omnibus test to identify a potential moderating effect of the environmental variables “taxonomic group,” “management on the control grassland,” “grassland type,” and “time since abandonment” (Table 2). The moderating effect of the four environmental variables was assessed in four different models, as not all studies accounted for all environmental variables simultaneously, and a different subset of studies was included in each mixed-effects model analysis. To account for multiple testing, a Bonferroni correction was employed, leading to a modified significance level ($P = \alpha/4 = 0.0125$; Nakagawa, 2004). If the omnibus test revealed an influence of one of the categorical environmental variables (i.e., “taxonomic group,” “management on the control grassland,” or “grassland type”), a subsequent sub-group analysis was realized, which can be seen as the counterpart to a post-hoc test providing the information for which of the categories biodiversity significantly increased or decreased after abandonment (Rossetti et al., 2017).

We assessed the robustness and generalizability of the statistical results, in relation to a potential publication bias (Gurevitch & Nakagawa, 2015). A publication bias can occur if the effect sizes in a meta-analysis are biased, for example, toward significant results or toward supporting only a certain narrative. The publication bias is also referred to as a “file-drawer-problem” alluding to non-significant results that are hidden in the drawer of researchers instead of being published. They are thus not found in a literature search and missing in a meta-analysis, which is biasing the results (Koricheva et al., 2013). We investigated the presence of publication bias visually based on a funnel plot (Sterne & Harbord, 2004; Sterne et al., 2011) and by means of Egger’s regression asymmetry test (Egger et al., 1997; Koricheva et al., 2013; adapted from Mupepele et al., 2021). Analyses were conducted in R 4.0.5 using the package “metafor” (Viechtbauer, 2010, see Appendix S9).

### RESULTS

Biodiversity was reduced in abandoned compared to managed grasslands (summary effect size: $-0.14 [-0.24; -0.04]$, Figure 1, Appendix S8). Only a small proportion of variance was linked to sampling variance ($I^2$ [level 1] = 1.09%). A high variability exists among studies demonstrating the importance of investigating environmental variables potentially explaining parts of this variance (between-study variance: Log-likelihood ratio test [LRT] = 18.79; $P < 0.0001$; $I^2$ [level 3] = 57.54%; within-study variance: $\text{LRT} = 1858.4$; $P < 0.0001$; $I^2$ [level 2] = 41.37%). Neither grassland management, such as mowing or grazing, nor the grassland type, such as dry or wet grassland, nor time that the grassland had been abandoned had an impact on the change in biodiversity after abandonment (Table 3, Appendix S7). There was, however, a significant difference between the taxonomic groups (Table 3, Model 1). Plant diversity decreased after abandonment (Figure 1, green diamond, Plant summary effect size: $-0.25 [-0.34; -0.16]$). Insects and birds did not show statistical evidence for a change in biodiversity, but a visual trend toward an increasing biodiversity.

#### 3.1 Publication bias

According to the funnel plot and Egger’s regression test, no publication bias was detected in our data (Appendix S6; intercept of Egger’s regression $= -0.82$; $t = -0.65$; $P = 0.52$).
4 DISCUSSION

Our meta-analysis synthesized findings across 39 studies with 90 effect sizes comparing managed and abandoned grasslands and demonstrated that biodiversity decreases after abandoning grassland management in Europe, which was driven by a loss in plant diversity. Insect and bird diversity showed a positive trend, which could indicate a trophic cascading effect, but additional studies would be needed to support this currently non-significant trend. Contrary to our hypotheses, we found no evidence for an influence of the type of management, such as mowing or grazing, the type of grassland, and the time since abandonment on the change in biodiversity.

4.1 Plant diversity in abandoned grasslands

Abandoning grassland management leads to succession in plant communities and can thus reduce plant species diversity (Shugart, 2013; Walcher et al., 2019). Due to the missing disturbances, such as animal trampling and biomass removal by mowing or grazing, plant litter accumulates. Plant litter can be beneficial for plants by conserving water in dry periods, but the overall effects on vegetation communities are negative (Pärtel et al., 2005; Valkó et al., 2012; Xiong & Nilsson, 1999). Litter may alter the physical and chemical environmental factors of the upper soil layer, which can reduce germination rates of certain species (Valkó et al., 2012). Additionally, the higher availability of nutrients contained in the litter causes eutrophication and increased productivity and canopy height. This is shifting resource competition of plants toward the availability of light (Hautier et al., 2009; Joyce, 2014) and thus, few fast-growing species might outcompete less dominant species, which are progressively replaced (Dierschke & Briemle, 2002; Hautier et al., 2009; Joyce, 2014; Otsus et al., 2014). With ongoing succession, the average vegetation height increases, and shrub encroachment as well as woody vegetation can inhibit the growth of short herbaceous species due to a lack of disturbance and light (Pápay et al., 2020; Pöyry et al., 2006). Our results found that abandonment...
decreases plant biodiversity and that management, such as mowing and subsequent biomass removal as a regular disturbance, is important for a positive response of plant diversity (Dengler et al., 2014; Pöyry et al., 2006; Tanneberger et al., 2022; Xiong & Nilsson, 1999). The general decrease of plant species after grassland abandonment does not exclude the existence of plant species specialized and dependent on abandonment or the process of succession and we are recognizing that the biology of certain species (i.e., grasses vs. herbs species) can strongly affect the reaction to a specific management (i.e., grazing vs. mowing, Steffan-Dewenter & Leschke, 2003). While the majority of case studies in our meta-analysis were focused on plants, the knowledge on grassland fauna is more limited (Dengler et al., 2014; Joyce, 2014; Walcher et al., 2019).

### 4.2 Insect diversity in abandoned grasslands

We found no significant effect of management abandonment on insects. The studies vary in the focal groups, such as ants, beetles, or butterflies, and thus they also vary in their traits, including their mobility, body size, and feeding and nesting needs. These differences can lead to different responses to management and its abandonment. For example, herbivorous insects directly depend on plants; however, they may react with a delay to changes in the lower trophic level, such as plant diversity. Three of the seven included studies looked at functional groups or traits of the insects, with only one study specifically looking at herbivorous insects (Fadda et al., 2008). The sample size was too low to further split insects into lower taxonomic or functional groups during the analysis. Likewise, the effects could differ between management types, with grazing having a different effect in comparison to mowing (Bonari et al., 2017) or between habitat types, with wet meadows having a different effect from dry meadows (Skórka et al., 2007). The lack of management could locally increase habitat heterogeneity with potentially positive effects for the insect population (Azcárate & Peco, 2012; Laiolo et al., 2004; WallisDeVries et al., 2002). Differences within species groups (i.e., large vs. small body size) also show diverging reactions to changes in the grasslands (Tonelli et al., 2018). Generalist species are usually more robust to changes and thus possibly less sensitive to management abandonment (Öckinger et al., 2006). In our analysis, only one study looked explicitly at specialist species and found that habitat type was the main driver and not management (Wiezik et al., 2019). Likewise, only four of the studies looked at the plant community in conjunction with the insect group, making it impossible to draw any conclusions on the influences of grassland abandonment on the overall insect communities. The decrease in disturbance is also known to explain an increase in abundance and diversity in arthropod communities (Morris, 2000), especially for insects that are also strongly related to soil (i.e., soil larvae, dormancy), which may be promoted by the lack of disturbance and accumulated litter during abandonment.

### 4.3 Bird diversity in abandoned grasslands

Similar to insects, we did not find significant effects of abandonment of grassland management for birds, which could be explained by the fact that abandonment initially has a positive effect on the diversity of fauna, and insects and birds may initially benefit from the increased structural complexity (Verholst et al., 2004). For example, less disturbance creates greater vegetation height for cover or more flowers for pollinators (Laiolo et al., 2004). However, if a site is no longer managed and in the long term, a thick layer of litter accumulates (Tanneberger et al., 2008, 2010) or the site becomes woody, grassland-dependent insect species will decline and, in turn, the birds that feed on those insects may decline (Købelsø & Lanz, 2018). On the one hand, birds have a larger habitat range than plants and insects, and thus the change or lack of management may not have any short-term implications on their community. On the other hand, insects depend on plants as a food source, and plants depend on insects for pollination. Likewise, birds rely on insects as food source and ground-nesting birds also on vegetation structure for nesting and cover (Arbeiter et al., 2008, 2020). Since each of these groups are interdependent on one another, we predicted that a significant decrease in plant species would also ultimately lead to a decrease of insect and bird species, which we could not confirm.

### 4.4 Influence of time since abandonment, grassland type, and management type

We expected that ongoing succession, and thus the time since abandonment, would have an influence on the difference of biodiversity between managed and abandoned grasslands. We could not confirm this effect; eventually including and accounting for the progression within long-term studies may shed more light on this relationship. While there are scientific records of short periods of abandonment promoting certain species and leading to
an increase in biodiversity, long-term abandonment often leads to population decline and local extinction events (Barabasz-Krasny, 2011; Bonari et al., 2017; Valkó et al., 2012). For instance, abandoned grasslands can still serve as a habitat for insects specialized on open land until woody vegetation encroaches (Wiezik et al., 2011). The time in which negative effects of abandonment arise have been shown to differ between different plant communities, depending on factors such as productivity (Bonari et al., 2017). Thus, the disruption of biodiversity seems to occur at different states of successions, which can be stable for several years to decades depending on the stage, abiotic and biotic factors and other variables such as management history (Walcher et al., 2019; Wiezik et al., 2011). Since succession can be fast or slow depending on the local conditions (Joyce, 2014), studies defining successional stages in addition to the number of years since management abandonment may support conclusions in biodiversity changes.

We also expected that different grassland types would influence biodiversity. Different types usually have different species composition and thus responses to environmental conditions and changes (e.g., Evans & Roekarts, 2019). However, we could not confirm a significant difference between grassland types in the biodiversity change after abandonment. In a previous meta-analysis, it was found that specialist plant species in wet grasslands almost disappear completely over time, whereas it was not so dramatic for dry grasslands (Diekmann et al., 2019). Likewise, differences between fauna composition have been found between the different types of grasslands, specifically for butterflies (Öckinger et al., 2006; Skórka et al., 2007), with abandonment of wet meadows having a greater, positive impact on the community. Eventually, a more equal distribution of effect sizes across the different grassland types could reveal differences between dry, mesic, and wet grasslands in biodiversity change after abandonment.

Different management practices are known to lead to different species communities in grasslands, especially for plants (Dierschke & Briemle, 2002; Kahmen et al., 2002; Kuhn et al., 2021; Rudmann-Maurer et al., 2008), but the effects on biodiversity are less apparent (Dengler et al., 2014). We expected that the management which had taken place before abandonment would have influenced the change in diversity. Grazing in comparison to mowing was found to promote higher levels of biodiversity, particularly for butterflies and ground beetles (Tälle et al., 2016). Abandonment of grazed sites could suffer from a loss of small-scale heterogeneity that was caused by trampling and defecation patterns (Dengler et al., 2014; Tälle et al., 2016). In our analysis, we did not find any significant influence of the management type taking place before abandonment, that is, grazing, mowing, or both. On the one hand, a possible explanation is that spatial context of the landscape is important with the difference between local and regional scale or the complexity of the landscape shaping the diversity of different communities (Gossner et al., 2016; Le Provost et al., 2021). On the other hand, temporal stability of management might be of higher importance for biodiversity than the type of management in grasslands (Eriksson et al., 2002). Likewise, historical management can play an important role for the established species community as well as the suitability of the present land-use (Tälle et al., 2016). Management as well as its abandonment also has an important impact on the soil community; however, current nature protection does not seem to benefit soil biodiversity (Ciobanu et al., 2019) or functions (Zeiss et al., 2022). Therefore, more tailored management and conservation approaches are needed not just for the aboveground communities, but also for the belowground communities (Guerra et al., 2022).

### 4.5 Conservation and future research

Grassland management has a long-standing tradition in European landscapes. Not only is there a diversity of grassland types, but grasslands are essential in promoting biodiversity and ecosystem services (Schils et al., 2022). In our analysis, we demonstrate that abandonment reduces biodiversity, most particularly plant species richness. Beyond plants, we encourage future comparative studies (using control sites) for insects (also including below ground species) and birds as our data did not yet reveal a clear understanding of how their diversity is affected by grassland management abandonment. We were further surprised that our literature search revealed missing studies in taxonomic groups other than plants, insects, and birds and the lack of studies studying the effects of specialists versus generalists. The industrialization of agriculture has changed grassland management as well as its diversity, involving both intensification in productive areas and abandonment in economically less attractive areas. Due to the previously non-uniform ways to report management intensity (e.g., “number of grazers/ha” in Jacquemyn et al., 2011; “estimated grazing pressure” in Laiolo et al., 2004), we were unable to include the management intensity on the control sites as a variable in our meta-analysis. Midolo et al. (2023) have suggested a uniform way of reporting disturbance indicator values, which would allow quantifying disturbance and intensification across different grasslands and studies. The bias toward plants, nonuniform methods, lack of a control, or incomplete data continue to be issues when
conducting a meta-analysis on grasslands and management (Slodowicz et al., 2023) and should be considered for future grassland studies. Considering different biodiversity facets or the spatial context of the landscape may also provide useful insight into understanding the biodiversity of the different communities. Given the overall decline in biodiversity after abandoning grassland management, we further encourage policy measures to support farmers maintaining their traditional, extensively managed grasslands.

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DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article (Appendix S9 and S10).

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